

BEHAVIOR AND ATTENDANCE PATTERNS OF THE FORK-TAILED STORM-PETREL

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ABSTRACT.—Behavior and attendance patterns of breeding Fork-tailed Storm-Petrels (*Oceanodroma furcata*) were monitored over two nesting seasons on the Barren Islands, Alaska. The asynchrony of egg laying and hatching shown by these birds apparently reflects the influence of several factors, including snow conditions on the breeding grounds, egg neglect during incubation, and food availability. Communication between breeding birds was characterized by auditory and tactile signals. Two distinct vocalizations were identified, one of which appears to be a sex-specific call given by males during pair formation. Generally, both adults were present in the burrow on the night of egg laying, and the male took the first incubation shift. Incubation shifts ranged from 1 to 5 days, with 2- and 3-day shifts being the most common. Growth parameters of the chicks, reproductive success, and breeding chronology varied considerably between years; this presumably relates to a difference in conditions affecting the availability of food. Adults apparently responded to changes in food availability during incubation by altering their attendance patterns. When conditions were good, incubation shifts were shorter, egg neglect was reduced, and chicks were brooded longer and were fed more frequently. Adults assisted the chick in emerging from the shell. Chicks became active late in the nestling stage and began to venture from the burrow several days prior to fledging. Adults continued to visit the chick during that time but may have reduced the amount of food delivered. Chicks exhibited a distinct pre-fledging weight loss. *Received 18 September 1979, accepted 26 July 1980.*

THE Fork-tailed Storm-Petrel (*Oceanodroma furcata*) is the northernmost of five species of storm-petrels that breed along the western coast of North America (A.O.U. 1957). Aside from recent work by Harris (1974), Boersma and Wheelwright (1979), Wheelwright and Boersma (1979), and Boersma et al. (1980), the only published accounts of Fork-tailed Storm-Petrels are incidental notes by early researchers such as Willet (1914), Bent (1922), Clay (1925), and Richardson (1960). This paper reports on a recent study of these birds conducted in 1977 and 1978 on the Barren Islands, Alaska. It describes several aspects of the behavior of Fork-tailed Storm-Petrels and examines the effect of an apparent difference in food availability on the attendance patterns of breeding adults. The inaccessibility of burrow-nesting birds often dictates the use of indirect methods of obtaining information. In this study, specially designed event recorders were used to monitor activity at five nests.

STUDY AREA AND METHODS

Located at the entrance to Cook Inlet between the Kenai Peninsula and Kodiak Island, the Barren Islands (58°55'N, 152°10'W) are some of the most productive and diverse seabird breeding grounds in central Alaska (Fig. 1). The vegetation and climate have been described by Bailey (1976), Manuwal and Boersma (1977), and Simons (1980). The large colonies on East Amatuli Island were studied from 20 May to 24 August 1977 and from 3 May to 27 August 1978.

Direct observation of a marked pair within an exposed burrow was carried out from a blind adjacent to the burrow using a Javelin night vision scope (Model #221). To supplement these observations, five event recorders were used to monitor the attendance patterns of the birds (Simons in prep.). A two-way switch enclosed in a section of plastic pipe and placed over the burrow entrance was used to determine the temporal pattern of entrances and exits at each burrow. A number of burrows, including those monitored with an event recorder, were modified by placing a clear plastic window and plywood cover over the nest chamber. Adults in these burrows were color-marked and observed daily to obtain additional

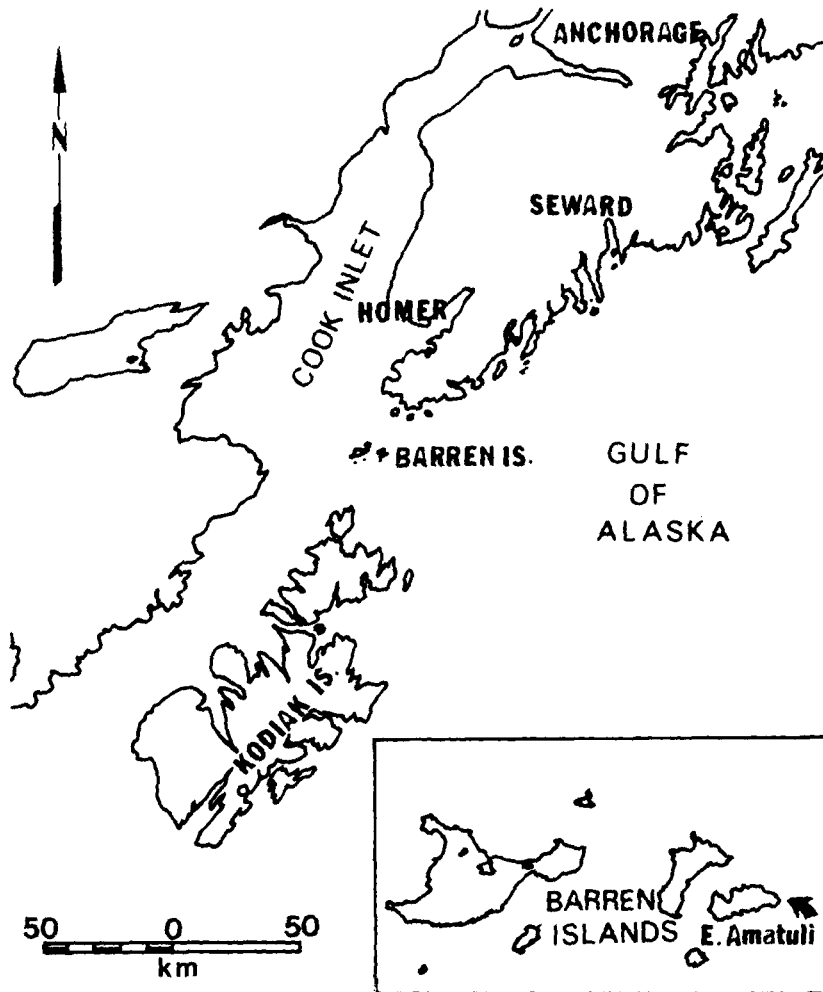


Fig. 1. Map of the Barren Islands, Alaska.

information on attendance patterns. Seven marked pairs were followed in 1977 and six in 1978. Chick growth data were collected daily using a 100-g Pesola scale; chicks were measured to the nearest 0.5 g. Growth calculations were based on a sample of 15 chicks in 1977 and 25 in 1978. Estimates of reproductive chronology and success were calculated from a sample of 176 nests in 1977 and 85 nests in 1978.

Growth equations were obtained employing the graphical method described by Ricklefs (1967, 1968). In Ricklefs' terminology, the equation for the logistic growth equation is $dW/dt = KW(1 - W)$, where W is the weight of the growing bird, K is a constant related to the overall growth rate, and t is time. Three other factors were also calculated for making interspecific growth comparisons. $Ka/4$ and $KR/4 \times 100$ represent the maximum instantaneous growth rate of the chick at the inflection point of the fitted logistic curve and may yield a better estimate of the overall growth rate than K (Hussel 1972). Ricklefs' t_{10-90} was also used and represents the time of growth from 10%–90% of the asymptote. It is calculated by the formula

$$t_{10-90} = \frac{(C_{90} - C_{10})}{dW/dt},$$

where C_{90} and C_{10} are conversion factors calculated from daily weights. Due to the irregularity of the weight data, a smooth curve was fitted by eye to the initial curves (Fig. 7) and used to compute the

TABLE 1. Variation in timing of breeding in relation to elevation, 29 July 1978.

Elevation	\bar{x} Chick weight (g)	\bar{x} Chick wing length (mm)	Burrows with eggs (%)
10 m	66.8 SD = 20.4 $n = 54$ chicks $t = 5.08, P < 0.01$	62.9 SD = 28.1 $n = 54$ chicks $t = 7.21, P < 0.01$	1.8 $n = 55$ burrows $z = 3.55, P < 0.01$
450 m	37.5 SD = 19.2 $n = 16$ chicks	24.9 SD = 11.8 $n = 16$ chicks	20 $n = 20$ burrows

growth constants. My early departure in 1977 limited the amount of chick growth data obtained after day 30, but because only the linear portion of the growth curve was used in calculating the growth constants, the data were adequate for comparing the growth parameters between years. Comparisons of feeding and visitation rates were also based on data from hatching to day 30.

Vocalizations were recorded on a Superscope C-104 portable cassette recorder with Sure Unisphere-6 microphone and a 14-inch parabolic reflector. Sonograms were recorded on a type B/65 Sona-graph manufactured by the Kay Elemetrics Company, Pine Brook, New Jersey.

Adults were sexed by laparotomy, and most birds recovered and flew off in good condition within 24 h. Of nine incubating adults that were sexed, five were found incubating within a week of their release.

RESULTS

The breeding cycle.—Fork-tailed Storm-Petrels were present in large numbers in the Barrens when I arrived in May of 1977 and 1978. D. Johnson and L. Smith, working on nearby Sugarloaf Island (1 km southeast of East Amatuli), reported that storm-petrels were numerous on that island when they arrived on 12 April 1978. Birds probably begin to arrive in late March, perhaps earlier in some years. Egg laying in 1977 began on 23 May, while in 1978 the first eggs were laid in late April. Egg laying began within 2 weeks of the time the snow cover disappeared from the nesting areas in 1978, and it appears that a portion of the population was prevented from initiating breeding due to snow conditions. On 29 July, 20 active burrows at an elevation of 450 m were at a much earlier stage in the breeding cycle than burrows located near sea level (Table 1). In addition, egg laying at a single nesting location often extended for over 5 weeks. Therefore, even though an individual breeding cycle takes about 4 months, birds may be found on East Amatuli over a 7-month span.

Vocalizations.—The Fork-tailed Storm-Petrel has two distinct calls. The most common (Fig. 2a), a raspy three-to-five syllable call, is used in a variety of contexts

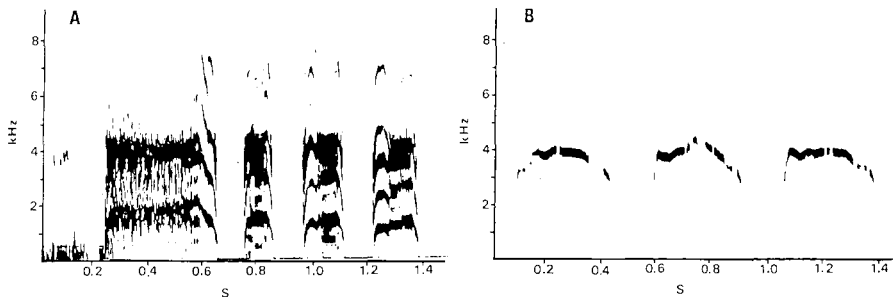


Fig. 2. Sonograms of Fork-tailed Storm-Petrel calls. A = typical four-syllable call; B = single-syllable male call.

by both sexes. It is often given by birds flying over the colony as well as by individuals involved in activities ranging from fighting to courtship on the ground and within burrows.

The second distinct vocalization (Fig. 2b) is a single-syllable call, which is often repeated many times. This call is used in a much more limited context, and it appears to be a sex-specific call used by males on the ground or within a burrow to attract a female. The function of the call was suggested by the behavior of a bird observed from a blind in 1977. The bird, which had been color-marked, apparently lost its mate sometime during incubation. It continued to incubate erratically for several weeks and then stopped returning to the burrow. After an absence of about 2 weeks, it reappeared in the burrow one evening and began giving the single-syllable call. The call attracted other birds, several of which responded by giving the three-to-five syllable call while flying over the burrow or calling from the ground outside the burrow. Eventually one individual entered the burrow, and the pair spent the next several hours calling back and forth, the marked bird giving the single-syllable call and the other bird giving the three-to-five syllable call. Outbursts of calling were often followed by bouts of mutual preening in which the birds alternated in carefully preening each other about the forehead, head, nape, and facial area for periods of up to 3 min. The pair remained in the burrow that evening, and early the next day they were sexed by dissection. The bird giving the single-syllable call was a male, and its partner was a female. In 1978, 11 birds captured giving this call on the ground or within burrows were sexed by laparotomy, and all proved to be males.

A single burrow was monitored nightly for 2 weeks prior to egg laying. Both members of the pair visited the burrow singly, at which time they constructed a small nest of dried grass and debris or rested quietly on the nest as if incubating. On three occasions both birds visited the burrow and spent the entire night together (approximately 3.5 h). These periods were characterized by mutual preening and vocalizations. Although no copulations by this pair were witnessed, three other copulations were observed from the blind. Two of these occurred within neighboring burrows following mutual preening and vocalizing, and a third occurred on the ground outside the blind.

Egg laying.—On 4 June, both adults arrived at the burrow shortly after dark, at approximately 2300, and spent the next hour alternating between mutual preening, calling, and exchanging places on the nest. At 0010 the birds exchanged places on the nest again, but this time the adult taking over assumed an unusual flattened posture and remained in that position for several minutes. It turned twice to nibble at its sides with its bill and then, as its mate rested nearby, it stood up to reveal a newly laid egg. It then turned and tucked the egg under its brood patch and began incubating. At 0100 the male walked to the incubating female, called several times using the three-to-five syllable call, and preened her on the forehead. At that point, the female rose from the egg, walked to the burrow entrance, and flew off without hesitation. The male began incubating.

Twelve birds incubating newly laid eggs were sexed. Of these, 10 were males and two were females. The two cases in which females took the first shift were in recorder-monitored burrows, and the males had not returned to their burrow on the night the egg was laid. The females remained on the nest during the day following egg laying and departed that evening.

Incubation.—Each member of a pair spent from 1 to 5 days in the burrow, and

TABLE 2. Fork-tailed Storm-Petrel incubation shifts.

Year	\bar{x} Number of incubation shifts per pair	\bar{x} Number of cold days per incubation period	\bar{x} Incubation shift length (days)	Total egg stage (days)
1977	15.3 SD = 2.5 $n = 7$ chicks $t = 2.68, P < 0.05$	9.6 SD = 3.8 $n = 7$ chicks $t = 2.54, P < 0.05$	2.6 SD = 1.0 $n = 103$ shifts $t = 2.48, P < 0.05$	50.8 SD = 4.1 $n = 9$ nests $t = 3.44, P < 0.01$
1978	18.5 SD = 1.6 $n = 6$ chicks	5.2 SD = 2.0 $n = 6$ chicks	2.3 SD = 0.9 $n = 151$ shifts	46.1 SD = 3.3 $n = 24$ nests

change-overs occurred at night. The sexes took approximately equal shares of incubation, but in an extreme instance one bird accounted for 63% of the incubation period. An incubation shift ended when an adult was relieved by its mate or when the incubating bird departed before being relieved. The frequency of cold eggs indicates the degree of synchrony between members of a pair (Table 2).

The mean number of incubation shifts per pair was higher in 1978 than in 1977, while the frequency of cold eggs and the length of the incubation period declined (Table 2). As a result, the mean incubation-shift length declined in 1978. The frequency distribution of the shifts illustrates the difference between the two years (Fig. 3). The frequency of 2-day shifts was significantly higher in 1978 than in 1977 ($z = 5.24, P < 0.001$) and reflects a corresponding reduction in 3-, 4-, and 5-day shifts in that year.

To determine the energetic costs of incubation, six adults were weighed before and after incubation spells of 24 h. The mean daily weight loss was 6.38% of initial body weight (SD = 1.88) over this period. Assuming an average adult weight of 58.6 g ($n = 33, SD = 3.5$), this would amount to an average weight loss of approximately 20% over a 3-day shift and 30% over a 5-day incubation shift. Because all of these birds were in the first or second day of their incubation shift, these estimates are probably somewhat high. In fact, Boersma et al. (1980) report a weight loss of 19% for one bird over a 5-day shift. Nevertheless, the estimates do suggest that the physiological costs of a 5-day shift are severe for a bird of this size, which, in part, explains the small number of 5-day shifts recorded.

Adults often meet in the burrow and spend varying amounts of time together prior to exchanging incubation duties ($n = 43, \bar{x} = 32.8$ min, SD = 38.4 min, range = 5–235 min). Behavior is similar to that during courtship and is characterized by quiet periods in which the birds rest side by side and by occasional outbursts

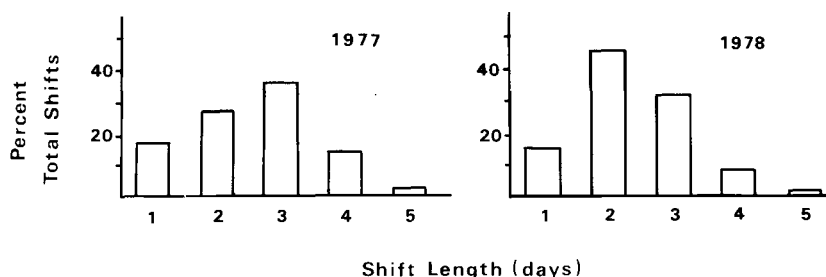


Fig. 3. Distribution of incubation shifts, 1977 and 1978. $n(1977) = 103$; $n(1978) = 151$.

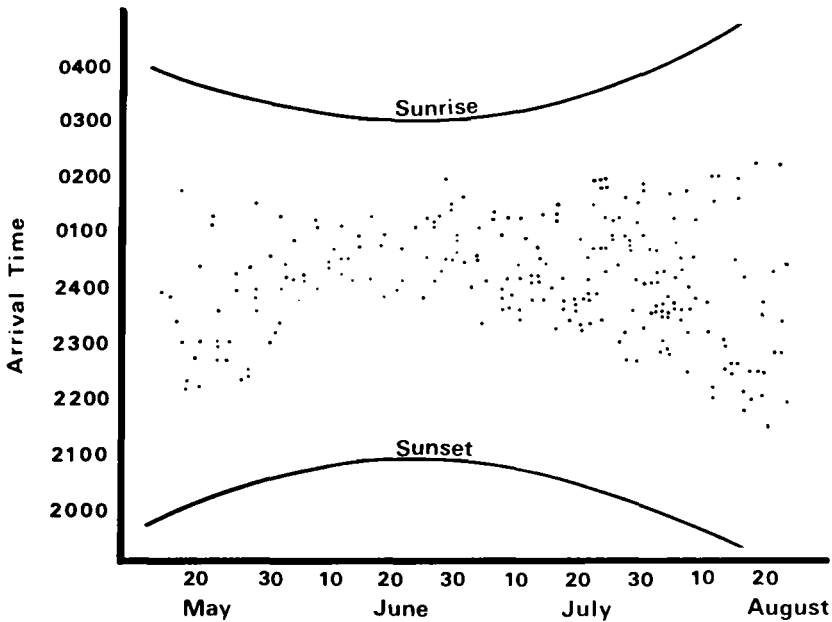


Fig. 4. Comparison of burrow arrival times of Fork-tailed Storm-Petrels with local sunrise and sunset.

of calling and mutual preening. In four burrows monitored throughout incubation, adults met an average of 10.7 times ($SD = 3.8$). In contrast, in three burrows monitored throughout the nestling stage adults met an average of 2.75 times ($SD = 0.95$; $t = 3.46$, $P < 0.01$). The difference reflects the different needs of the incubation and nestling periods. Pairs that synchronize their activity during incubation presumably reduce egg neglect. During the nestling period the benefits adults obtain by meeting in the burrow, such as reinforcement of the pair bond, may be outweighed by the additional foraging time gained when visits to the burrow are brief.

Breeding Fork-tailed Storm-Petrels seldom return to the burrow during incubation without relieving their mate. I noted only seven instances in over 500 recorder-monitored nights in which a bird entered a burrow and remained for a period of time without relieving its mate. It is unlikely that these were strange birds investigating the burrow, because my observations from the blind indicate that intruders are always promptly driven off by the incubating bird. In these seven cases the incubating bird was in the first or second day of its incubation shift and remained in the burrow for another 1–3 days. Perhaps the condition of the incubating bird determines whether a change-over will occur. In general, it appears that, unless an individual has just initiated its shift and is capable of remaining for several more days, it is most advantageous to switch whenever its mate arrives.

Although petrels began to arrive shortly after sunset, birds continued to arrive at their burrows all night (Fig. 4). Two birds departed up to 4 h after sunrise, indicating that, although these birds are for the most part strictly nocturnal, they will infrequently venture from the colony in broad daylight.

The nestling stage.—I observed a nest continuously through the hatching process and found that the presence of an adult during and immediately following hatching may be critical to the survival of the chick. The adult assisted the chick in hatching

TABLE 3. Reproductive parameters during the nestling stage.^a

Year	\bar{x} Brooding period (days)	\bar{x} Number of feeding visits per day	\bar{x} Estimated food load size (g)	Estimated reproductive success (chicks fledged/eggs laid)
1977	3.4 SD = 1.4 $n = 7$ chicks $t = 1.89, P < 0.05$	0.7 SD = 0.6 $n = 100$ visits $t = 4.88, P < 0.01$	8.0 SD = 4.0 $n = 75$ loads NS	0.47 $n = 176$ nests $z = 4.03, P < 0.01$
1978	4.5 SD = 1.4 $n = 30$ chicks	1.1 SD = 0.7 $n = 92$ visits	8.0 SD = 3.8 $n = 85$ loads	0.68 $n = 85$ nests

^a Food data estimated over period from hatching to day 30.

by placing its bill inside of the partially opened shell and shaking its head from side to side. This may be a common behavior, as I often found that the shell had been partially picked away on eggs that did not hatch. When the chick was free of the shell, the adult brooded it immediately and continued to do so until the chick's down was dry. Chicks were commonly brooded for a total of 1–8 days following hatching; the length of the brooding period varied from year to year (Table 3).

Within 2 h of hatching the adult began to feed the chick. I observed the birds frequently during the 3-day brooding period, and it appeared that the chick was fed at 3- to 4-h intervals. Feeding was often initiated by the chick. It jostled the adult and called constantly, and, in response, the adult oriented itself at 90° to the chick and allowed it to feed from its lower mandible and the back of its throat (Fig. 5). The chick often fed in this manner for 2 or 3 min at a time.

The early nestling stage was a period of high mortality for Fork-tailed Storm-Petrel chicks, during which time they were dependent on the frequent attention of



Fig. 5. Adult Fork-tailed Storm-Petrel feeding its chick.

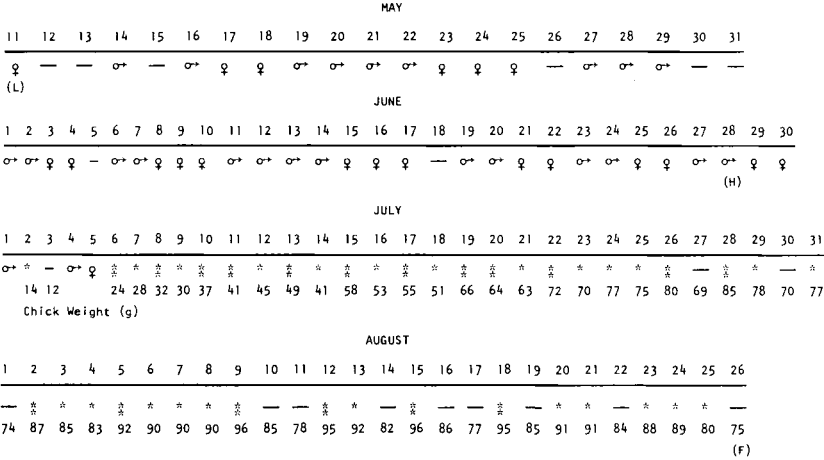


Fig. 6. A typical attendance pattern of a pair of breeding Fork-tailed Storm-Petrels. Asterisks indicate the estimated number of feeding visits each evening. L = egg laid; H = egg hatched; F = chick fledged.

their parents for survival. Of the chick mortality observed over the 2 yr, 78% occurred in chicks less than 3 weeks old ($n = 261$ nests). This mortality was apparently related to the amount of time the adults spent with the chicks during the nestling period. Visits during the first half of the nestling period were longer ($\bar{x} = 71.1$ min, $n = 64$, $SD = 74.1$) than visits in the second half of the nestling period ($\bar{x} = 23.9$ min, $n = 59$, $SD = 30.5$; $t = 4.7$, $P < 0.001$). This is consistent with the observation that adults frequently brooded young chicks for up to 3 h a night when they returned to feed them early in the nestling period but stopped brooding after the chick was about 3 weeks old.

The frequency of visits and food loads delivered by adults was highly variable (Fig. 6). Feeding visits varied from two per night to one every 4 nights. By directly observing a color-marked pair and weighing their chick before and after feedings, I was able to determine the quantity of food delivered and attendance patterns of the individual birds. The pair was observed for two 1-week periods, one following hatching and the other late in the nestling period. Adults shared equally in feeding the chick, and individual loads varied from less than 3 g to almost 19 g. Adults were able to deliver large amounts of food to the chick in a single evening, and this occasionally resulted in chick weight gains of over 65%. Adults delivered loads equal to 29% of mean adult weight at the time, and this may represent the limit of their capabilities (Ashmole 1971).

Feeding frequency and load size were also estimated from recorder-monitored burrows by noting both the sequence of entrances and exits indicated by the recorder and changes in chick weight each day (Table 3). Estimated load size remained constant both years, while feeding frequency increased in 1978. In addition, a variation in load size through the season was noted in 1978, with mean load size increasing from 8.0 g ($n = 85$, $SD = 3.8$) in the first half of the nestling stage to 10.4 g ($n = 67$, $SD = 3.8$) in the second half ($t = 3.63$, $P < 0.01$).

Growth curves constructed from mean daily chick weights [n (1977) = 15, n (1978) = 25] indicate that chick growth rates were lower in 1977 than in 1978 (Fig. 7). The calculated growth rate constants (Ricklefs 1968) also reflect the relative

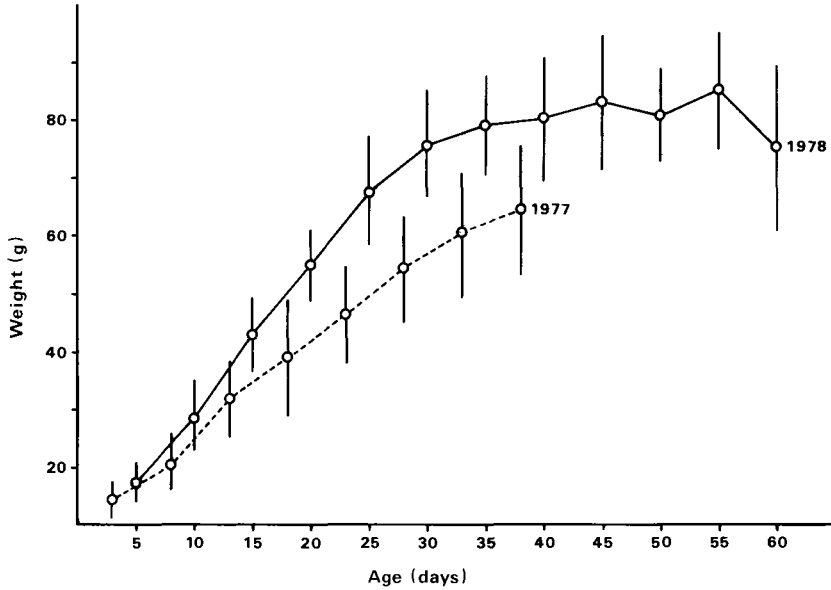


Fig. 7. Weight gain of Fork-tailed Storm-Petrel chicks 1977 and 1978, $n(1977) = 15$; $n(1978) = 25$. Vertical lines represent one standard deviation on either side of the mean.

differences in chick growth rates between the two years (Table 4). Estimated reproductive success was also lower in 1977 (Table 3).

Fledging.—The mean nestling period for 20 Fork-tailed Storm-Petrel chicks in 1978 was 58.4 days (SD = 2.23, range 51–61 days). Chicks exhibited a distinct pre-fledging weight loss, reaching peak weight approximately 8 days prior to fledging. They lost an average of 1.87 g per day before fledging at a mean weight of 73.4 g (SD = 7.45 g), or 122.4% of mean adult weight (Fig. 8). Data from three burrows monitored with recorders suggest that the adults do not abandon their chicks prior to fledging but that the amount of food consumed by chicks during that period is reduced. The frequency of visits by adults was not significantly reduced before fledging, while estimated mean load size over the week before fledging was ($\bar{x} = 10.4$, $n = 67$, SD = 3.8; $t = 5.04$, $P < 0.01$).

Chicks ventured from the burrow several days before fledging, sometimes five or

TABLE 4. Fork-tailed Storm-Petrel reproductive parameters during 1977 and 1978.^a

	1977	1978
<i>n</i>	15	25
Asymptote <i>a</i> (g)	74	85
Adult weight <i>W</i> (g) ^a	60	60
$R = a/W$	1.23	1.42
Fledging weight <i>FW</i> (g)	—	73.43
FW/W (%)	—	122.38
<i>K</i>	0.107	0.132
$Ka/4$ (g/day)	1.98	2.81
$KR/4 \times 100$ (%/day)	3.29	4.69
t_{10-90} (days)	41.05	33.27

^a Ricklefs (1967).

^b Manuwal and Boersma (1977).

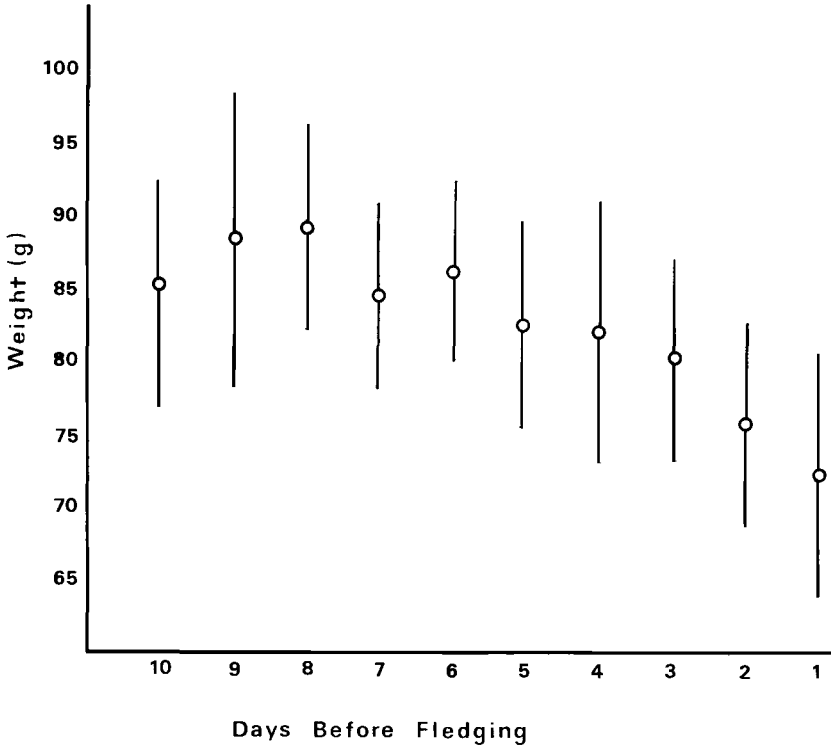


Fig. 8. Prefledging weight recession of Fork-tailed Storm-Petrel chicks, $n = 30$. Vertical lines represent one standard deviation on either side of the mean.

six times a night. In the three burrows monitored, the chicks initially left their burrows shortly after dark but returned a number of times before departing at approximately 2300. Two burrows were monitored for a week following fledging. One was not visited during that period, and in the other both adults apparently returned briefly to the burrow on the night following the chick's departure.

DISCUSSION

The means of communication used by breeding Fork-tailed Storm-Petrels illustrate adaptations to the environment in which they must reproduce. The use of auditory and tactile signals predominates in exchanges between members of a pair, and these represent efficient modes of communication in their nocturnal environment (Marler 1967). When thousands of birds congregate in high-density nesting colonies, which is often the case in this species, individuals are faced with the problem of trying to communicate in a "noisy neighborhood" (Smith 1977). Complex or lengthy vocalizations are of little value in this environment, and the short, simple, distinct, and repetitive vocalizations used by Fork-tailed Storm-Petrels at the colony presumably reduce signalling errors. The sex-specific, single-syllable call is an effective method of advertisement and, due to its intensity, pattern, and pitch, is easily located amidst the cacophony so characteristic of a storm-petrel colony. This is not the case in all other Procellariiformes. Some, such as *Puffinus* spp., nest in large, very dense colonies and have long and rather complex vocalizations (J. Warham

pers. comm.). There is indirect evidence that sex-specific calls are found in other Procellariiformes (Warham 1977), but only this study and recent work by Brooke (1978) have shown their importance.

The burrow appears to be vital as a focal point of the reproductive effort (Davis 1957, Allan 1962). Pairs spend considerable amounts of time together in the burrow, beginning several weeks prior to egg laying, and continue to meet periodically in the burrow for up to 4 months. Arrival times give no indication that adults are together away from the colony, and thus it seems that the integrity of the nest site is essential to a successful reproductive effort. This is especially true during the nestling period, when adults may only meet in the burrow two or three times over a period of almost 2 months. Work on the Barren Islands over the past 4 yr (Boersma et al. 1980) indicates a high degree of nest-site and mate fidelity in this species, which is similar to the pattern found in Leach's Storm-Petrel (*Oceanodroma leucorhoa*) by Morse and Buchheister (1979).

The tendency for males to take the first incubation shift has been documented in several Procellariiformes (Warham 1964). This allows the female to return to sea immediately after laying to rebuild energy stores depleted in the production of the egg. In the Fork-tailed Storm-Petrel the egg is about 22% of adult weight, which represents a considerable initial female investment in reproduction.

Assistance provided by the adult to the hatching chick presumably helps reduce chick mortality. Chicks that were deserted by their parents before their down was dry invariably died. Because an adult cannot be certain when its mate will return, assistance to the chick seems to represent a means of influencing the time of hatching, of presumably reducing energy expenditure by the chick during this critical period, and of lowering the probability that an adult will have to depart prematurely.

The importance of food resources in shaping the reproductive strategies of sea birds by influencing reproductive success is well established (Ashmole 1963, 1971; Lack 1967, 1968; Harris 1969, Boersma 1978). Many Procellariiformes are adapted to utilize an often limited and distant food supply (Warham 1964, Lack 1967, Ashmole 1971), and activity during incubation appears to be affected by changes in this resource (Kendeigh 1940, Matthews 1954, Harris 1969). Unfortunately, we know very little about the feeding ecology of Fork-tailed Storm-Petrels. Recent work by Sanger et al. (MS), Lensink et al. (1978), and Wiens et al. (1978) has improved our knowledge of the feeding habits and distribution of Procellariiformes in Alaska, but we still know very little about where Fork-tailed Storm-Petrels from the Barren Islands are foraging, much less what they are eating and feeding their chicks. Nevertheless, there were clear differences in the breeding biology and behavior of the Fork-tailed Storm-Petrels studied in 1977 and 1978. The facts that the onset of breeding was later, chick growth rates were reduced, and overall reproductive success was lower in 1977 indicate that conditions for breeding were better in 1978 than in 1977. The difference in conditions appeared to relate directly or indirectly to the availability of food resources. This could have been caused by a variety of factors, including differences in prey type, density, location, and distribution or oceanographic and weather conditions on the feeding grounds. It is not at all clear what factors were responsible, but it is clear that breeding petrels responded by altering their colony-attendance patterns throughout the breeding season. In 1978, when conditions were good and the birds were able to meet their metabolic needs more quickly, shorter incubation shifts predominated, and egg neglect was reduced. In contrast, in 1977 incubation shifts were longer, the synchrony between members of

a pair was reduced, and egg neglect and the length of incubation period increased. Harris (1969) found a similar pattern in the Aububon's Shearwater (*Puffinus lherminieri*), and Boersma and Wheelwright (1979) have demonstrated the direct relationship between egg neglect and incubation period in Fork-tailed Storm-Petrels.

The ability of the chick to go for several days without food has been reported in a number of related species (Roberts 1940, Richdale 1963, Serventy 1967) and represents an adaptation to fluctuations in food availability. Chicks are also capable of consuming large quantities of food when it is available. In this study, the maximum chick weight gain recorded was 65%, although Harris (1966) has documented gains of over 100% in the Manx Shearwater (*Puffinus puffinus*). In addition, the variability of arrival times implies that food resources are widely dispersed and also suggests the possibility that some individuals may be feeding at night. The length of the brooding period was increased when conditions were good, and that may have contributed to the reduction in chick mortality noted in 1978. Chicks were also fed more that year, and adults responded by increasing their visitation rate rather than increasing the size of the load delivered. The reasons for this response are not clear but may be related to an optimization of feeding based on the constraints of central-place foraging such as prey distribution, load size, and foraging distance (Orians and Pearson 1979). Although Harris (1966) noted that nutrition did not influence the length of the nestling period in the Manx Shearwater, he pointed out that, as in this study, it does influence chick growth rates and fledging weight, both of which are certainly related to fledging survival and fitness of the adults.

The asynchrony of breeding exhibited by this population is unique among the 15 species of sea birds breeding in the Barren Islands and may also be related to the food supply. Most species of sea birds breeding at high latitudes appear to be adapted to a short-term abundance of food (Ashmole 1971). This adaptation seems to account for the higher survival rate of early hatched chicks in species such as the Manx Shearwater (Perrins 1966), but its importance as a selective force in Fork-tailed Storm-Petrels is unknown. Although such factors as snow cover (Sealy 1975, this study) and egg neglect may account for some of the asynchrony, food resources for storm-petrels around the Barren Islands are probably a more important factor and must remain above some minimum level throughout the summer in order to permit the initiation of breeding over such an extended period. This is not to say that breeding conditions are consistently good for Fork-tailed Storm-Petrels throughout the season or from year to year. In fact, this study indicates that the capacity of these birds to alter their colony attendance patterns is one means they have of responding to fluctuations in resource availability and that it provides them with the flexibility required to breed in the harsh and unpredictable environment of the Gulf of Alaska.

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