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EGG NEGLECT IN THE PROCELLARIIFORMES: REPRODUCTIVE ADAPTATIONS IN THE FORK-TAILED STORM-PETREL

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The eggs of many procellariiform birds may still hatch even though temporarily abandoned during the incubation period. Distant foraging and long incubation periods, characteristic of these birds, increase the probability that storms or undependable food resources will delay an individual's returning to relieve its incubating partner. Consequently, tolerance to chilling by the embryo has evolved to a greater degree in the Procellariiformes than in other orders. This paper reports the incidence of egg neglect in the Fork-tailed Storm-Petrel (*Oceanodroma furcata*), and discusses the adaptive significance and costs of egg neglect in the Procellariiformes.

STUDY AREA AND METHODS

Between 14 May and 6 September 1976, and between 20 May and 24 August 1977, we observed Fork-tailed Storm-Petrels on East Amatuli Island, Barren Islands (58°55′N, 152°10′W) at the entrance of Cook Inlet, Alaska (see Bailey 1976). In 1976, late in the incubation period, we found 89 nests with eggs and visited them at least once every five days from 8–21 July to watch interrupted incubation. The following year, before egg laying had begun, we established a sample plot of 113 likely nest sites which we checked daily to determine exact egg-laying dates. The 59 active nests were thereafter checked daily to see if an adult was present. Since storm-petrels desert the nest with little provocation, we tried to minimize disturbance by placing a toothpick "gate" across the entrance of the nest burrow. If a toothpick had been knocked over (indicating that a bird may have left or arrived), or if there was any doubt whether an adult was present, we slowly reached into the burrow until we touched an incubating adult or the egg. In shallow burrows, where the nest was visible, it was unnecessary to disturb the adult. If the egg was warm, we assumed that an incubating adult was present. Only when eggs were cold, and therefore unattended, did we remove and weigh them. Adults, chicks and eggs were weighed with 50 g and 100 g Pesola scales to 0.1 g and 0.5 g, respectively.

NEST SITE DISTURBANCE

In the sample plot checked daily in 1977, 58% of the eggs hatched (n = 59), while in a control plot checked only four times late in the incubation period 84% of the eggs hatched (n = 100). In 1976 in a control plot checked four times late in incubation, 70% of the eggs hatched (n = 89). Hatching success in the control plots may be slightly overestimated because egg loss from predation and parental rejection early in the incubation period before the initial observation was unknown. Daily observations of nests, however, apparently contributed to a reduced hatching success. Allan (1962) and Harris (1969), assuming that their observations did not reduce hatching success, reported hatching successes of 49% and 60%, respectively, in the Madeiran Storm-Petrel (*Oceanodroma castro*), which are similar to hatching success in our sample plot. Wilbur (1969), in contrast, calculated breeding success of 98% for Leach's Storm-Petrel (*O. leucorhoa*).

Two observations on the proportion of unattended nests in the control plot in 1977 (17% and 34%) were within the range of egg-neglect in the sample plot, suggesting that our observations did not significantly influence the incidence of interrupted incubation. Since Fork-tailed Storm-Petrels arrive and leave the island only at night, egg-neglect was calculated in days rather than hours.

RESULTS

The Fork-tailed Storm-Petrel embryo, more than any other avian embryo studied, can tolerate frequent and extended periods of neglect at low temperatures. Of 33 nests in which eggs hatched, the mean cumulative number of days of egg-neglect was 11.0. Daytime air temperatures in the burrows averaged 10.0°C (Wheelwright and Boersma 1979). The mean duration of periods of egg-neglect was 1.7 days (n = 229). Most commonly, eggs that hatched had been neglected for one or two days at a time, but nine eggs hatched after being neglected continuously for four days, five eggs for five days, and one egg for seven days. Depending upon the total amount of egg-neglect, incubation periods of the Fork-tailed Storm-Petrel extended from 37 to 68 days, with a mean of 49.8 days (n = 33). The duration of the incubation period was directly proportional to the number of days of egg-neglect (Fig. 1). Eggs neglected 11 days (the mean number of days of egg-neglect in the sample) or less during the incubation period hatched, on the average, 46.3 days after laying. When egg-neglect exceeded 11 days, the mean incubation period increased to 54.6 days (Table 1). One egg that had been neglected for a total of 31 days pipped just before we left the island, 71 days after it had been laid. The mean weight of adults captured in bur-

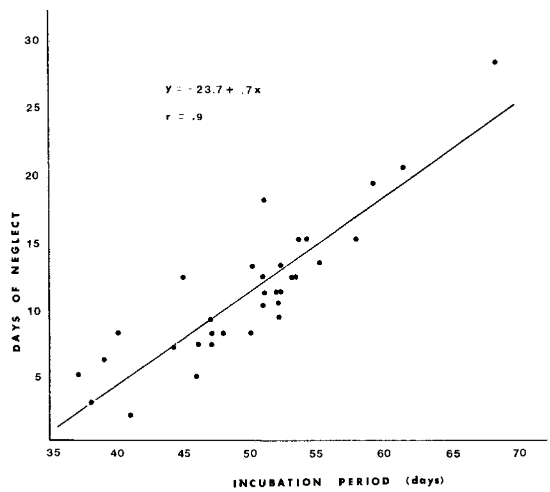

FIGURE 1. Relationship between egg-neglect and duration of the incubation period in Fork-tailed Storm-Petrels (n = 33).

rows where eggs had been neglected (n = 14) was less than that of more faithful incubators (n = 19), although the difference was not statistically significant (Table 1).

In 1977, the proportion of unattended nests of Fork-tailed Storm-Petrels increased during the summer. Egg-neglect was not significantly correlated with rainfall or wind on the island in 1976 or 1977 (Fig. 2). Herring Gulls (*Larus argentatus*; Drent 1970, MacRoberts and MacRoberts 1972) and other open nesters (Skutch 1962) incubate more faithfully during inclement weather. For Fork-tailed Storm-Petrels, burrow nesters who feed far from the island, poor weather conditions where birds actually foraged may be more likely to increase interruptions in incubation. The increase in egg-neglect throughout the summer may have been due to a decline in food availability as well as the fact that the sample included late nesters, which neglected their eggs more often than early nesters. Eggs laid before 30 May 1977 were neglected on the average 9.1 days and had a mean incubation period of 47.9 days (n = 13). Those laid between 30 May and 4 June were neglected an average of 12.8 days and had an incubation period of 51.7 days (n = 11), while those laid after 4 June had an average of 14.4 days of egg-neglect and a mean incubation period of 52.7 days (n = 10).

The frequency of egg-neglect also increased during the incubation period (Fig. 3). (The high incidence of egg-neglect when the incubation period exceeded 55 days was due to the small sample comprised of irregular incubators.) Because egg-neglect presumably results when the incubating bird leaves to feed and its partner fails to return to incubate, egg-neglect should increase with the breeding season as birds are increasingly taxed by the reproductive effort. The mean weight of adult Fork-tailed Storm-Petrels decreased throughout the incubation period. Individuals captured by mist-netting in the middle of a colony showed a steady decline in weight as the breeding season progressed. The mean weight late in June was 60.6 g (n = 81, σ = 4.4); early July 58.7 g (n = 105, σ = 3.4) mid-July, 57.2 g (n = 87, σ = 3.9); and late July 54.8 g (n = 26, σ = 2.6). Some of the birds were nonbreeders; however, late in the breeding season, when fewer nonbreeders visited the island, the trend continued.

During its development an avian embryo metabolizes yolk and loses water (see Drent 1975). At the end of the incubation period in birds previously studied, about 60% of the yolk is exhausted, the remainder being drawn into the abdominal cavity and absorbed within 5–7 days after hatching (Romanoff 1960). Water loss accounts for 75% of total egg weight loss (Simkiss 1974). We found that weight loss of the egg, relative to initial

TABLE 1. Fork-tailed Storm-Petrels: mean incubation period, egg weight loss, chick mortality, and adult weight for relatively neglected eggs versus attended eggs. All eggs in the sample hatched. (σ = standard deviation.)

Variable	Nests with 11 or fewer days of egg neglect (n = 19)		Nests with more than 11 days of egg neglect (n = 14)	
	$\bar{x}$	σ	$\bar{x}$	σ
Mean number of days of egg-neglect	7.6	2.6	15.5	4.5
Mean length of incubation period (days)**	46.3	5.1	54.6	5.6
Mean adult weight on day of hatching (g)	62.3	4.2	60.6	6.3
Mean egg weight at laying (g)	12.4	1.1	12.6	1.0
Mean egg width (cm)	2.6	.1	2.6	.1
Mean egg length (cm)	3.5	.1	3.5	.1
Percent weight loss of egg*	12.9	4.5	16.7	3.9
Chick mortality (within 10 days of hatching)	26%		43%	

* Means are significantly different ($P = <.01$).
** Means are significantly different ($P = <.001$).

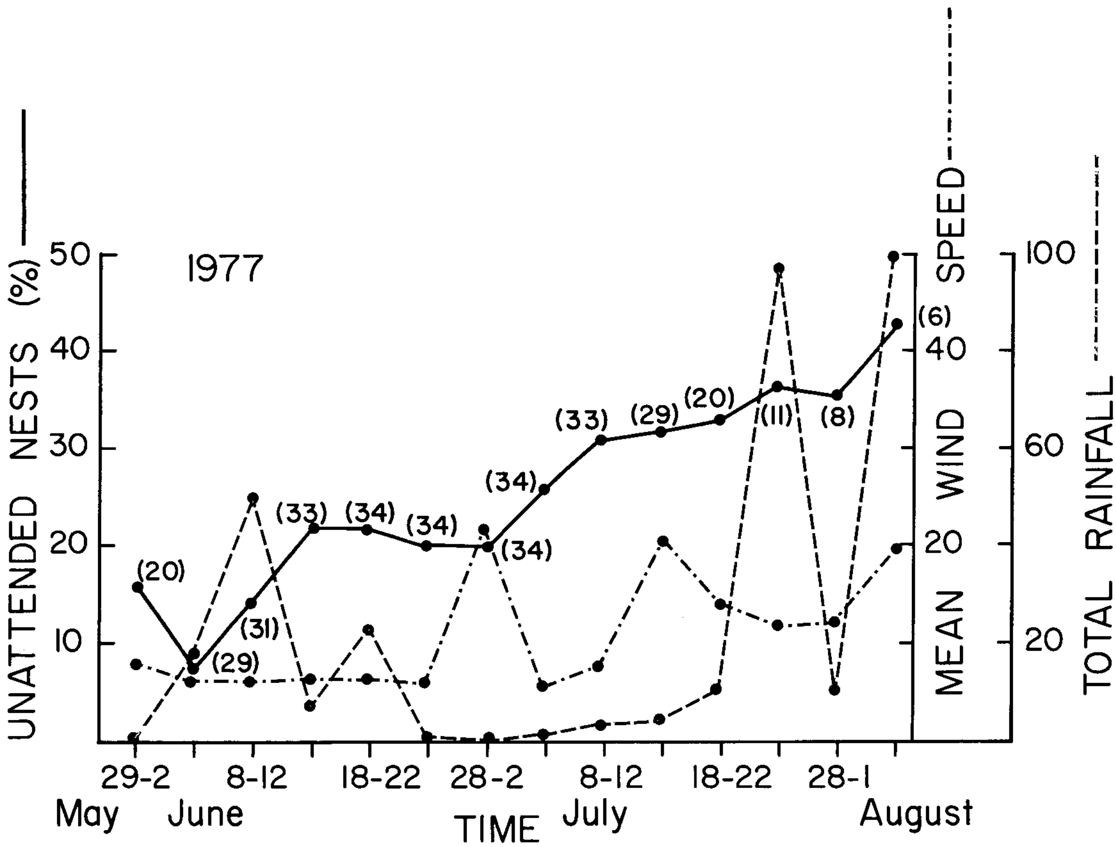

FIGURE 2. Frequency of Fork-tailed Storm-Petrel egg-neglect, mean wind speed (averaged over five-day intervals; km/h), and rainfall (five-day totals; mm/week), during the breeding season, 1977. (Sample sizes in parentheses.)

weight, increased with egg-neglect, principally because of water loss, but also probably due to the additional metabolic demands of the extended incubation period (Fig. 4). The eggs that had been neglected more than 11 days showed a mean weight loss of 16.7%, significantly more than the 12.9% for those that had been neglected 11 days or less (Table 1).

Fork-tailed Storm-Petrel nestlings were brooded irregularly following hatching for an average of 5.3 days. Most chick mortality occurred in the first 10 days, especially when the chicks were unvisited and unfed. Chick mortality rose with egg neglect (Fig. 5). When eggs were neglected more than the mean of 11 days, chick mortality was 43%, whereas when they were neglected 11 days or less, mortality was 26% (Table 1). Chick mortality was only 8% when egg-neglect was less than 9 days (n = 12) and 0% when egg-neglect was less than 8 days (n = 7). Nestlings may also have died as a consequence of parental failure to brood, rather than depletion of yolk reserves alone. During the first five days after hatching, chicks from eggs that were neglected less than 11 days (n = 15) were brooded significantly more ($P < .001$, t-test) than chicks from neglected eggs (n = 11). Furthermore, chicks that died were not brooded (n = 13) as much on the first three days after hatch-

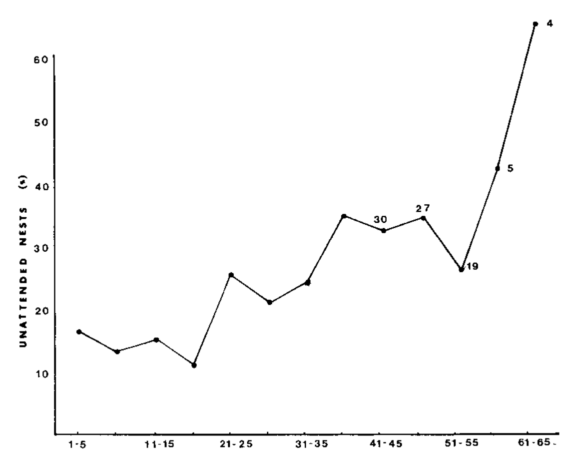

FIGURE 3. Frequency of egg-neglect (averaged over five-day intervals) in the Fork-tailed Storm-Petrel during the incubation period, 1977 (n = 33, except where indicated).

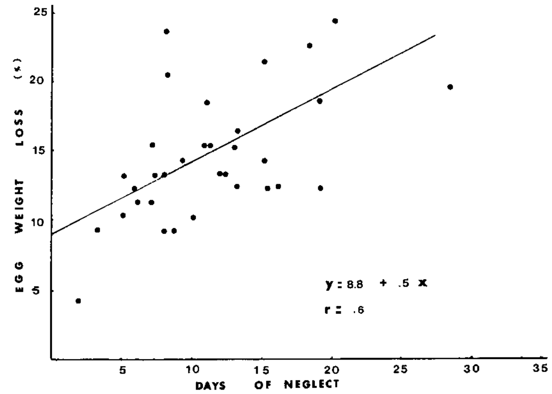

FIGURE 4. Relationship between egg-neglect and relative weight loss of the egg in Fork-tailed Storm-Petrels (n = 32).

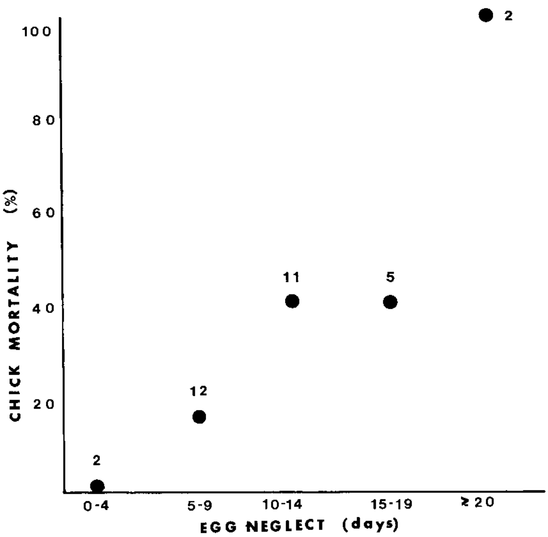

FIGURE 5. Relationship between egg-neglect and chick mortality (within 10 days after hatching) in Fork-tailed Storm Petrels. (Sample sizes above points.)

ing as those chicks that survived (n = 19, $P < .001$, t-test).

Chick weight on day one is not a good index of the actual weight of newly hatched chicks because parents may have fed the young before we weighed it. Other body dimensions, however, should be reliable indices of body size. The differences in mean initial lengths of body parts between neglected eggs and non-brooded chicks compared to tended eggs and brooded chicks were not significant; nevertheless, the direction of departure was consistent, which suggests that chicks from neglected eggs and those that were not brooded were smaller (Table 2). To determine whether chicks from neglected eggs were significantly smaller and whether they remained so, we compared the mean size of body parts of known-aged chicks who survived from neglected and non-neglected eggs, using a Mann-Whitney U test (Table 3). Chicks from neglected eggs were consistently smaller than those from more faithfully incubated eggs until 20 days of age ($P < .05$). Furthermore, dimensions (wing, tarsus and culmen length) of chicks at hatching were good predictors of relative size at day 20 ($P < .001$, .001, and .004, respectively; Spearman rank correlation coefficient). Tarsus length at hatching was not correlated with tarsus length at 40 to 45 days of age (n = 22, Spearman rank correlation = $P < .45$). Neglected chicks who survive, therefore, are not necessarily smaller adults.

Parents can feed chicks as much as 30 g on

TABLE 2. Body measurements of Fork-tailed Storm-Petrel chicks from neglected versus non-neglected eggs in 1977, and of chicks brooded versus not brooded on day one in 1976.

	Chicks from eggs neglected < 11 days 1977			Chicks from eggs neglected > 11 days 1977		
Body measurement	n	x̄	σ	n	x̄	σ
Culmen length (cm)	19	.94	.04	13	.93	.05
Tarsus (cm)	19	1.42	.14	13	1.41	.08
Wing (cm)	19	1.49	.14	13	1.47	.08
Weight (g)	19	9.2	1.2	13	9.4	1.1
	Brooded chicks 1976			Non-brooded chicks 1976		
	n	x̄	σ	n	x̄	σ
Culmen length (cm)	39	.95	.04	14	.94	.08
Culmen depth (cm)*	39	.40	.02	14	.39	.02
Wing (cm)	39	1.34	.13	14	1.29	.08
Tarsus (cm)*	39	1.42	.05	14	1.40	.06
Foot (cm)	39	1.24	.08	13	1.22	.10
Weight (g)**	39	10.8	2.2	14	8.8	1.3

* Difference between means is significant $P < .05$ t-test.
** Difference between means is significant $P < .005$ t-test.

TABLE 3. Mann-Whitney U probability values showing that chicks from eggs neglected 11 days or less are larger than those from eggs unattended more than 11 days. Ratios, (e.g., 11/7), represent sample sizes of the two groups: eggs neglected $\leqslant$11 days/eggs neglected >11 days (* = $P < .05$).

Character	Day 1	Day 5	Day 10	Day 15	Day 20	Day 25	Day 30
Culmen length	$P = 0.023$* 11/7	$P = 0.015$* 11/7	$P = 0.017$* 11/7	$P = 0.04$* 11/6	$P = 0.044$* 11/6	$P = 0.045$* 11/5	$P = 0.059$ 10/4
Tarsus	$P = 0.001$* 11/7	$P = 0.004$* 11/7	$P = 0.006$* 11/7	$P = 0.002$* 11/6	$P = 0.044$* 11/6	$P = 0.097$ 11/5	$P = 0.059$ 10/4
Wing	$P = 0.006$* 11/7	$P = 0.015$* 11/7	$P = 0.017$* 11/7	$P = 0.005$* 11/6	$P = 0.009$* 11/6	$P = 0.014$* 11/5	$P = 0.090$ 10/4
Weight	$P = 0.409$ 11/7	$P = 0.111$ 11/7	$P = 0.236$ 11/7	$P = 0.129$ 11/7	$P = 0.242$ 11/6	$P = 0.476$ 11/5	$P = 0.145$ 10/4

one night, so that variations in feeding time and amount make mass a less reliable indicator of size. Growth patterns of chicks from the two groups were not significantly different, although the mean weight of chicks from neglected eggs was lower on all but two days of the first 26 days following hatching (Kolmogorov-Smirnov = $P > .1$; Fig. 6). Thus chicks from neglected eggs appear to be smaller at hatching and remain small for at least the first 20 days.

Depletion of the yolk reserve due to egg-neglect could account for the smaller size of newly-hatched chicks. Yolk supplies ordinarily committed to growth may have been diverted to maintenance when the chicks were un-

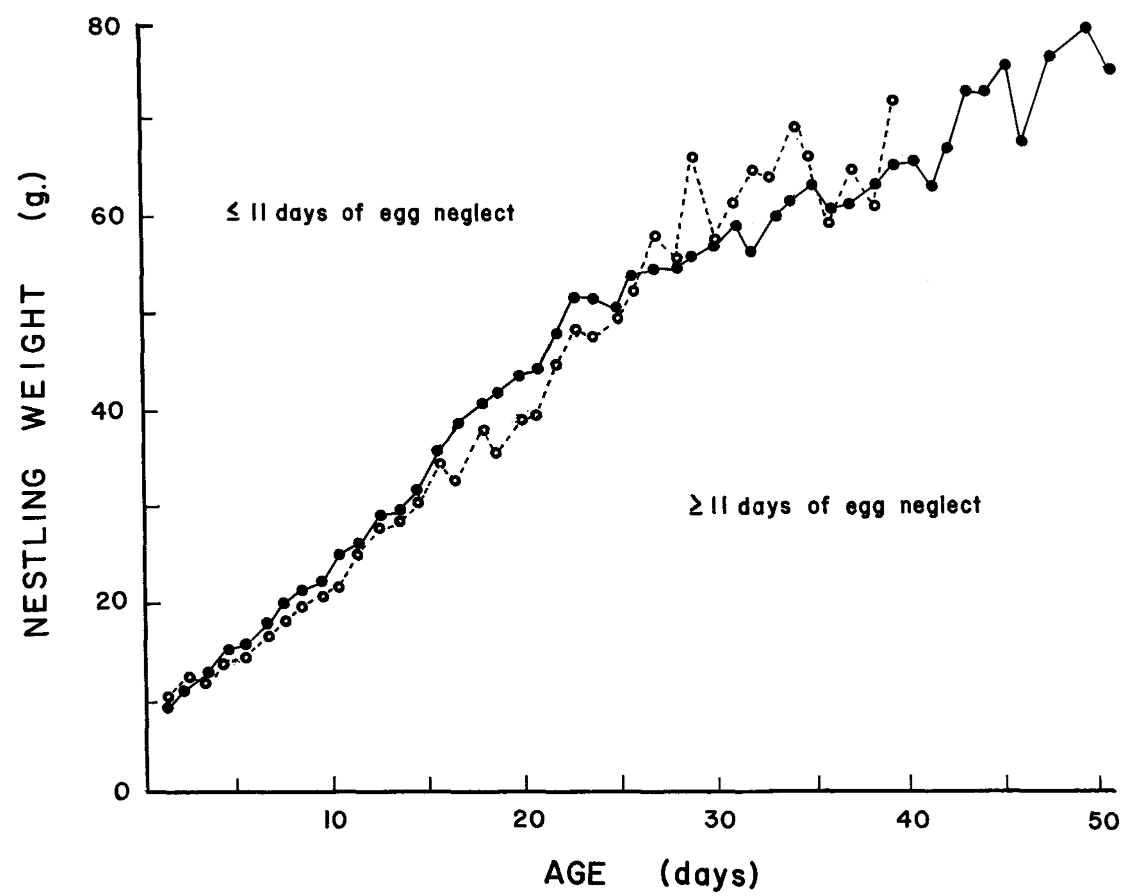

FIGURE 6. Fork-tailed Storm-Petrel mean chick weights from nests where egg-neglect exceeded 11 days (n = 7) versus those where egg-neglect was 11 days or less (n = 12).

attended. Alternately, the growth of chicks from eggs that had been much neglected could have reflected a continuation of parental inattentiveness in feeding the chick. However, this did not seem to be the case. In nests where eggs had been neglected more than 11 days, chicks went unfed only on 28% of the nights (determined by a chick weight loss of more than 2 g in 24 h), whereas the group with 11 or fewer days of egg-neglect was not fed on 34% of the nights although the loads of food may have been greater.

DISCUSSION

Many procellariiform birds neglect their eggs, although none has been shown to do so as much as the Fork-tailed Storm-Petrel. Egg-neglect of several hours to five days has been reported in the Royal Albatross (*Diomedea epomophora*), Laysan Albatross (*D. immutabilis*), Manx Shearwater (*Puffinus puffinus*), Sooty Shearwater (*P. griseus*; Matthews 1954 and references therein), Galapagos Albatross (*D. irrorata*; Harris 1973), Gray-faced Petrel (*Pterodroma macroptera*; Imber 1976), Snow Petrel (*Pagodroma nivea*; Brown 1966), Mottled Petrel (*Pterodroma inexpectata*; Warham et al. 1977), Dove Prion (*Pachyptila desolata*; Tickell 1962), Fairy Prion (*P. turtur*; Richdale 1965a), White-faced Storm-Petrel (*Pelagodroma marina*; Richdale 1965b), Wilson's Storm-Petrel (*Oceanites oceanicus*; Roberts 1940, Beck and Brown 1972, Pefaur 1974), Black-bellied Storm-Petrel (*Fregetta tropica*; Beck and Brown 1971), Storm-Petrel (*Hydrobates pelagicus*: 11 days of neglect, Davis 1957), Madeiran Storm-Petrel (Harris 1969), Galapagos Storm-Petrel (*Oceanodroma tethys*; Harris 1969), and Leach's Storm-Petrel (Matthews 1954, Wilbur 1969).

The most significant effect of egg-neglect in the Fork-tailed Storm-Petrel is to prolong the incubation period. The same thing happens in the Manx Shearwater (Matthews 1954), Gray-faced Petrel (Imber 1976), Mottled Petrel (Warham et al. 1977), and Wilson's Storm-Petrel (Beck and Brown 1972). Similarly, Marshall (1942) and Nisbet (1975) discovered that nocturnal desertion induced by predators delayed hatching in Common Terns (*Sterna hirundo*).

Factors that cause variation in the incubation period in other species include initial egg weight, air temperature (Drent 1975 and references therein, Parsons 1972), body temperature of the incubating bird (Bergtold, in Warham 1971), and body weight of the female (Warham 1971). For Fork-tailed Storm-Petrels, egg-neglect more than any of these factors determined the incubation period.

Although the mean actual incubation period of the Fork-tailed Storm-Petrel was 49.7 days, the net incubation period (the total number of days that the egg was actually attended) averaged 38.6 days, which is similar to the recorded incubation periods of other storm-petrels: Madeiran Storm-Petrel, 39–51 days (Harris 1969); Black-bellied Storm-Petrel, 38–44 days (Beck and Brown 1971); Wilson's Storm-Petrel, 38–43 days (Beck and Brown 1972); Storm-Petrel, 41 days (Davis 1957); and Leach's Storm-Petrel, 41–42 days (Wilbur 1969). These species are not known to neglect their eggs for long periods, which may explain their shorter incubation periods.

In other procellariiform species, the frequency of egg-neglect, where known, is significantly lower than in the Fork-tailed Storm-Petrel. Wilbur (1969) found 12% of the eggs of Leach's Storm-Petrel unattended during a single visit to previously undisturbed nests. Fewer than 2% of the eggs of Manx Shearwaters (Matthews 1954) were found unattended, prompting Matthews to question the survival value of resistance to chilling in embryos of albatrosses and shearwaters. Yet even if the incidence of egg-neglect were only 2% in a species with an incubation period of about 50 days (such as the Manx Shearwater) each pair would, on the average, neglect its egg one day during incubation. Pairs that neglected embryos intolerant of chilling would suffer complete breeding failure that season and a subsequent decrease in fitness relative to other members of the population.

Prévost and Bourlière (1955) suggested that egg-neglect enabled petrels to modify the length of the incubation period so that the chick fledged when food is most abundant. This is unlikely in the case of the Fork-tailed Storm-Petrel for several reasons. The costs of egg-neglect reveal themselves initially in weight loss of the egg. Because chicks hatch with a yolk reserve that allows them to survive for some time without food, the risk of mortality would be expected to rise if the reserve had been depleted during an incubation period prolonged by interrupted incubation.

The risk of hatching failure increases with interrupted incubation, probably outweighing any benefits of retarded hatching. Interrupted incubation reduces hatching success in Ringed Turtle Doves (*Streptopelia risoria*; Peakall and Peakall 1973), Common Terns (Nisbet 1975), and various game and domestic fowl (MacMillan and Eberhardt 1953). Sensitivity to incubation interruption increases during later stages of incubation in Ring-billed Gulls (*Larus delawarensis*) (Hunter et al. 1976) and pheasants and domestic chickens (Moreng and Bryand 1956). Matthews (1954) observed the opposite effect in Manx Shearwaters. Chick mortality in Fork-tailed Storm-Petrels increases substantially with egg-neglect.

Because the breeding season at high latitudes is delayed by snow and ice over the burrow and abbreviated by severe fall storms, any increment to the already considerable incubation and nestling periods of procellariiforms would be disadvantageous. Finally, it is unlikely that hatching is delayed until the time when food is most abundant because we found that hatching was highly asynchronous within the population, extending from 26 June until 24 August in 1976 and from 3 July until 19 August in 1977.

Tolerance of a procellariiform embryo to chilling is an adaptation that mollifies the reproductive penalties of interrupted incubation. It is not without costs, however, for inattentive birds forfeit some degree of hatching success, chick viability, and chick size. The risk of reduced reproductive success in one breeding season due to egg-neglect must be compensated for by an increase in an individual's total fitness if egg-neglect is adaptive. Because of the embryo's tolerance to chilling, underweight adults who are feeding do not have to return soon to incubate. They can continue foraging without risking certain nest failure, instead of possibly endangering future reproductive opportunities by returning to incubate without having fed.

We found that egg-neglect increased and adult weight declined during the breeding season. Late in the incubation period, therefore, when faced with the immediate "decision" of whether to return to incubate or to continue foraging, an adult should be more likely to neglect the egg. Alternatively, the distribution of food may have changed as the season progressed. If the food resource moves farther away from the colony, is depleted inshore by foraging, or becomes more patchy, storm-petrels would be forced to fly farther to feed or to spend more time foraging. Egg-neglect should increase because the probability of failing to return rises with both distance and time of foraging.

There is, of course, some upper limit to the amount of neglect an embryo can survive. At what point should an incubating bird abandon the egg? The "decision" to continue incubating or to desert the egg depends upon the probability that the egg will hatch (which diminishes with egg-neglect) and the costs involved in incubation. If the costs of incubation, such as forfeiture of foraging time or exposure to predation on the nest, are high and reduce the probability of future reproduction, individuals should invest little extra time and energy in an egg that has not hatched at the end of the expected incubation period. If, on the other hand, continuing incubation does not lower reproductive value substantially, individuals should continue to incubate for a longer time. We found that the mean interval between laying and desertion of eggs that did not hatch was 60.4 days ($n = 17$), about 60% more than the minimum observed incubation period, 37 days. One banded storm-petrel continued to incubate after 81 days. Many species will incubate 50–100% more than the normal incubation period (Skutch 1962, Holcomb 1970). If age-specific mortality occurs, the optimal incubation commitment should vary. Older birds, who have fewer future reproductive opportunities, would be expected to devote a greater effort to reproduction once they begin nesting than younger birds (Williams 1966) and to incubate for a longer period in excess of the normal incubation period.

Procellariiform birds are adapted for a pelagic existence where food resources are frequently undependable (Lack 1968, Warham 1971). Both sexes alternate incubation duties, and the evolution of tolerance to chilling in the embryo may permit their long incubation shifts. In the Fork-tailed Storm-Petrel incubation shifts typically last two to three days, and may be as long as five days. Chilling tolerance and long incubation shifts enable storm-petrels to forage at greater distances from the nest. Billings (1968) showed in homing experiments that Leach's Storm-Petrels may travel more than 250 km per day and still gain weight. As a result, storm-petrels may take advantage of rich food resources and thereby encounter less competition for food.

The probability that storms or other factors would prevent a storm-petrel from returning to relieve its incubating partner increases with foraging distance. Furthermore, for species which are nocturnal at the colony, the "target time" (hours of darkness) for returning to the colony is briefer at high latitudes. Where darkness lasts only two to three hours each night, if a storm-petrel foraging far from the island is delayed by a sudden head wind or storm, it may easily be prevented from returning on a given night. Accordingly, we can made several predictions about patterns of egg-neglect which should hold true for other groups with similar habits. For similar species of storm-petrels that forage at different distances from the colony, egg-neglect will be more common in the more distant forager. Leach's Storm-Petrels would be expected to neglect their eggs more than Fork-tailed Storm-Petrels or Ashy Storm-Petrels (*Oceanodroma homochroa*) where they co-occur, because Leach's Storm-Petrel forages at a greater distance (Ainley et al. 1974, Crossin 1974, Harris 1974). Within a species that is nocturnal at the colony there will be a latitudinal gradient in egg-neglect, which should increase with latitude and decreasing night length during the breeding season. These trends should be true except where other factors override them. For example, at very high latitudes, where extreme temperatures are lethal to an unattended egg, neglect should be infrequent. At low latitudes, egg-neglect should not be expected in species that nest in exposed places where the egg is subject to solar radiation or high air temperatures. Nesting in holes reduces the effect of extreme temperatures and predation, particularly at low latitudes. Several species with protected nests abandon the eggs during the day in tropical Africa (Koenig 1956). Similarly, where egg predation (see Richdale 1952, Tickell and Pinder 1975) or intraspecific competition for nest sites is high (see Harris 1969), the advantages of egg-neglect are outweighed by the potential loss of the egg or nest.

SUMMARY

Many procellariiform birds regularly neglect to incubate their eggs. The embryo of the Fork-tailed Storm-Petrel, in particular, can tolerate frequent parental neglect. Of 33 nests in which chicks hatched, the mean number of days of egg-neglect was 11.0. Embryos survived intervals of up to seven days of continuous desertion during which burrow temperatures averaged 10°C. Depending upon the incidence of egg-neglect, incubation periods extended from 37–68 days ($\bar{x}$ = 49.8 days). Hatching appeared to be determined by the number of days of actual incubation rather than the length of the entire incubation period, including egg-neglect. Increased neglect of eggs was associated with loss of egg weight, parental inattentiveness of the chick during the first five days, smaller hatchlings, and higher chick mortality. Tolerance of embryos to chilling is adaptive in an environment where storms are severe and unpredictable and food resources are patchy. We predict that species of storm-petrels that forage at a distance or breed at high latitudes will be found to neglect their eggs.

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RECENT PUBLICATION

A Field Guide to the Nests, Eggs and Nestlings of North American Birds.—Colin Harrison. 1978. William Collins Publishers, Inc., Cleveland, Ohio. 416 p. $11.95. This book follows the same plan as the author's guide to European nests, eggs, and nestlings. Identification keys lead to the species accounts, where nesting habitat, nest structure, breeding season, eggs, incubation, nestling, and nestling period are described succinctly. The book is illustrated with many drawings and color paintings of nests and nestlings by Philip Burton and over 620 color photographs of individual eggs. A waterproof cover adds to its practicality for field use. In addition to serving its intended purpose, the book is useful as a source of basic information on the breeding habits of North American birds. Compare it with *Hal H.* Harrison's field guide to nests in the Peterson Field Guide Series (1975. Houghton Mifflin Co.).