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COMPARATIVE BIOLOGY OF THE BURROWING PETRELS OF THE CROZET ISLANDS

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ABSTRACT

This paper presents, as well as some earlier data, the results of a study of the burrowing petrels of the Crozet Islands (South Indian Ocean) made during the East Island expedition of September 1981 to February 1982.

The 16 petrels are discussed and analysed in the following taxonomic groups: 4 gadfly petrels, 5 prions, 2 *Procellaria* petrels, 3 storm petrels and 2 diving petrels. For each group, biometric data and the breeding biology of each species are given. The timing of events (first return to land, laying, hatching, fledging), nest reoccupation, incubation schedule, chick growth and chick-feeding pattern were the main study topics.

Abundance cycles during pairing, temporary egg desertions, nest selection, comparison with other localities and particularly ecological segregation of the petrels are discussed.

INTRODUCTION

The Crozet Islands, discovered in 1772 by the French navigator Nicolas Marion-Dufresne, lie in the Indian Ocean between longitudes 50°00′ and 52°30′ E and latitudes 45°50′and 46°30′ S.

A recent study (Gamberoni *et al.* 1982) showed that the Antarctic Convergence is displaced northwards in the Crozet - Kerguelen region by the shelves of these island groups. The Crozet Islands are more than 300 km south of the Polar Front but north of the limit of the subsurface temperature minimum between 48° and 49° S. Thus, the chief hydrological characteristic of this region is the limited extent of subantarctic waters because the Antarctic and Subtropical Convergences are very close together (43° and 41° respectively).

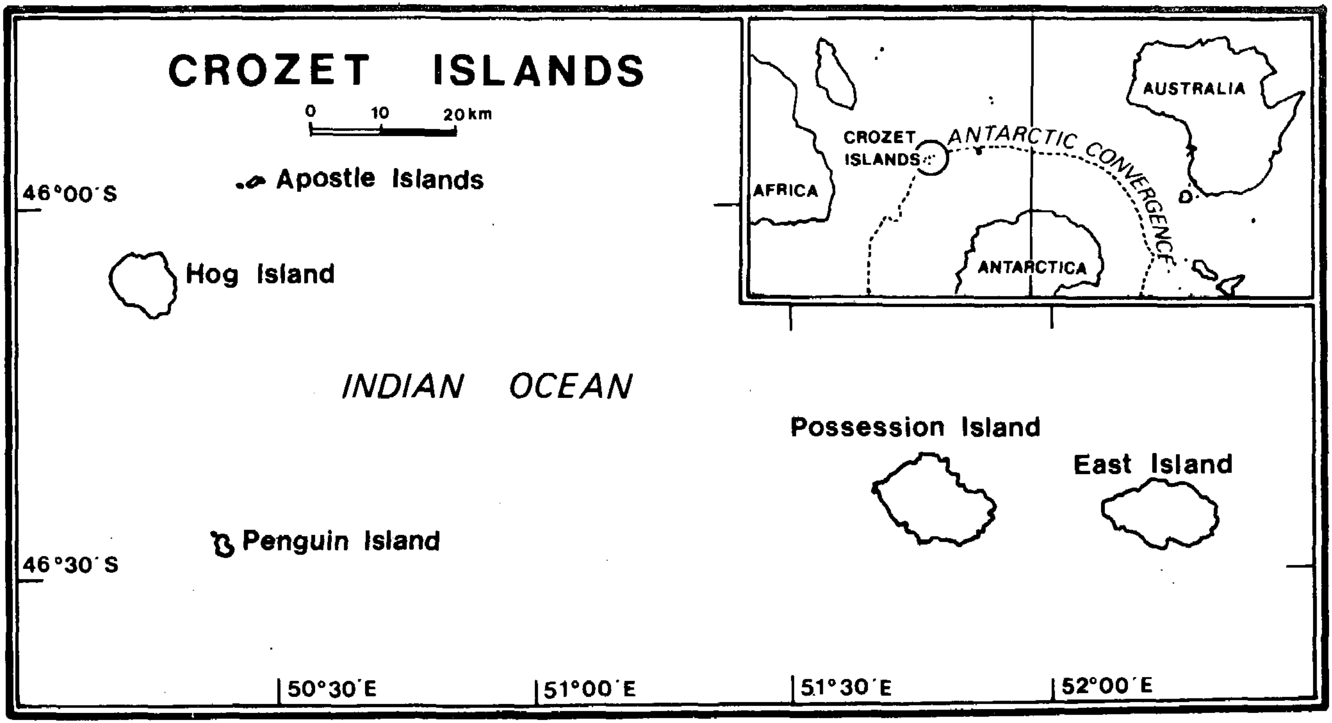

FIGURE 1 — Location and map of the Crozet Islands

The Crozet Islands are scattered over about 150 km east to west and have an estimated total land area of about 500 km². There are two groups of islands (Fig. 1); to the west, Hog Island, Penguin Island and Apostle Islands, and to the east, Possession Island and East Island. The islands are volcanic in origin and are small (the largest, Possession Island, is 18 km on its longest side), but the topography is complex and rises to quite a high altitude. The highest point is 1050 m on East Island. The coastline alternates between cliffs and beaches of sand or boulders. The interior consists of large glacial valleys separated by rocky ridges or high plateaus. The tundra-type vegetation (no trees occur on the Crozets) does not extend higher than 300 m a.s.l.

The climate is severe, even for the "roaring forties". The temperatures are cold, the mean annual temperature being + 4.6°C. There is a small variation in temperature between the warmest month (February, + 7.7°C) and the coldest (September, + 2.8°C), but the climate is characterised by violent winds, which have a mean annual speed of 12 m/s (43 km/h) and a maximum of 70 m/s (252 km/h). For example, in 1980 the wind blew at speeds of more than 115 km/h on 93 days. Sunshine hours are low overall (a monthly mean of 103 hours) and rainfall is high (2470 mm per annum). During winter, snowfalls are frequent but there is no permanent snow on the islands.

We have shown elsewhere (Jouventin *et al.* 1984) that the Crozet Islands shelter a rich seabird community. East Island has the most birds of the group. Of the 34 seabird species breeding on the Crozets, 32 are on East Island, which lacks introduced predators (cats and rats). This island is the breeding ground of 23 procellariiformes (5 albatrosses, 13 procellarids, 3 storm petrels and 2 diving petrels) compared with 15 on Possession Island, 8 on Hog Island, 18 on Penguin Island and 15 on Apostle Islands. Of these 23 species, 15 nest in burrows. The only burrowing species of the Crozets missing on East Island is the White-headed Petrel (*Pterodroma lessonii*), which nests only on Possession Island. Studies of burrowing petrels of the Crozet group are therefore best done on East Island.

A study of this kind was lacking. The whole breeding cycle of some of these petrels — *Pterodroma brevirostris* (Mougin 1969), *P. lessonii* (Barré 1976), *Procellaria aequinoctialis* (Mougin 1970, 1971), and *Procellaria cinerea* (Barrat 1974, Despin 1976) — had been studied on Possession Island. Partial studies on most of the burrowing petrels had resulted from summer expeditions to East Island (Despin *et al.* 1972) and Hog Island (Derenne *et al.* 1976, Derenne & Mougin 1976) for limited periods of time. A complete study of all the burrowing petrels had still to be done, and we attempted this on East Island from September 1981 to March 1982.

METHODS

We marked occupied burrows during pairing of the birds as soon as possible after the adults returned to land. We judged this by listening to the diurnal and nocturnal vocal activity of the pairs and by closing the entrances of burrows suspected of occupation and seeing if they were reopened by the next morning. For monitoring, we dug observation windows above the nesting chamber of each burrow and rearranged nests among rocks. We marked study nests and, whenever possible, ringed both birds in each pair on a different leg to simplify identification. For the more timid species we occasionally ringed only one of the pair or marked them with paint to reduce handling.

To compare the growth of chicks of the various species, we measured and weighed them at 3-day intervals to calculate the mean growth-rates. To study chick feeding we weighed chicks daily. An increase in weight or stable weight between two weighings was considered to represent a feeding. For each nest we divided the number of nights with chick feeding by the total number of nights studied to get the frequency of feedings, F. To calculate the sojourn at sea per adult we have used the formula

$$1 - F = (1 - p)^2$$

where p is the probability of a visit to the nest by an adult. We draw from this that

$$p = 1 - \sqrt{1 - F}$$

The actual number of visits by the parents during the study period is then equal to 2 pn, n being the total number of nights studied. Finally, the interval between two visits by the same adult is equal to $\frac{1}{p}$.

GADFLY PETRELS

On the Crozet Islands, the genus *Pterodroma* is represented by four species, the Great-winged Petrel *(P. macroptera),* the White-headed Petrel *(P. lessonii),* the Kerguelen Petrel *(P. brevirostris)* and the Soft-plumaged Petrel *(P. mollis).*

Table 1 shows the measurements of the birds from this locality (partly from Prévost 1970, Despin *et al.* 1972 and Barré 1976), and Table 2 shows the chronology of their breeding cycles (partly from Warham 1956, Mougin 1969, Despin *et al.* 1972, Barré 1976, Imber 1976).

The White-headed Petrel and the Soft-plumaged Petrel are summer breeders. White-headed Petrels occupy their colonies from September to May, whereas Soft-plumaged Petrels breed from September to April. The rather long breeding cycle of the Great-winged Petrel is centred on the winter season, its return to land being in February. Fledging occurs from October to December. Between mid-December and the beginning of February, the adults are absent from their colonies. The breeding cycle of the Kerguelen Petrel, which lasts a little less than 6 months, is the shortest of the four species. It begins in August, before the end of winter, and ends in February.

During its long non-breeding season, the Kerguelen Petrel visits its colonies frequently (Mougin 1969). Between the first returns to land and laying, pairing is long for the gadfly petrels (Table 2), except for the Kerguelen Petrel.

Reoccupation of burrows

Soft-plumaged Petrel: 32 burrows were inspected daily. Occupation of burrows was low at the end of September but increased progressively during October, reaching a maximum in the last 10 days of the month. Thereafter, it diminished up to the beginning of December, when the first layings began (Fig. 2). The occupation of burrows increased regularly between the 80th and 51st days before laying, attaining a maximum between the 50th and 41st days.

TABLE 1 —Weights (g) and measurements (mm) of *Pterodroma* species

	P.macroptera	P.lessonii	P.brevirostris	P.mollis
Weight				
Mean ±S.D.	560 ±58	770 ±15	331 ±40	302 ±23
Range (n)	455-680(28)	750-780(3)	210-400(29)	245-360(72)
Wing				
Mean ±S.D.	306 ±7	309	259 ±8	253 ±5
Range (n)	293-320(29)	305-319(5)	231-275(33)	238-265(76)
Culmen				
Mean ±S.D.	36.4 ±1.2	38.5	27.0 ±1.4	28.5 ±1.0
Range (n)	33.5-38.8(29)	37.8-39.5(6)	24.5-29.0(33)	26.0-31.8(76)
Tarsus				
Mean ±S.D.	43.8 ±1.4	45.9	38.5 ±1.5	35.8 ±1.0
Range (n)	41.2-48.0(29)	43.0-48.5(5)	35.5-41.0(33)	33.5-38.0(76)

TABLE 2 —Timing and duration of events during the breeding cycle of *Pterodroma* species. Values in brackets indicate estimates from data available in other localities.

	P.macroptera	P.lessonii	P.brevirostris	P.mollis
Visits observed during the post breeding period	No	No	Yes	No
First return on land	7 feb 71 15 feb 82	sep	9-28 aug 68	before 20 sep 81
Length of pre-laying period (days)	(75)	80	53 range 43-63(6)	⩾88
Laying period Mean ±S.D. Range (n)	(25 apr - 10 jun)	late nov - early dec	10 oct 68 ±1 15 oct 81 ±6 9-13 oct 68(9) 2-25 oct 81(17)	16 dec 81 ± 6 9-28 dec (17)
Period from laying to hatching (days) Mean ±S.D. Range (n)		60 (1)	58.7 ±5.7 54-65(3)	52.0 ± 2.6 49-55 (6)
Real incubation period (days) Mean ±S.D. Range (n)			49.3 ±1.8 47-51(7)	50.2 ±0.8 49-51(6)
Hatching period Mean ±S.D. Range (n)	(20 jun.-late jul.)	late jan - early feb	28 nov 68 ±2 10 dec 81 ±6 27-30 nov 68(4) 30 nov -17 dec 81(7)	7 feb 82 ±5 2-16 feb (7)
Fledging period (days)		>100	62(61-63)(2)	
Departure of fledglings from the colony Mean ±S.D. Range (n)	4 nov 81 ±14 16 oct -11 dec (35)	1-15 may	27-29 jan 68 23 jan -3 feb 71 29 jan -18 feb 82	

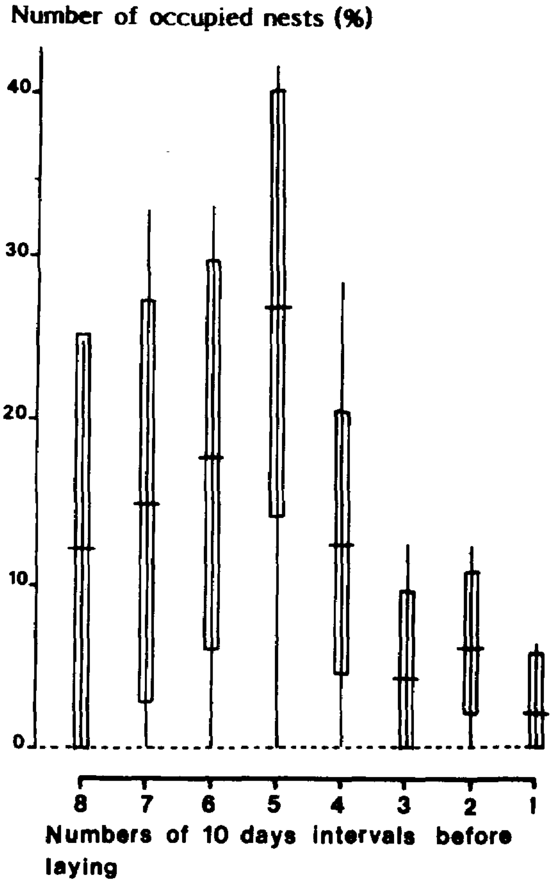

FIGURE 2 — Nest attendance by *Pterodroma mollis* before laying on Crozet

It then diminished rapidly for 10 days, and remained low for the month before laying. Individual visits lasted 1.3 ± 0.7 days (n=153, range 1-6 days), 79.1% of them lasting not more than 1 day.

Kerguelen Petrel: A high diurnal occupation of the colonies on Possession Island was noted at the end of August: 33.3% of nests during the second 10-day period of the month and 10.2% during the third 10-day period were visited by at least one adult each day. Of the total number of visits 86.4% lasted no more than 1 day and 13.6% lasted 2 days (mean 1.1 ± 0.4 days). In September and early October, visits became fewer or strictly nocturnal with no birds observed during the day in the 11 nests studied. It was the same on East Island during the last days of pairing. Of the 16 nests monitored before laying (5-28 days of observation), nest visits occurred on only 2 out of the total of 285 nest-days, or 0.7%. Thus, this species has a long prelaying exodus by both sexes.

Activity of non-breeders

In the Soft-plumaged Petrel, non-breeders exceeded breeders. Out of 32 burrows studied, only 36 of the total of 88 banded birds bred. That is, 59.1% of the birds were non-breeders. Of the 88 birds, 82 (93.2%) did not use more than one burrow throughout courtship and 6 (6.8%) used two. Each of the 32 burrows studied was visited by 2.94 ± 1.64 birds (range 1-7). Some nests of the Soft-plumaged Petrel were more frequented than others; these were the ones in which eggs were subsequently laid. The 15 burrows in which no laying occurred were frequented by 2.07 ± 1.33 birds (range 1-5), whereas the 17 burrows where the petrels did lay were frequented by 3.71 ± 1.53 birds (range 2-7), the two values being significantly different ($t=2.82$; $p < 0.01$).

Nest occupation rate was higher in the Kerguelen Petrel. On East Island, 17 eggs were laid in 23 burrows (73.9%), and on Possession Island in 1968, 9 eggs were laid in 11 occupied burrows (82%) (Mougin 1969).

Most Soft-plumaged Petrels were faithful to one partner throughout courtship in spite of an enormous abundance of birds. For 64 paired birds observed at this time, 61 (95.3%) kept the same partner, 2 (3.1%) courted two partners in succession and only 1 (1.6%) courted three.

Laying

At the end of the prelaying exodus, most of the females came ashore only very briefly. They first returned on the night of laying (94% of females) and only 6% first returned on the night before the night of laying (17 birds).

The laying dates for gadfly petrels on Crozet are given in Table 2. For most, the laying period was short. It lasted 24 days (17 layings) for the Kerguelen Petrel on East Island in 1981, 5 days (9 layings) for the same species on Possession Island in 1968 (Mougin 1969), and 20 days (17 layings) for the Soft-plumaged Petrel on East Island. For *Pterodroma lessonii* on Possession Island, the laying period lasted from 21 November to 12 December (Barré 1976). Data are lacking for the Great-winged Petrel but results from New Zealand (Imber 1976) and the fledging period on East Island suggest that the laying period could last 5-6 weeks.

Egg measurements of gadfly petrels from Crozet are given in Table 3. The Kerguelen Petrel eggs and those of the Soft-plumaged Petrel are indistinguishable by their weight and volume but differ in shape, the eggs

TABLE 3 —Weights (g) and dimensions (mm) of eggs of *Pterodroma* species

	P. lessonii	*P. brevirostris*	*P. mollis*
Weight			
Mean ± S.D.	99	55.5 ± 1.9	57.1 ± 3.5
Range (n)	93-105 (2)	54-59 (8)	52-67 (22)
Length			
Mean ± S.D.	70.3 ± 1.0	56.8 ± 1.8	59.4 ± 1.9
Range (n)	69.5-71.4 (3)	53.7-60.5 (22)	55.0-63.0 (36)
Breadth			
Mean ± S.D.	51.7 ± 1.5	43.9 ± 1.2	42.8 ± 1.2
Range (n)	50.0-52.8 (3)	41.2-46.8 (22)	40.0-45.2 (36)

of *P. mollis* being more elongated than those of *P. brevirostris*. The ratio of egg weight to adult weight is 12.9% in *P. lessonii*, 16.8% in *P. brevirostris* and 18.9% in *P. mollis*. We do not have the same data for *P. macroptera*, although, if these are similar to those in New Zealand, the ratio would be 15.5% (Imber 1976).

Incubation

Incubation shifts were studied only for the Kerguelen Petrel and the Soft-plumaged Petrel (Tables 4 and 5, Fig. 3). Shifts were long in both species (average 9-10 days) except for the first shift of the female. As hatching approached, these shifts shortened for the Kerguelen Petrel. In both species, incubation is divided into five or six shifts. The female does more numerous and shorter shifts than the male, but the two sexes incubate for about the same time. Table 5 shows that small differences can exist from year to year in the same species, but they are not significant.

Temporary egg desertions during incubation were particularly frequent for the Kerguelen Petrel on East Island in 1981-82. They were especially noticeable at the beginning of incubation (at the end of the female's first shift) when the return of the males was not synchronous. Thereafter desertions were much shorter and fewer. The egg's resistance to low temperatures for long periods is remarkable: 9 days on average for three eggs that hatched. These temporary desertions are not constant for the Kerguelen Petrel and did not occur in 1968 on Possession Island (Mougin 1969). However, they were much less frequent in 1981-82 on East Island for Soft-plumaged Petrel than for Kerguelen Petrel: of six eggs that hatched, three were deserted once for a maximum of four days.

Thus, the Kerguelen Petrel's sojourns at sea were long during the 1981-1982 incubation, the incubation shifts for both sexes were long, and there were numerous desertions of the egg. The sojourns for the Soft-plumaged Petrel were not as long (11 days average) as for the Kerguelen Petrel (13 days).

The hatching dates of gadfly petrels from Crozet are given in Table 2. Due to the repeated egg desertions during incubation in 1981, hatching for the Kerguelen Petrel was later than in 1968 (Mougin 1969). This was also true for the Soft-plumaged Petrel, the hatching period in 1981-1982 being 2-16 February compared with 21 January-8 February 11 years before (Despin *et al.* 1972).

Incubation in three Kerguelen Petrel nests lasted for a mean of 58.7 days (54-65 days). These eggs were deserted for a total of 9.0 days (4-14 days). If we subtract one figure from the other, we get an actual incubation mean length of 49.7 (48-51) days. The figure obtained in 1968 on four eggs from Possession Island, 49.0 (47-51) days (Mougin 1969), was very similar. The same was true for six Soft-plumaged Petrel nests where the total apparent incubation length was 52.0 (49-55) days. After subtracting 1.8 days of desertion time, we get the actual incubation mean length of 50.2 (49-51) days. The incubation length for the White-headed Petrel on Crozet is 60 days (Barré 1976) but is not known for the Great-winged Petrel. Imber (1976) showed 54.6 (53-57) days to be the average incubation length for this species in New Zealand.

TABLE 4 — Incubating shifts and egg desertions in *Pterodroma brevirostris* and *P. mollis*

	Length of stay in burrow (days)		Length of desertion (days)		Desertion frequency (per cent)	
	Pterodroma		Pterodroma		Pterodroma	
	brevirostris	mollis	brevirostris	mollis	brevirostris	mollis
First shift (♀)						
Mean ± S.D.	4.6 ± 3.4	2.3 ± 1.6	4.3 ± 4.8	1.2 ± 1.8	67	33
Range	(0-9)	(0.5-5)	(0-11)	(0-4)		
Second shift (♂)						
Mean ± S.D.	13.9 ± 3.6	12.5 ± 1.6	1.7 ± 2.1	0	67	0
Range	(10-21)	(11-14)	(0-4)			
Third shift (♀)						
Mean ± S.D.	13.7 ± 2.5	12.8 ± 1.7	1.0 ± 1.7	0.7 ± 1.6	33	17
Range	(11-16)	(10-15)	(0-3)	(0-4)		
Fourth shift (♂)						
Mean ± S.D.	8.3 ± 2.0	12.5 ± 2.1	0.5 ± 1.2	0	17	0
Range	(7-12)	(10-15)	(0-3)			
Fifth shift (♀)						
Mean ± S.D.	7.3 ± 2.9	11.0 ± 1.3	0	0	0	0
Range	(4-9)	(10-13)				

TABLE 5 — Incubation schedule in *Pterodroma brevirostris* and *P. mollis*

		P. brevirostris		P. mollis
		1981-1982	1968-1969	1981-1982
INCUBATION				
Mean length of a shift (days)				
both sexes	mean ± S.D.	9.3 ± 4.1	10.1 ± 4.4	9.9 ± 4.6
	range (n)	1-16 (16)	2-20 (30)	0.5-15 (31)
male	mean ± S.D.	10.1 ± 3.3	12.5 ± 3.6	11.6 ± 3.6
	range (n)	7-15 (7)	7-20 (12)	1-15 (13)
female	mean ± S.D.	8.7 ± 4.7	8.5 ± 4.3	8.7 ± 5.0
	range (n)	1-16 (9)	2-17 (18)	0.5-15 (18)
DESERTION				
Mean number of periods per nest				
	mean ± S.D.	2.0 ± 1.0	-	0.5 ± 0.5
	range (n)	1-3 (3)		0-1 (6)
Total length per nest (days)				
	mean ± S.D.	9.0 ± 5.0	-	1.8 ± 2.0
	range (n)	4-14 (3)		0-4 (6)
Mean length of a period (days)				
	mean ± S.D.	4.5 ± 3.3	-	3.7 ± 0.6
	range (n)	2-11 (6)		3-4 (3)
Frequency of nest-reliefs with desertion (per cent)				
	mean ± S.D.	46.7 ± 25.7	-	11.7 ± 12.9
	range (n)	25.0-75.0 (3)		0-25.0 (6)
STAYS AT SEA				
Mean length (days)				
both sexes	mean ± S.D.	12.7 ± 5.5	10.1 ± 4.4	11.0 ± 4.5
	range (n)	4-22 (16)	2-20 (30)	0.5-17 (30)
male	mean ± S.D.	11.7 ± 5.1	8.5 ± 4.3	9.3 ± 4.9
	range (n)	4-20 (9)	2-17 (18)	0.5-17 (18)
female	mean ± S.D.	14.0 ± 6.1	12.5 ± 3.6	13.4 ± 2.2
	range (n)	8-22 (7)	7-20 (12)	10-17 (12)

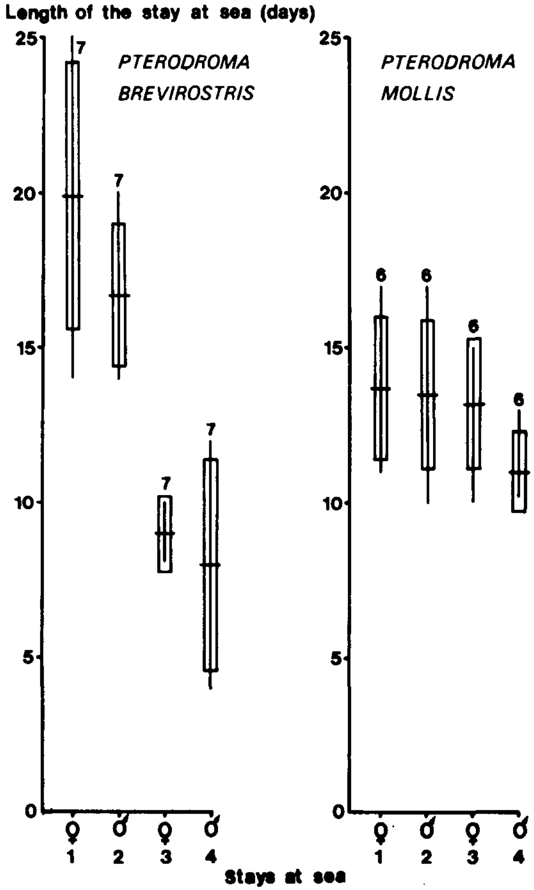

FIGURE 3 — Duration of sojourns at sea in *Pterodroma brevirostris* and *Pterodroma mollis* during each incubation shift. Mean ± standard deviation, range and sample size

These gadfly petrel chicks were able to survive without the additional warmth of a parent within 48 hours after hatching. This is called *thermic emancipation.*

Chick growth

Weight gain and growth of chicks are given in Fig. 4-9 and in Table 6. Because of the timing of our visit we missed the end of growth of the Soft-plumaged Petrel and the beginning of growth of the Great-winged Petrel. The Soft-plumaged Petrel was monitored for the first month after hatching and the Great-winged Petrel for the last two months of its stay on land. Only the Kerguelen Petrel was studied from hatching to fledging. The White-headed Petrel had already been studied by Barré (1976).

TABLE 6 — Weight growth in *Pterodroma brevirostris* and *P. macroptera* chicks

	P.macroptera	P.brevirostris 1981-1982	P.brevirostris 1970-1971
Weight at birth			
Weight (g)			
Mean ±S.D.		42.4 ±21.8	
Range (n)		45-58(4)	
Percent adult weight		12.8	
Maximum weight			
Weight (g)			
Mean ±S.D.	653 ±99	410 ±68	440
Range (n)	470-870(15)	340-475(3)	385-460
Percent adult weight	117	124	133
Age at peak weight (days)			
Mean ±S.D.	81 ±15	43 ±5	52
Range (n)	57-111(15)	38-48(3)	
Weight at fledging			
Weight (g)			
Mean ±S.D.	461 ±77	233	310
Range (n)	305-570(15)	221-245(2)	220-380
Percent adult weight	82	70	94

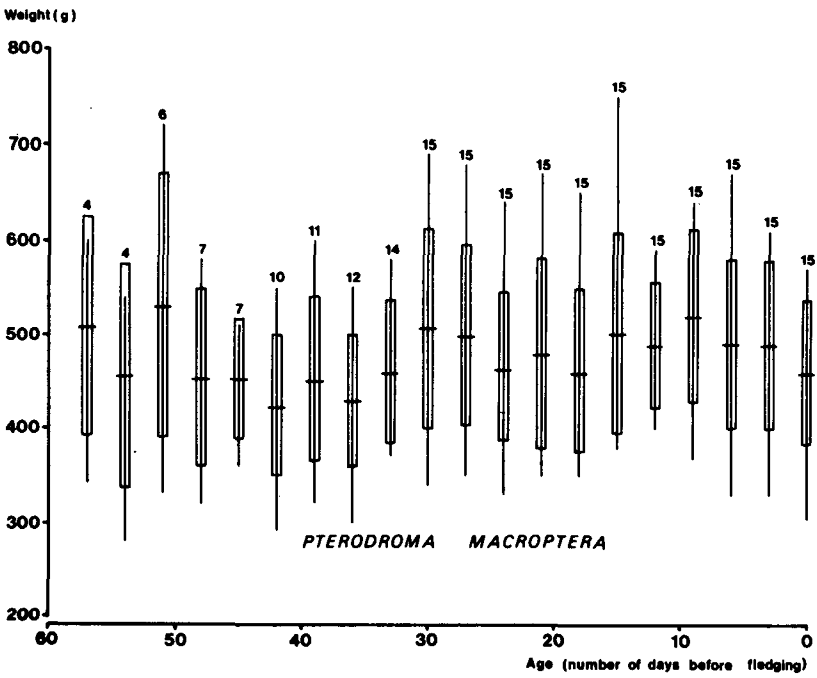

FIGURE 4 — Weight increase in *Pterodroma macroptera* chicks. Mean ± standard deviation, range and sample size

There were two periods in weight growth. The rate of weight gain for the Kerguelen Petrel in three-day periods was 26.5 ± 18.5% for the first 15 days after hatching and 13.8 ± 14.9% for the second. For the Soft-plumaged Petrel it was 20.1 ± 19.2% and 10.8 ± 9.7%. When the Great-winged Petrel and Kerguelen Petrel chicks were two-thirds of the way to fledging, they weighed 20% more than the adults. In the last third of growth the Kerguelen Petrel chicks lost 30-40% of their maximum weight at a rate of decrease of 4.1 ± 8.7%. At fledging the chicks weighed 70 - 80% of the adult weight.

These results vary from year to year. Table 6 shows that the maximum weight and fledging weight for the Kerguelen Petrel were far less in 1981-1982 than 11 years before (Despin *et al.* 1972).

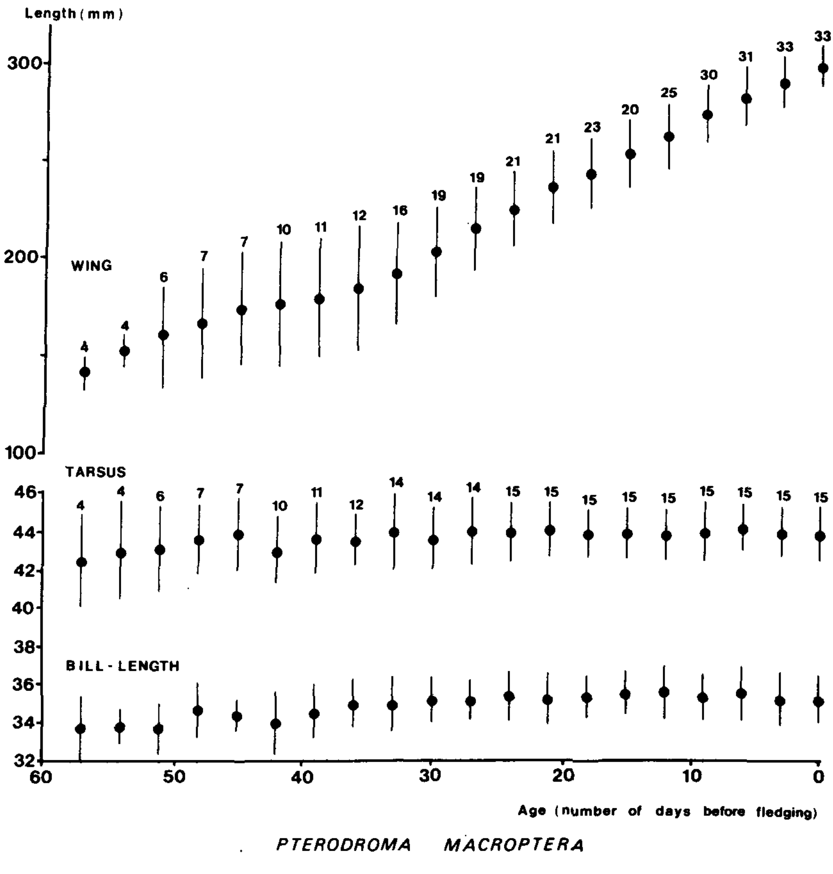

FIGURE 5 — Growth of wing, tarsus and bill length in *Pterodroma macroptera* chicks. Mean ± standard deviation and sample size

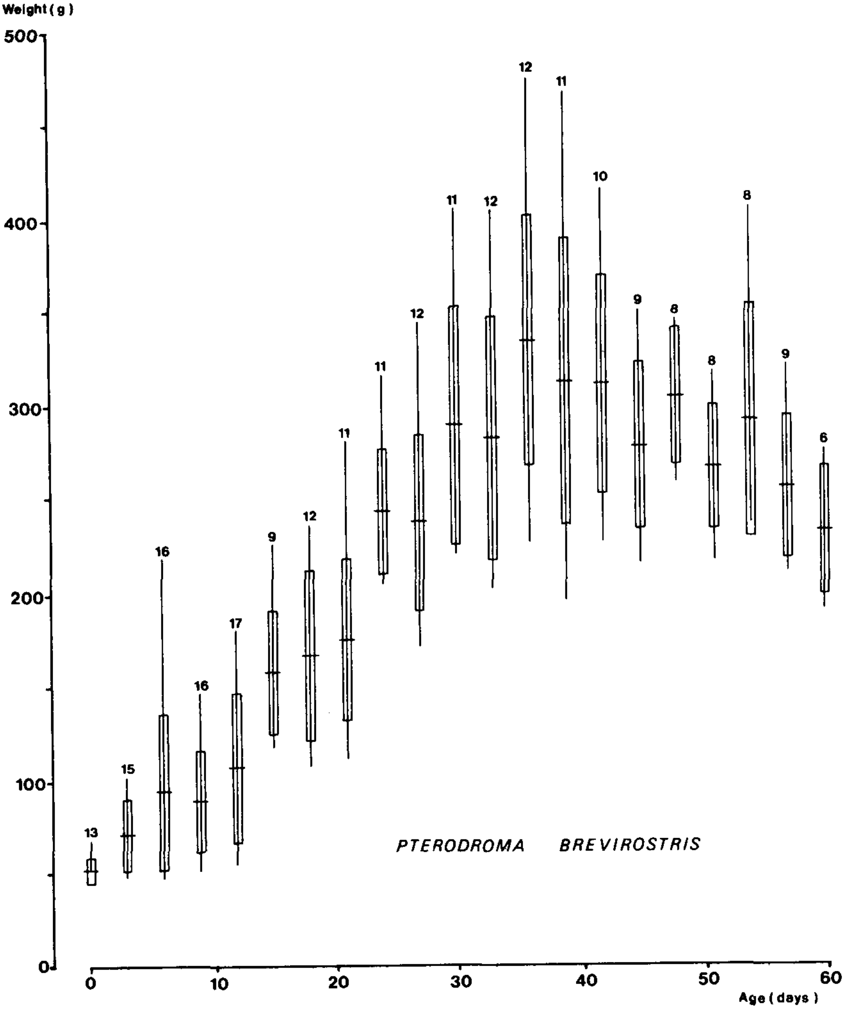

FIGURE 6 — Weight increase in *Pterodroma brevirostris* chicks. Mean ± standard deviation, range and sample size

The growth of the Great-winged Petrel was slightly different. Maximum weight was followed by a weight loss 37 ± 15 days before fledging. Variation between individuals was considerable, with periods of weight loss lasting 7-61 days for the 15 chicks studied. Some chicks gained weight while others were losing it, but the mean weight of our 15 chicks remained constant during the last two months of growth (Fig. 4). As usual, wing growth occurred in two stages. Before the appearance of the primaries it was slow, the average rate of increase in three-day periods reaching 5.2 ± 4.3% for the Kerguelen Petrel and 5.5 ± 3.2% for the Soft-plumaged Petrel. With the appearance of the primaries, it was more rapid and nearly constant until fledging, the rate of increase being 14.5 ± 8.3% for the Kerguelen Petrel, 11.5 ± 8.3% for the Soft-plumaged Petrel and only 4.1 ± 17% for the Great-winged Petrel. Adult size was not always reached by the time the chicks fledged.

The culmen and tarsus also developed in two stages, rapidly at first and then slowing down or even totally stopping as in the Great-winged Petrel for the last two months in the nest. All reached adult measurements by the time they fledged.

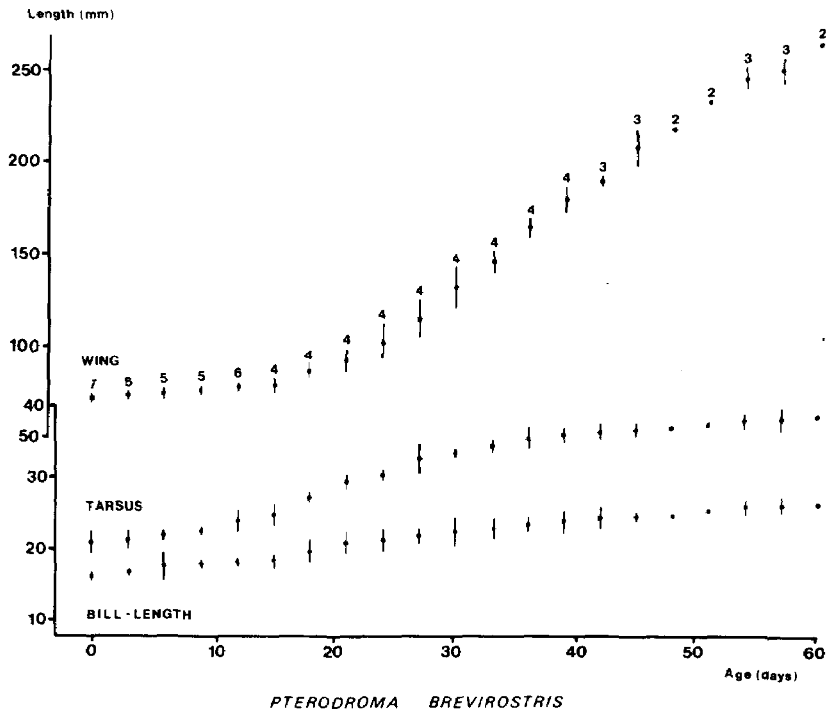

FIGURE 7 — Growth of wing, tarsus and bill length in *Pterodroma brevirostris* chicks. Mean ± standard deviation and sample size

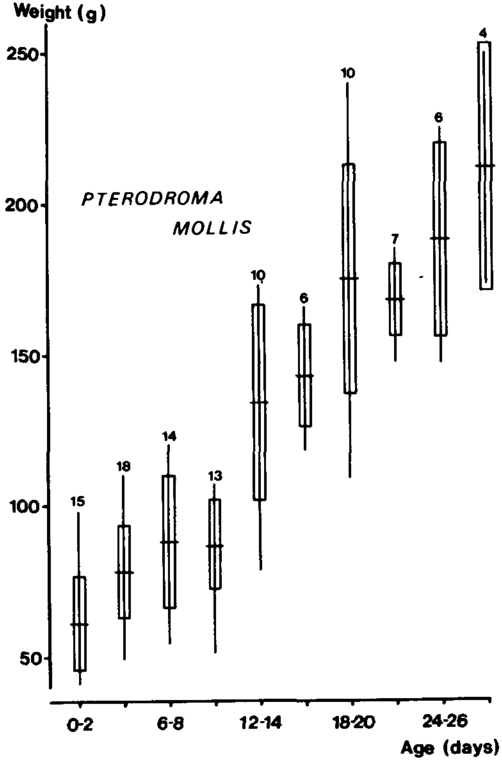

FIGURE 8 — Weight increase in *Pterodroma mollis* chicks. Mean ± standard deviation, range and sample size

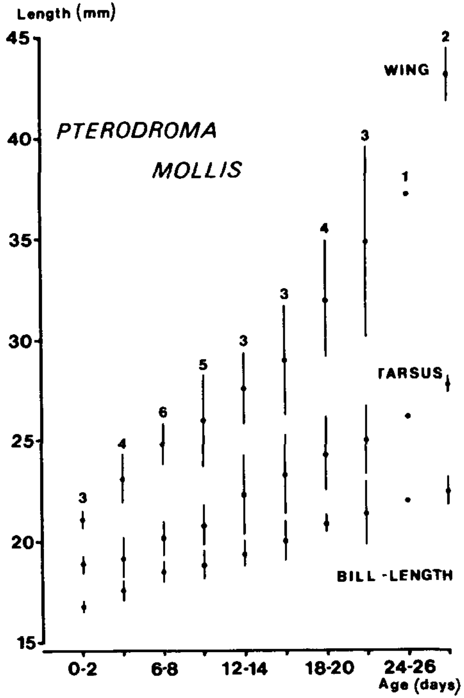

FIGURE 9 — Growth of wing, tarsus and bill length in *Pterodroma mollis* chicks. Mean ± standard deviation and sample size

The feeding of chicks was studied for the Soft-plumaged Petrel during the weight-gain period, during the weight-decrease period for the Great-winged Petrel and for the whole growth of the Kerguelen Petrel. Similar work was not done on the White-headed Petrel. These results are given in Table 7. The Soft-plumaged Petrel received its first feed sooner than the Kerguelen Petrel and was fed more often during its period of weight gain, although it was fed only half the amount of that given to the Kerguelen Petrel. This explains the Soft-plumaged Petrel's lower rate of growth.

During the period of weight decrease, the Great-winged Petrel chicks were fed more often than Kerguelen Petrel chicks. After each feed the chicks gained approximately 10% of their previous weight, rather less than Kerguelen Petrel chicks, which gained about 22%.

If we compare the results obtained for the Kerguelen Petrel during these two periods, we see that the weight loss towards the end of rearing is caused by a decrease in feeding frequency, rather than a decrease in the feed size (27-22% of the chick weight). Here again, differences exist from year to year. During the period of weight decrease in 1970-1971 (Despin *et al.* 1972) chicks were fed every 3.6 nights, rather more often than 11 years later. However, the reduction of feeds at the end of growth was similar.

During the chick's period of weight gain, the average time each adult spent at sea was 4.4 days for the Soft-plumaged Petrel and 5.1 days for the Kerguelen Petrel. During the weight decrease phase, the adult Kerguelen Petrels spent up to 10.2 days at sea, but the adult Great-winged Petrels spent up to 5.5 days away.

Fledging

The fledging dates of the chicks are given in Table 2. The Great-winged Petrel chicks fledged over a longer period (57 days) than did the Kerguelen Petrel chicks (21 days). Most chick departures took place at the beginning of the fledging period (75% in the first month), and so the long fledging period was due to a few late departures. Departures of the Kerguelen Petrel were later than those observed previously (Despin *et al.* 1972, Mougin 1969). The dates of our stay on East Island did not allow us to observe the fledging of the Soft-plumaged Petrel chicks, and so we do not know the fledging period.

The departures of the chicks did not end the breeding cycle for the Kerguelen Petrel. Birds continued to visit the colony after fledging for the whole of February at least, and perhaps even later (Despin *et al.* 1972). The first visit to land during the non-breeding season occurred in March or April, and so the birds were not absent from their breeding colonies for long.

E PETREL AND PRIONS

Five species of prion breed on the Crozet Islands: the Blue Petrel *(Halobaena caerulea)*, the Salvin's Prion *(Pachyptila salvini)*, the Antarctic Prion *(P. desolata)*, the Thin-billed Prion *(P. belcheri)* and the Fairy Prion *(P. turtur)*. The measurements are given in Table 8 (partly from Despin *et al.* 1972 and Derenne & Mougin 1976) and the timing of the different phases of the breeding cycle in Table 9 (partly from Paulian 1953, Tickell 1962, Richdale 1965, Despin *et al.* 1972, Derenne & Mougin 1976, and Strange 1980).

The Blue Petrel and the prions of the Crozet Islands are summer breeders but their breeding cycles are timed differently. Three of them, Salvin's Prion, the Thin-billed Prion and the Fairy Prion, are rather well synchronised, with laying occurring at the end of November and the beginning of December. The Antarctic Prion lays a month later (end of December) and the Blue Petrel a month earlier (end of October).

For all the above species the breeding season is short, lasting a maximum of five or six months between the first returns to land for courtship and the last fledging of the chicks. During winter, the Blue Petrel often returns to land in the Kerguelen Islands (Paulian 1953) and probably on Crozet also. The Fairy Prion continues to visit its colonies for some time after fledging (Derenne & Mougin 1976), whereas the Salvin's Prion does not. Winter data for the Antarctic Prion and the Thin-billed Prion are lacking. Between the first returns to land and the first laying, pairing is comparatively short for the prions on the Crozet Islands, lasting about 50-75 days according to the species (Table 9).

TABLE 7 — Chick-feeding pattern in three *Pterodroma* species

		P. macroptera	P. brevirostris	P. mollis
Period of increase in weight				
Number of chicks weighed		-	4	6
Number of weighings		-	141	90
Number of nights with visits (percent of total number of nights studied)	Mean ± S.D. Range	-	35.6 ± 4.1 30.6-40.6	40.4 ± 7.0 31.6-50.0
Interval between meals (days)	Mean ± S.D. Range	-	2.56 ± 0.34 2.18-3.00	2.26 ± 0.46 1.71-2.89
Weight increase per 24 hours when the chick is fed (g)	Mean ± S.D. Range (n)		59.7 ± 38.1 1-168 (150)	33.7 ± 19.5 2-73 (38)
Period of decrease in weight				
Number of chicks weighed		25	3	-
Number of weighings		222	52	
Number of nights with visits (percent of total number of nights studied)	Mean ± S.D. Range	33.2 ± 12.3 11.1-55.6	18.7 ± 3.5 16.7-22.7	-
Interval between meals (days)	Mean ± S.D. Range	3.25 ± 1.61 1.50-8.74	5.20 ± 0.93 4.13-5.74	-
Weight increase per 24 hours when the chick is fed (g)	Mean ± S.D. Range (n)	56.7 ± 44.1 0-200 (72)	70.3 ± 36.2 34-134 (8)	-
Total growth period				
Number of chicks weighed		-	3	-
Number of weighings			157	
Number of nights with visits (percent of total number of nights studied)	Mean ± S.D. Range	-	31.4 ± 2.5 29.1-34.1	-
Interval between meals (days)	Mean ± S.D. Range	-	2.93 ± 0.26 2.66-3.17	-
Weight increase per 24 hours when the chick is fed (g)	Mean ± S.D. Range (n)	-	61.9 ± 38.3 1-168 (47)	-

TABLE 8 — Weights (g) and measurements (mm) of *Halobaena caerulea* and *Pachyptila* species

Species	H. caerulea	P. salvini		P. desolata	P. belcheri	P. turtur	
Locality	East I	East I	Hog I	East I	East I	East I	Hog I
Weight (g)							
Mean ± S.D.	212 ± 22	170 ± 11	159 ± 13	138	129 ± 9	139 ± 17	132 ± 6
Range (n)	171-253 (27)	140-200 (63)	130-210 (85)	116-160 (2)	115-135 (4)	118-169 (21)	122-148 (18)
Wing length (mm)							
Mean ± S.D.	216 ± 4	195 ± 5	192 ± 5	185 ± 4	183 ± 4	178 ± 4	180 ± 4
Range (n)	208-224 (30)	185-205 (63)	184-207 (89)	182-190 (3)	177-185 (4)	168-186 (23)	170-185 (18)
Culmen length (mm)							
Mean ± S.D.	26.9 ± 0.7	30.2 ± 3.7	30.2 ± 1.0	27.7 ± 1.5	25.3 ± 1.1	22.1 ± 1.1	22.1 ± 1.1
Range (n)	25.5-28.5 (30)	28.0-35.3 (64)	27.5-32.2 (89)	26.0-29.0 (3)	24.5-27.0 (4)	20.0-24.0 (24)	21.0-25.0 (18)
Culmen breadth (mm)							
Mean ± S.D.	-	17.2 ± 0.7	16.9 ± 0.8	13.9 ± 1.3	10.8 ± 0.7	11.1 ± 0.7	11.4 ± 0.9
Range (n)		15.5-18.6 (63)	15.2-18.5 (89)	12.5-15.0 (3)	10.2-11.8 (4)	10.2-12.8 (15)	10.5-12.2 (18)
Tarsus length (mm)							
Mean ± S.D.	34.3 ± 1.5	34.0 ± 1.2	33.8 ± 1.1	34.2 ± 0.8	34.9 ± 1.4	32.5 ± 1.3	32.7 ± 1.4
Range (n)	31.2-38.2 (30)	31.2-37.5 (63)	31.0-36.8 (89)	33.5-35.0 (3)	34.0-37.0 (4)	30.0-35.0 (24)	30.2-36.0 (18)

Reoccupation of burrows and pairing

Reoccupation of burrows by Salvin's Prion was studied by daily observations. The nest-visiting rates during this period reached a maximum in the last 10 days in October and the first 10 days in November (Fig. 10). This was followed by a minimum, corresponding with a prelaying exodus in the second 10 days of November. During pairing, Salvin's Prion was periodically present in large numbers on land. These periods of high abundance and activity in the colonies were brief (a few days to a week long) and were separated by intervals of 7.4 ± 2.4 days (range 5.4-12.0 days). Figure 11 shows the same data plotted against the laying date. The number of Salvin's Prion present on land reached a maximum shortly after reoccupation of the burrows. The numbers then rapidly decreased, reaching the first minimum on the 50th day before laying. The numbers reached a second maximum on the 30th day before laying, followed by a rapid decrease corresponding to the prelaying exodus in the last 15 days of pairing.

We lack further information on the Crozets owing to the late discovery of the Blue Petrel burrows and the difficulty of gaining access to prion colonies.

Of 367 visits noted during the pairing of Salvin's Prion, 85.3% lasted a day, 12.3% lasted two days, 2.2% lasted three days, and 0.2% lasted four days (an average of 1.2 ±0.5 days). There were many paired birds that did not lay. Of the daily monitored burrows, 58 were visited by 202 birds, of which only 43 pairs eventually laid eggs (a non-breeding percentage of 57.4%). Of these 202 birds, 182 (90.1%) visited only one burrow, 18 (8.9%) visited two burrows and 2 (1.0%) visited three burrows. Each of the 58 observed burrows was visited by an average of 3.86 ± 2.01 Salvin's Prions (range 1-10), although burrows in which eggs were eventually laid attracted 4.32 ± 2.01 birds per burrow (range 2-10) and those that remained empty attracted 3.00 ± 1.75 birds per burrow (range 1-7), the two values being significantly different ($p < 0.01$).

Of 149 paired birds, 132 (88.6%) were faithful to only one partner during courtship, 15 (10.1%) courted two successively and 2 (1.3%) courted three. For 53 Salvin's Prion's nests, 96% of the females returned to land on the night of laying, 2% returned the night before, and 2% returned two nights before laying. Corresponding figures for the Blue Petrel were 20%, 60% and 20% for 23 nests.

Laying

Table 9 shows the chronology of laying for the Blue Petrel and prion species on the Crozet Islands. The laying period is short (10 days) for the Blue Petrel and longer (3 weeks) for Salvin's Prion. Sample numbers of the other species were too low to be useful but data on these species from other localities show laying periods of similar length (Tickell 1962, Harper 1976, Strange 1980).

Egg measurements of three of the species from Crozet are given in Table 10 (partly from Despin *et al.* 1972). The ratio of egg weight to adult weight was 17.6% for the Blue Petrel and 21.2% for Salvin's Prion.

TABLE 9 — Timing and duration of events during the breeding cycle of the prions. Values in brackets indicate estimates from data available in other localities.

	H.caerulea	P.salvini	P.desolata	P.belcheri	P.turtur
First returns on land	early sep	before third decade sep	late oct	early sep	late sep
Length of pre-laying period (days)	(50)	≥69	(60)	(75)	
Egg-laying					
Mean ±S.D.	27 oct 81 ±2	29 nov 81 ± 5			
Range (n)	23-31 oct (23)	18 nov -10 dec (62)	late dec	(20 nov -5 dec)	10-15 nov
Period from laying to hatching (days)					
Mean ±S.D.		49.6 ±3.4			
Range (n)	52(1)	46-55(6)			(56)
Real incubation period (days)					
Mean ±S.D.		44.8 ±1.7			
Range (n)	46(1)	42-47(6)			
Chick hatching					
Mean ±S.D.	18 dec 81 ±1	23 jan 74 ± 6 15 jan 82 ± 5			
Range (n)	16-20 dec (8)	4-18 jan 71 14 jan -10 feb 74 (52) 7-25 jan 82 (15)	eearly feb	5 jan -18 jan	mid jan
Fledging period (days)					
Mean ±S.D.		59.7 ±2.7			
Range (n)	43(2)	54-65(34)			
Departure of fledglings from the colony					
Mean ±S.D.		23 mar 74 ±6			
Range (n)	29 jan -7 feb	13 mar -4 apr (39)	(late mar)	23 feb -10 mar	early mar

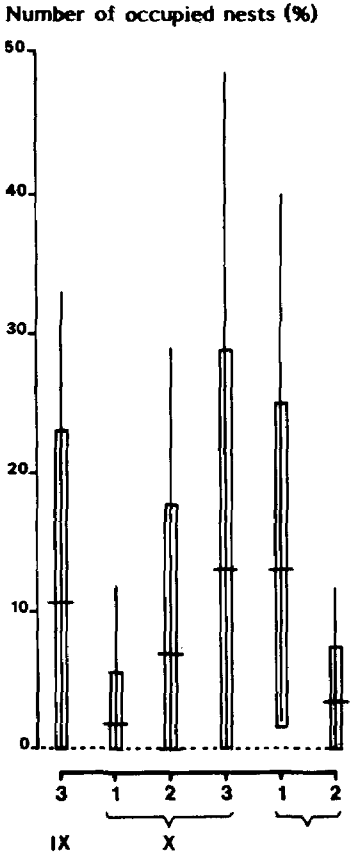

FIGURE 10 — Nest attendance by *Pachyptila salvini* from September to November

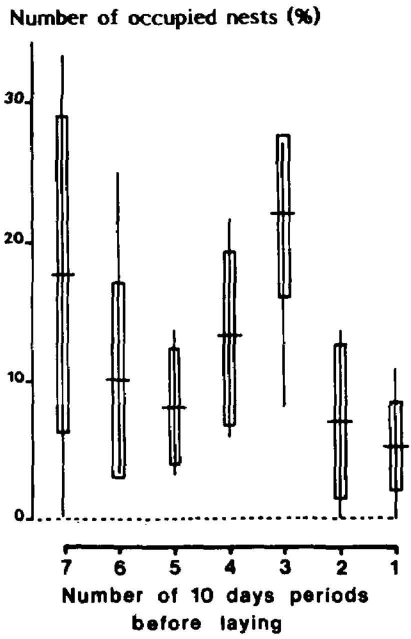

FIGURE 11 — Nest attendance by *Pachyptila salvini* before laying

We have already mentioned the very high proportion of non-breeding birds (almost 60%) observed for Salvin's Prion. The proportion of visited burrows that had no egg laid was also high, 20 out of 58 (34.5%), but 62 eggs were laid in 53 observed burrows. In 47 of these nests (88.7%) one laying occurred, in 3 (5.7%) of them two pairs laid in succession, and in the other 3 nests (5.7%) three pairs laid.

Incubation

Incubation shifts were studied for the Blue Petrel and Salvin's Prion. The results given in Table 11 show a rather distinct difference between the two species. In both species, the female's first shift is shorter and the male's longer than those that follow. Although incubation periods are of similar length (46 days for *Halobaena caerulea* and 45 days for *Pachyptila salvini*), the shifts of the Blue Petrel are fewer and longer than those of Salvin's Prion (Table 12). Work distribution between the sexes is similar for both species.

TABLE 10 — Weights (g) and dimensions (mm) of eggs of *Halobaena caerulea* and *Pachyptila* species

	H.caerulea	P.salvini	P.belcheri
Weight			
Mean ±S.D.	38.3 ±2.6	36.1 ±1.1	
Range (n)	33-43(20)	34-38(15)	
Length			
Mean ±S.D.	51.1 ±1.4	49.2 ±1.5	48.6
Range (n)	48.5-54.5(21)	45.7-52.4(65)	46.0-51.1(2)
Breadth			
Mean ±S.D.	37.7 ±1.0	35.7 ±1.1	34.6
Range (n)	35.5-39.1(21)	33.5-38.7(65)	33.0-36.2(2)

TABLE 11 — Incubation shifts and egg desertions in *Halobaena caerulea* and *Pachyptila salvini*

	Length of stay in burrow (days)		Length of desertion (days)		Desertion frequency (per cent)	
	H. caerulea	P. salvini	H. caerulea	P. salvini	H.caerulea	P.salvini
First shift (♀)						
Mean ± S.D.	1.5 ± 0.6	2.9 ± 2.5	0	0	0	0
Range (n)	1-2 (4)	0.5-7 (6)	(4)	(6)	(4)	(6)
Second shift (♂)						
Mean ± S.D.	12.7 ± 2.9	9.0 ± 1.5	0.3 ± 0.6	0.5 ± 1.2	33	17
Range (n)	11-16 (3)	7-11 (6)	0-1 (3)	0-3 (6)	(3)	(6)
Third shift (♀)						
Mean ± S.D.	8.9 ± 1.4	7.2 ± 1.0	4.3 ± 2.2	0.7 ± 0.8	88	33
Range (n)	7-11 (8)	6-9 (6)	0-7 (8)	0-3 (6)	(8)	(6)
Fourth shift (♂)						
Mean ± S.D.	8.0 ± 2.3	7.5 ± 1.4	2.3 ± 2.3	1.5 ± 0.5	75	100
Range (n)	4-10 (8)	6-9 (6)	0-6 (8)	1-2 (6)	(8)	(6)
Fifth shift (♀)						
Mean ± S.D.	7.6 ± 1.7	6.8 ± 1.0	0.9 ± 1.9	1.0 ± 1.1	29	50
Range (n)	6-10 (7)	5-8 (6)	0-5 (7)	0-2 (6)	(7)	(6)
Sixth shift (♂)						
Mean ± S.D.	8.0 ± 2.2	7.0 ± 1.3	0	0.2 ± 0.4	0	17
Range (n)	5-10 (4)	6-9 (6)	(4)	0-1 (6)	(4)	(6)
Seventh shift (♀)						
Mean ± S.D.	-	5.0 ± 2.5	-	1.2 ± 2.2	-	40
Range (n)		2-8 (5)		0-5 (5)		(5)
Eighth shift (♂)						
Mean	-	5.0	-	0	-	0
Range (n)		3-7 (2)		(2)		(2)

TABLE 12 — Incubation schedule in *Halobaena caerulea* and *Pachyptila salvini*

	H.caerulea	P.salvini
INCUBATION		
Mean length of a shift (days)		
both sexes		
Mean ±S.D.	7.8 ±3.2	6.5 ±2.4
Range (n)	1-16(34)	0.5-11(43)
male		
Mean ±S.D.	8.9 ±2.9	7.6 ±2.8
Range (n)	4-16(15)	3-11(20)
female		
Mean ±S.D.	6.8 ±3.2	5.5 ±2.5
Range (n)	1-11(19)	0.5-9(23)
DESERTION		
Mean number of periods per nest		
Mean ±S.D.	2.0 ±0.8	2.5 ±1.0
Range (n)	1-3(4)	1-4(6)
Total length per nest (days)		
Mean ±S.D.	5.6 ±1.7	4.8 ±2.5
Range (n)	4-8(4)	1-8(6)
Mean length of a period (days)		
Mean ±S.D.	2.9 ±1.9	1.9 ±1.1
Range (n)	1-5(8)	1-5(15)
Frequency of nest-reliefs with desertion (per cent)		
Mean ±S.D.	43.3 ±11.5	41.2 ±17.4
Range (n)	33.3-60.0(4)	14.3-66.7(6)
STAYS AT SEA		
Mean length (days)		
both sexes		
Mean ±S.D.	10.0 ±4.6	7.8 ±3.0
Range (n)	1-16(23)	0.5-13(43)
male		
Mean ±S.D.	8.3 ±5.2	6.8 ±3.3
Range (n)	1-15(12)	0.5-11(23)
female		
Mean ±S.D.	11.8 ±3.2	9.0 ±2.2
Range (n)	5-16(11)	3-13(20)

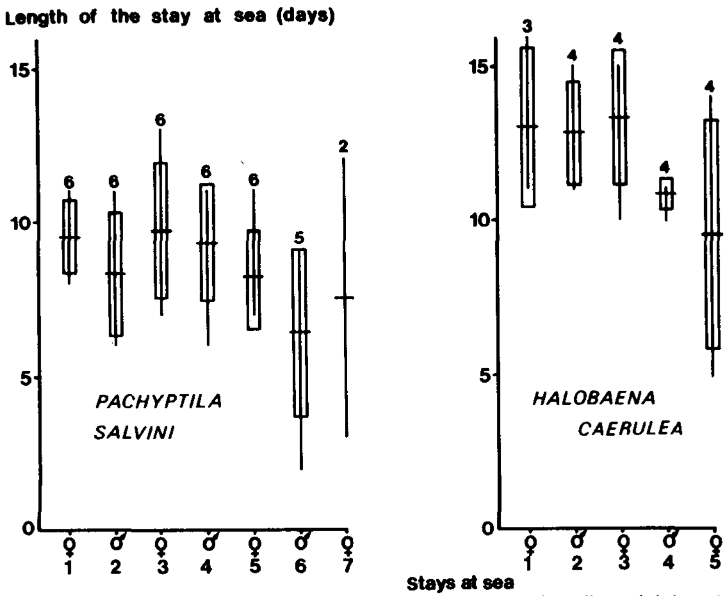

FIGURE 12 — Duration of sojourns at sea in *Pachyptila salvini* and *Halobaena caerulea* throughout incubation. Mean ± standard deviation, range and sample size

We obtained only a small amount of similar information about the other prions on the Crozet Islands. For the Fairy Prion, one male's first incubation shift lasted at least eight days and another at least five days, with a desertion of two days before the female returned.

The eggs were deserted fairly frequently during incubation, two or three times for a total of five or six days in both the Blue Petrel and Salvin's Prion (Tables 11 and 12). The longest and most frequent desertions occurred in the middle of incubation, that is, after the third shift for *Halobaena caerulea* and after the fourth for *Pachyptila salvini*.

Sojourns at sea for both sexes were relatively long in the two species studied. However, they were more numerous and shorter ($t = 2.35$; $p < 0.05$) for Salvin's Prion than for the Blue Petrel, and in both species, longer for females than for males (Fig. 12). The dates of hatching for the Crozet prions and Blue Petrel are given in Table 9. As in the laying dates, the hatching dates were similar for Salvin's Prion, the Thin-billed Prion and the Fairy Prion, later for the Antarctic Prion and earlier for the Blue Petrel. Hatching was highly synchronised for the Blue Petrel, where all hatching occurred over five days. For Salvin's Prion, at least, small differences exist from year to year; the similar values obtained in 1971 and 1982 are significantly earlier than those of 1974 (Derenne & Mougin 1976).

The total and actual incubation lengths are given in Table 9. A characteristic of this group is that all the species studied so far have an actual incubation length averaging 45-47 days.

The thermic emancipation of prion chicks on Crozet was early, usually a few hours after hatching.

Chick growth

Weight gain data for Blue Petrel and Salvin's Prion chicks are given in Tables 13 and 14 and Figures 13 and 14. Chick growth was rapid at first, slowing down until the chick reached a maximum weight of about 15% more than the adult. By this time the chick was about three-quarters fully fledged. The rate of weight gain in 3-day periods was $19.3 \pm 24.0\%$ in the Blue Petrel and $13.8 \pm 19.6\%$ in Salvin's Prion, which had a longer rearing period. Thereafter chicks lost approximately 15% of their maximum weight at a rate of $0.6 \pm 4.8\%$ for the Blue Petrel and $0.9 \pm 3.4\%$ for Salvin's Prion. For both species fledging weight was slightly less than the adult weight.

As shown in Fig. 15 and the growth curves published elsewhere (Derenne & Mougin 1976), the wing growth was slow before the appearance of the primaries, becoming more rapid with the appearance of these feathers, then slowing down as fledging approached. The average rate of wing growth in 3-day periods was $17.2 \pm 12.4\%$ for the Blue Petrel and $12.4 \pm 8.7\%$ for Salvin's Prion. At fledging, the wings of the chicks of both species measured approximately 90% of those of the adults.

As usual the rather rapid growth of the culmen and tarsus in young chicks slowed down as fledging approached, almost stopping in the Salvin's Prion. At fledging, full development was reached in both species. We do not have similar data for the other prions of Crozet.

TABLE 13 — Weight growth in *Halobaena caerulea* and *Pachyptila salvini* chicks

	H.caerulea	P.salvini
Weight at birth		
Weight (g.)		
Mean ±S.D.	37.5	26.0 ±3.7
Range (n)	37-38(2)	21-32(8)
Percent adult weight	18	16
Maximum weight		
Weight (g.)		
Mean ±S.D.	240	186 ±29
Range (n)	220-260(2)	140-270(17)
Percent adult weight	113	117
Age at peak weight (days)		
Mean ±S.D.	33	44 ±11
Range (n)	31-34(2)	25-61(17)
Weight at fledging		
Weight (g.)		
Mean ±S.D.	208	154 ±22
Range (n)	200-215(2)	115-200(17)
Percent adult weight	98	97

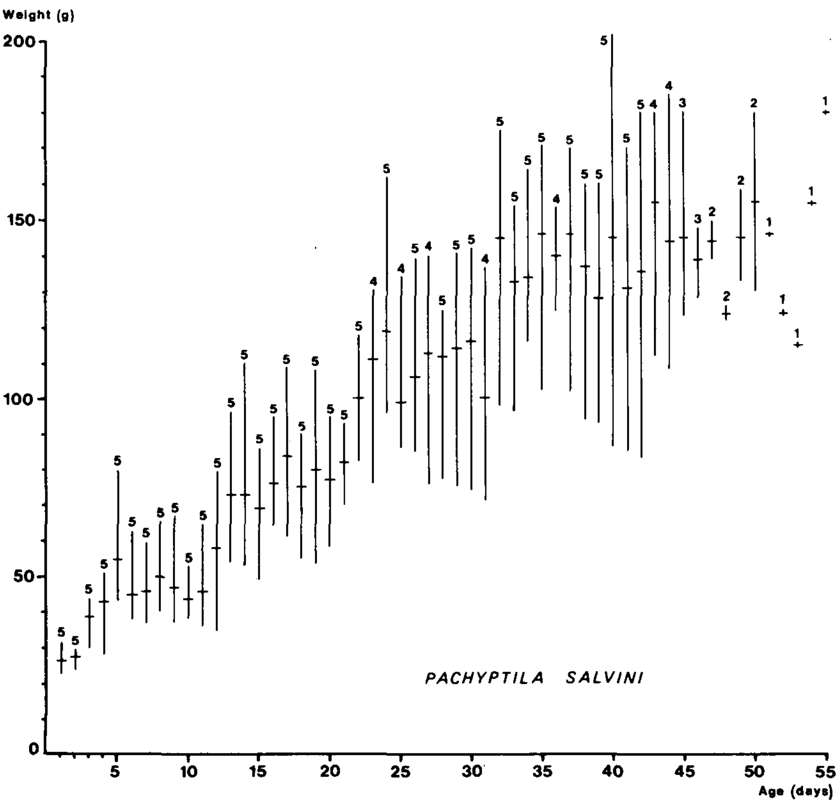

FIGURE 13 — Weight increase in *Pachyptila salvini* chicks. Mean, range and sample size

TABLE 15 — Chick-feeding pattern in *Halobaena caerulea* and *Pachyptila salvini*

Period of increase in weight		H. caerulea	P. salvini
Number of chicks weighed		9	7
Number of weighings		68	272
Number of nights with visits (percent of total number of nights studied)	Mean ± S.D. Range	54.4 ± 7.5 40.0-66.7	54.4 ± 9.7 41.5-71.8
Interval between meals (days)	Mean ± S.D. Range	1.57 ± 0.29 1.18-2.22	1.59 ± 0.34 1.07-2.13
Weight increase per 24 hours when the chick is fed (g)	Mean ± S.D. Range (n)	30.6 ± 24.9 0-127 (38)	18.1 ± 14.2 0-53 (119)
Period of decrease in weight			
Number of chicks weighed		5	6
Number of weighings		33	37
Number of nights with visits (percent of total number of nights studied)	Mean ± S.D. Range	23.1 ± 10.0 12.5-33.3	38.6 ± 10.0 25.0-50.0
Interval between meals (days)	Mean ± S.D. Range	4.83 ± 2.31 2.72-7.74	2.47 ± 0.77 1.71-3.73
Weight increase per 24 hours when the chick is fed (g)	Mean ± S.D. Range (n)	25.6 ± 12.8 8-44 (7)	16.4 ± 13.2 0-36 (14)
Total growth period			
Number of chicks weighed		10	10
Number of weighings		108	270
Number of nights with visits (percent of total number of nights studied)	Mean ± S.D. Range	42.8 ± 12.3 25.0-60.0	49.5 ± 5.8 41.4-57.1
Interval between meals (days)	Mean ± S.D. Range	2.29 ± 0.90 1.36-3.73	1.75 ± 0.25 1.45-2.13
Weight increase per 24 hours when the chick is fed (g)	Mean ± S.D. Range (n)	29.8 ± 23.5 0-127 (45)	18.0 ± 14.0 0-53 (133)

The average length of time spent at sea by the breeding birds during the period of chick weight loss was 8.1 days in the Blue Petrel compared with 3.1 days during the earlier period of weight gain. A smaller increase from 3.1 to 4.6 days occurred with the Salvin's Prion.

Fledging

The dates of fledging are given in Table 9. The departure period was brief in all species, never exceeding 3 weeks.

The fledging period on Crozet is particularly short for the Blue Petrel (43 days) and particularly long for Salvin's Prion (60 days, Derenne & Mougin 1976). Data for the other prions on Crozet are lacking, but in other localities where they have been studied, the fledging period for prions is usually about 50 days (Richdale 1944, 1965, Tickell 1962, Strange 1980).

GENUS PROCELLARIA

Of the four species of *Procellaria,* two nest on the Crozet Islands: the White-chinned Petrel *(P. aequinoctialis)* and the Grey Petrel *(P. cinerea).* Table 16 gives the measurements of these birds and Table 17 the timing of their breeding cycles (partly from Mougin 1970 and 1971, Despin *et al.* 1972, Barrat 1974, Despin 1976). These relatively large petrels have a long breeding season with eight or nine months passing between the first return of adults to land for pairing and their last departure (much later than the last fledging). Neither petrel on Crozet has ever been observed ashore during the non-breeding season. The White-chinned Petrel is a summer breeder; the Grey Petrel nests in winter.

TABLE 16 — Weights (g) and measurements (mm) of *Procellaria* petrels

	P. aequinoctialis	*P. cinerea*
Weight (g)		
Mean ± S.D.	1213 ± 134	1073 ± 137
Range (n)	980-1885 (87)	950-1220 (3)
Wing length (mm)		
Mean ± S.D.	372 ± 11	345 ± 4
Range (n)	350-395 (30)	340-350 (5)
Culmen length (mm)		
Mean ± S.D.	52.3 ± 2.0	46.3 ± 1.9
Range (n)	47.0-56.0 (30)	44.5-49.0 (5)
Tarsus length (mm)		
Mean ± S.D.	65.0 ± 2.4	64.0 ± 3.4
Range (n)	61.0-70.0 (30)	62.0-70.0 (5)

TABLE 17 — Timing and duration of events during the breeding cycle of *Procellaria* petrels

	P. aequinoctialis	*P. cinerea*
First returns on land	15 sep 66 16 sep 68	early feb
Length of pre-laying period (days)		
Mean ±S.D.	48.6 ±9.6	45
Range (n)	36-68(17)	
Laying period		
Mean ±S.D.	22 nov 68 ±13 21 nov 81 ±4	second fortnight of mar
Range (n)	8 nov -20dec 68 (19) 18-25 nov 81(3)	
Length of incubation (days)		
Mean	57.5	60
Range (n)	57-58(2)	
Hatching period		
Mean ±S.D.	12 jan 68 ±5 12 jan 69 ±1 11 jan 71 ±7 12 jan 82 ±2	second fortnight may
Range (n)	2-16 jan 68(6) 11-13 jan 69(2) 6-16 jan 71(2) 10-14 jan 82(4)	
Fledging period (days)		
Mean ±S.D.	95.7 ±4.9	110
Range (n)	91-105(6)	
Departure of fledglings from the colony		
Mean ±S.D.	17 apr 68 ±8	mid sep
Range (n)	4-29 apr (6)	
Last departure of adults	7 may 68	20 oct 82

Reoccupation of burrows and pairing

Compared with the length of the breeding period, pairing (from first reoccupation of a burrow until laying) is relatively short on Crozet, lasting for about 45-50 days for both species. The 60 White-chinned Petrel nests studied showed an important variation in the daily rate of occupation (Fig. 16). For the first 30 days of courtship (from mid-September to mid-October) the rate was constant, declining as a result of the prelaying exodus of both sexes to become rather low at the end of October and the beginning of November. Figure 17 shows the mean rate of occupation of the 13 nests in which eggs were laid, plotted against the mean laying date of those 13 nests, recalculated from Mougin 1970. The rate of visiting was nearly constant between the 50th and the 21st day before laying, but in the last 20 days before laying, the prelaying exodus depopulated the colonies and only 5% of the nests were visited daily. Of the 174 observed periods of time spent on land, 76.4% did not last longer than a day, 17.2% lasted two days, 5.2% lasted three days, 0.6% lasted five days and 0.6% lasted six days (an average of 1.3 ± 0.7 days).

Many non-breeding White-chinned Petrels were on land during courtship (Mougin 1970). Thirty-one nests were visited by 69 birds, of which only 19 pairs eventually nested (44.9% non-breeders). Of these 69 birds, 50 (72.5%) visited only one burrow, 13 (18.8%) visited two, 5 (7.2%) visited three, and 1 (1.5%) visited six. Each of the 31 nests was visited by an average of 3.19 ± 1.96 birds (range 1-10), but there appeared to be no significant difference

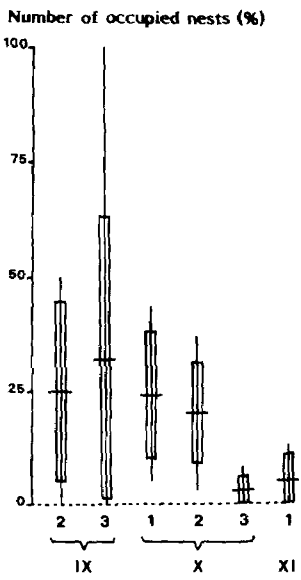

FIGURE 16 — Nest attendance by *Procellaria aequinoctialis* from September to November

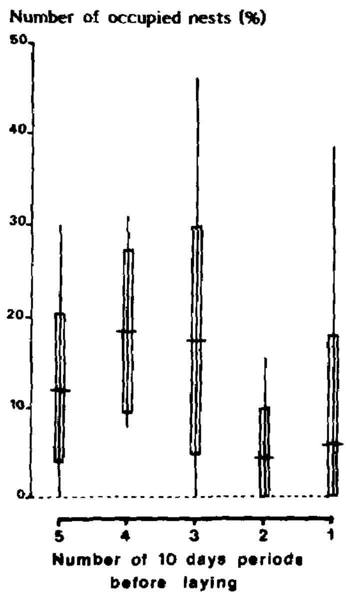

FIGURE 17 — Nest attendance by *Procellaria aequinoctialis* from September to November

between burrows in which eggs were laid (3.06 ± 2.01 birds, range 2-10) and those that remained empty (3.29 ± 1.94 birds, range 1-7).

The high mobility of adults during pairing did not stop after laying. Of the 32 nests monitored daily during chick rearing, Mougin (1970) observed on average 2.00 ± 0.95 birds visiting each nest (range 1-4) and 1.23 ± 0.58 nests frequented by each bird (range 1-4).

During pairing, 35 birds were observed accompanied by a partner. Of these, 33 birds were faithful to only one partner, 1 had two partners, and 1 had three. No similar work was done for the Grey Petrel.

Laying

The White-chinned Petrel females returned just before laying, that is, at the end of the prelaying exodus. Laying took place on the night of return in 64% and on the next night in 36% (14 nests, Mougin 1970). Eggs of the White-chinned Petrel are laid at the end of the spring and those of the Grey Petrel at the beginning of autumn, the dates being fairly consistent from year to year (Table 17). Laying can be well spread. A month and a half has been recorded for the White-chinned Petrel, but almost three-quarters of the eggs were laid in the first 15 days and a few late breeders extended this time by another month (Mougin 1970).

Egg measurements are given in Table 18 (partly from Mougin 1970, Despin *et al.* 1972 and Barrat 1974). The ratio of egg weight to adult weight is 10.4% for the White-chinned Petrel and about 10.3% for the Grey Petrel (Barrat 1974).

As well as the high proportion of non-breeders already mentioned for *Procellaria aequinoctialis,* in a high proportion of nests no eggs were laid (13 out of 31 nests studied, or 42%). Nineteen eggs were laid in the 18 other nests, a second pair laying in one nest where a first pair had lost its egg.

Incubation

The incubation shifts of the White-chinned Petrel are shown in Fig. 18 (data from Mougin 1970 and 1971). As usual, females spent only a short time on the nest after laying. The following shifts were longer, but shortened after the fifth. The shifts of the males lasted for an average of 9.5 ± 2.2 days (range 5-13 days for 13 shifts) and those of the females 6.1 ± 4.3 days (range 1-15 for 18 shifts). For 4 nests the number of shifts was 6 or 7. In total, the female's share of the incubation was 45% and the male's 55%. No temporary egg desertions were observed for any successful breeders. Temporary desertions resulted eventually in total desertion (Mougin 1970). During incubation, the time spent at sea was equal to the time spent on land, the total incubation period lasting for an average of 57.5 days (Mougin 1971).

We do not have similar data on the Grey Petrel for the Crozets or any other breeding locality, although the incubation period for the Grey Petrel on Crozet was about 2 months, similar to that of the White-chinned Petrel.

Grey Petrel chicks hatched at the end of autumn and the White-chinned Petrel chicks in the middle of summer (Table 17). We have pointed out the short hatching period for the White-chinned Petrel (15 days from first to last hatching), which contrasts with the long laying period. Late layings were rare and were usually abandoned during incubation, reducing the length of the hatching period. The synchrony of hatching from year to year is remarkable with a mean hatching date of 12 January in 1968, 1969 and 1982 and 11 January in 1971.

The chicks of both the White-chinned Petrel (Mougin 1970) and the Grey Petrel became thermically emancipated very quickly, brooding ceasing a few hours after hatching, but the chicks continued to be accompanied by a parent for the next 24-72 hours.

TABLE 18 — Weights (g) and dimensions (mm) of *Procellaria* petrel eggs

	P. aequinoctialis	*P. cinerea*
Weight (g)		
Mean ± S.D.	126 ± 8	-
Range (n)	115-140 (8)	
Length (mm)		
Mean ± S.D.	82.2 ± 3.4	79.2
Range (n)	77.3-90.0 (17)	78.4-80.0 (2)
Breadth (mm)		
Mean ± S.D.	53.8 ± 1.4	56.2
Range (n)	51.3-56.6 (17)	55.2-57.2 (2)

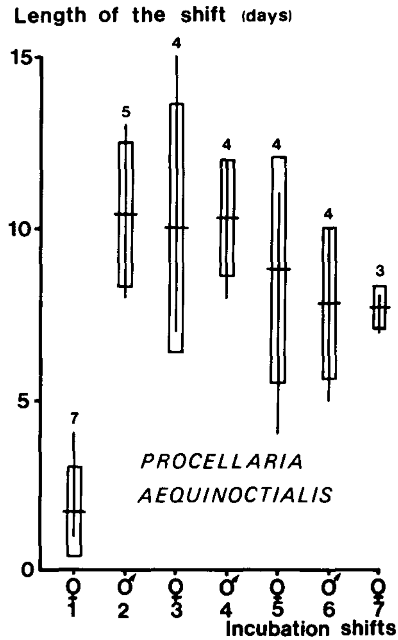

FIGURE 18 — Length of incubation shifts in *Procellaria aequinoctialis.* Mean ± standard deviation, range and sample size

Chick growth

Weight increase is given in Table 19 (partly from Mougin 1970, Barrat 1974, Despin 1976). The rate of increase in weight in 3-day periods for the White-chinned Petrel reached 15.3%. The chicks reached a maximum weight of 17% more than the adult weight after two-thirds of the fledging period. The chicks then lost 30% of their maximum weight at a rate of weight decrease in 3-day periods of 1.9%.

The Grey Petrel chicks' rate of increase in weight of 6.9% in 3-day periods was much less than that of the White-chinned Petrel. The chicks reached a maximum weight of 37% more than the adult weight by the time that they were three-quarters fledged. The weight loss that followed was much less than that of the White-chinned Petrel, 14% of their maximum weight being lost at a rate of 2.3% in 3-day periods.

The rate of wing growth in 3-day periods was remarkably low for the White-chinned Petrel (8.6%), but even lower for the Grey Petrel (7.1%). Adult length was usually not reached by the time the chicks fledged. The culmen and tarsus grew slowly in both species but almost reached adult measurements by fledging.

While chick feeding of the White-chinned Petrel was studied only during the weight-gain period, the whole of rearing for the Grey Petrel (Table 20) was observed for a single bird and the weight-decrease period for another one. During the weight-gain period, the White-chinned Petrel chicks were fed less often than those of the Grey Petrel, but the meals were larger. This could explain the more rapid growth of the White-chinned Petrel chicks. During the weight-decrease period, the Grey Petrel chicks were fed less often but the size of the meals remained the same. This slow reduction of feeding probably explains the smaller weight loss during the weight-decrease period, at least for the chicks studied.

During the chicks' weight-increase period, the adult White-chinned Petrels spent an average of 3.8 days at sea, compared with 3.2 days for the Grey Petrel. During the chicks' weight-decrease period the Grey Petrel spent an average of 3.8 days at sea.

Fledging

The Grey Petrel chicks fledged at the beginning of spring and the White-chinned Petrel chicks in the middle of autumn, both fledging periods lasting about 3 weeks (Table 17). The time from hatching to fledging differed for the two species, about 96 days for the White-chinned Petrel and 110-120 days for the Grey Petrel (slightly shorter than for the only other winter breeder on Crozet, the Great-winged Petrel - *Pterodroma macroptera*).

STORM PETRELS

Three species of storm petrels breed on the Crozet archipelago, the Wilson's Storm Petrel *(Oceanites oceanicus)*, the Grey-backed Storm Petrel *(Garrodia nereis)* and the Black-bellied Storm Petrel *(Fregetta tropica)*. Table 21 shows the measurements of these birds (partly from Prévost 1970, Despin *et al.* 1972) and Table 22 the timing of their breeding cycles (partly from Beck & Brown 1971 and 1972, Despin *et al.* 1972, Lacan 1972, Turner 1980).

TABLE 19 — Weight growth in *Procellaria* petrel chicks

	P.aequinoctialis	P.cinerea
Weight at birth		
Weight (g.)	94(1)	
Maximum weight		
Weight (g.)		
Mean ±S.D.	1417 ±203	1447 ±216
Range (n)	1200-1740(6)	1200-1600(3)
Percent adult weight	117	137
Age at peak weight (days)		
Mean ±S.D.	58.8 ±8.4	84.5
Range (n)	48-70(6)	75-94(2)
Weight at fledging		
Weight (g.)		
Mean ±S.D.	1000 ±200	1207 ±136
Range (n)	680-1230(6)	1050-1290(3)
Percent adult weight	82	112

TABLE 20 — Chick-feeding pattern in *Procellaria* petrels

		P.aequinoctialis	P.cinerea
Period of increase in weight			
Number of chicks weighed		6	1
Number of weighings		156	94
Number of nights with visits (percent of total number of nights studied)	Mean ±S.D. Range	45.4 ±7.8 35.7-55.6	53.2
Interval between meals (days)	Mean ±S.D. Range	1.97 ±0.42 1.50-2.52	1.58
Weight increase per 24 hours when the chick is fed (g)	Mean ±S.D. Range (n)	133.1 ±102.6 0-530(72)	112.0 ±93.7 0-420(50)
Period of decrease in weight			
Number of chicks weighed			2
Number of weighings			30
Number of nights with visits (percent of total number of nights studied)	Mean Range		45.8 41.7-50.0
Interval between meals (days)	Mean Range		1.92 1.71-2.12
Weight increase per 24 hours when the chick is fed (g)	Mean ±S.D. Range (n)		113.1 ±160.7 10-590(13)
Total growth period			
Number of chicks weighed			1
Number of weighings			118
Number of nights with visits (percent of total number of nights studied)			50.8
Interval between meals (days)			1.67
Weight increse per 24 hours when the chick is fed (g)	Mean ±S.D. Range (n)		112.3 ±109.3 0-590(63)

TABLE 21 — Weights (g) and measurements (mm) of storm petrels

	O. oceanicus	G. nereis	F. tropica
Weight (g)			
Mean ± S.D.	32 ± 3	32 ± 5	52 ± 3
Range (n)	27-39 (31)	25-42 (16)	43-59 (38)
Wing length (mm)			
Mean ± S.D.	143 ± 4	127 ± 6	163 ± 5
Range (n)	134-154 (29)	116-134 (18)	155-175 (54)
Culmen length (mm)			
Mean ± S.D.	12.1 ± 0.4	13.6 ± 0.7	15.4 ± 0.6
Range (n)	11.4-13.0 (30)	12.5-15.0 (18)	14.2-17.0 (54)
Tarsus length (mm)			
Mean ± S.D.	34.8 ± 1.1	32.6 ± 1.4	40.9 ± 1.4
Range (n)	32.5-37.0 (30)	30.0-34.0 (18)	38.2-44.5 (54)

TABLE 22 — Timing and duration of events during the breeding cycle of the storm petrels. Values in brackets indicate estimates from data available from other localities.

	O.oceanicus	G.nereis	F.tropica
First return on land	16 nov 81	17 oct 81	27 sep 81
Length of pre-laying period (days)	45	60	80
Laying period			
Mean ±S.D.	2 jan 82 ±10		20 dec ±5
Range (n)	18 dec -15 jan (20)	15-29 dec 70	15-31 dec (7)
Period from laying to hatching (days)			
Mean ±S.D.	49.7 ±5.4		
Range (n)	44-59(6)		61(1)
Real incubation period (days)			
Mean ±S.D.	35.7 ±1.8		
Range (n)	33-38(6)		39(1)
Hatching period			
Mean ±S.D.	16 feb 82 ±10		7 feb 82 ±8
Range (n)	31 jan -2 mar (6)	1-13 feb 71	31 jan -16 feb (3)
Departure of fledglings from the colony	[late mar -early apr]		[mid apr]

The Black-bellied Storm Petrel is much larger than the other two species, which are about the same size. The length of the breeding reflects these size differences. The period between the first return to land of the adults and the last departure of the fledglings is 5 months in *Oceanites oceanicus*, 6 months in *Garrodia nereis* and 7 months in *Fregetta tropica*. All breed in summer. Although pairing begins at different times of the year for each species (September to November), the chicks fledge at the same time (end of March to beginning of April). The colonies of the three species are probably deserted between the breeding seasons as these birds are almost absent around the Crozet Islands in winter (Stahl, Weimerskirch, unpubl.).

Reoccupation of burrows and pairing

The courtship period varied between species, lasting about 1.5 months for Wilson's Storm Petrel, 2 months for the Grey-backed Storm Petrel and almost 3 months for the Black-bellied Storm Petrel (Table 22).

During pairing, the colonies were visited periodically by *Fregetta tropica* and *Garrodia nereis*. For *F. tropica*, the periods of abundance occurred every 15.5 ± 1.5 days, the last cycle before laying being shorter (9.8 days). For *G. nereis*, the cycles measured 16.5 ± 0.7 days. Nothing similar was observed for the Wilson's Storm Petrel, for which the number of visits made each night remained fairly constant. We noticed, however, that visiting decreased between the 43rd and the 27th day before laying, with more regular visiting (almost daily) occurring between the 26th and the 14th day before laying. A desertion then occurred, lasting until laying (the prelaying exodus). All visits were brief, none lasting more than one day.

Table 23 shows the reoccupation of burrows for Wilson's Storm Petrel and the Black-bellied Storm Petrel. For the Wilson's Storm Petrel (21 nests) and the Black-bellied Storm Petrel (4 nests), the time the females spent on the nest before laying was brief because they returned to land only on the night of laying.

Laying

Although the three Storm Petrels first returned to land in different months, their laying was well synchronised, in the second half of December in *Fregetta tropica* and *Garrodia nereis* and from the second half of December to the beginning of January in *Oceanites oceanicus*. The laying period lasted 15 days for the first two species and about 1 month for Wilson's Storm Petrel, the laying of the eggs being evenly distributed throughout this period in all three species (Table 22).

Table 24 shows the measurements of eggs from the Crozet Islands (partly from Despin *et al.* 1972). The ratio of the egg weight to the adult weight was approximately the same for the three species, 30.0% in Wilson's Storm Petrel, 28.1% in the Grey-backed Storm Petrel and 28.8% in the Black-bellied Storm Petrel.

TABLE 23 — The nest reoccupation by the storm petrels

	O. oceanicus	F. tropica
Number of birds observed	52	32
Breeders	42 (80.8 %)	6 (18.8 %)
Non breeders	10 (19.2 %)	26 (81.2 %)
Number of nests studied	25	17
Nests with egg-laying	21 (84.0 %)	3 (18.0 %)
Nests without egg-laying	4 (16.0 %)	14 (82.0 %)
Number of birds per burrow		
Mean ± S.D	2.1 ± 0.4	1.9 ± 1.0
Range	(1-3)	(1-5)
Number of burrows visited per bird	1	1
Number of mates per bird		
Mean ± S.D	1.1 ± 0.3	1.1 ± 0.3
Range	(1-2)	(1-2)

TABLE 24 — Weights (g) and dimensions (mm) of storm petrel eggs

	O. oceanicus	G. nereis	F. tropica
Weight (g)			
Mean ± S.D.	9.6 ± 1.6	9.0 ± 0.7	15.0 ± 1.2
Range (n)	8-15 (16)	8.5-10 (8)	14-17 (5)
Length (mm)			
Mean ± S.D.	31.5 ± 1.1	33.2 ± 1.9	37.0 ± 2.1
Range (n)	30.0-33.1 (16)	31.6-37.5 (8)	34.6-39.9 (5)
Breadth (mm)			
Mean ± S.D	22.9 ± 0.8	24.3 ± 1.1	26.8 ± 0.6
Range (n)	21.2-24.3 (16)	22.7-25.7 (8)	26.1-27.5 (5)

Incubation

The incubation shifts were studied for Wilson's Storm Petrel and the Black-bellied Storm Petrel. The results, given in Table 25, show a rather large difference between the two species ($t = 8.15$, $p < 0.001$). During incubation, the shifts of both sexes are significantly shorter for *Oceanites oceanicus* than for *Fregetta tropica* although no changes in the length of the shifts were observed as incubation progressed in both species. Incubation was shared equally between the sexes. We have no detailed data for the Grey-backed Storm Petrel. Four observations of shift length varied from 1 to 3 days (average 1.5 days), a figure similar to that for the Wilson's Storm Petrel.

Poor synchronisation of the changing of shifts between the two partners meant that there were frequent desertions at the end of the incubation spells for both Wilson's Storm Petrel and the Black-bellied Storm Petrel. Up to 18 desertions were noted for a single nest for a total length of up to one month without damage to the egg. No significant difference in egg desertions was seen between the male and the female (Tables 25 and 26). The small amount of data obtained for the Grey-backed Storm Petrel concerned a single nest for which three shifts were observed, each followed by a desertion. Each desertion lasted 3.0 ± 2.0 days (range 1-5 days).

For Wilson's Storm Petrel, desertions also occurred during incubation shifts. These desertions were observed in only 9.4% of the 159 shifts studied, each lasting an average of 1.2 ± 0.4 days (range 1-2 days for 15 desertions). Desertions of this kind also occurred in the Grey-backed Storm Petrel but were not observed in the Black-bellied Storm Petrel.

Periods of time spent at sea by both sexes were relatively long, the Black-bellied Storm Petrel spending longer at sea ($p<0.01$) than Wilson's Storm Petrel (Fig. 19 and 20). For the Grey-backed Storm Petrel, three sojourns at sea lasted 4.0 ± 3.6 days (range 1-8 days).

The eggs hatched in the first half of February for *Fregetta tropica* and *Garrodia nereis* and during the whole of February for *Oceanites oceanicus* (Table 22). The total incubation period differed between species, but with the many desertions allowed for, the actual incubation times were very similar. For Wilson's Storm Petrel, the average of 49.7 ± 5.4 days of total incubation minus 14.0 ± 7.0 days of desertions gave an actual incubation period of 35.7 ± 1.8 days (6 nests). A highly significant correlation ($r = 0.99$, $n = 6$) exists

TABLE 25 — Incubation shifts and egg desertions in *Oceanites oceanicus* and *Fregetta tropica*

	Length of stay in burrow (days)		Length of desertion (days)		Desertion frequency (per cent)	
	O. oceanicus	F. tropica	O. oceanicus	F. tropica	O. oceanicus	F. tropica
First shift (♀)						
Mean ± S.D.	0.6 ± 0.2	1.7 ± 0.6	0.6 ± 0.9	4.7 ± 2.1	41.2	100
Range (n)	0.5-1 (19)	1-2 (3)	0-3 (17)	3-7 (3)		
Second shift (♂)						
Mean ± S.D.	1.8 ± 0.8	3.7 ± 2.9	1.3 ± 1.4	2.3 ± 0.6	66.7	100
Range (n)	1-3 (16)	2-7 (3)	0-5 (15)	2-3 (3)		
Third shift (♀)						
Mean ± S.D.	1.4 ± 0.6	3.7 ± 1.2	1.1 ± 1.8	2.7 ± 1.2	50.0	100
Range (n)	1-3 (14)	3-5 (3)	0-6 (14)	2-4 (3)		
Fourth shift (♂)						
Mean ± S.D.	2.4 ± 1.3	3.5 ± 1.0	0.3 ± 0.5	4 (1)	25.0	100
Range (n)	1-4 (13)	3-5 (3)	0-1 (12)			
Fifth shift (♀)						
Mean ± S.D.	2.2 ± 0.9	3.8 ± 1.0	1.5 ± 2.4	1.3 ± 1.2	50.0	67
Range (n)	1-3 (12)	3-5 (3)	0-8 (14)	0-2 (3)		
Sixth shift (♂)						
Mean ± S.D.	1.9 ± 0.9	3.3 ± 1.5	0.6 ± 0.7	3.7 ± 3.8	50.0	100
Range (n)	1-3 (14)	2-5 (3)	0-2 (14)	1-8 (3)		
Seventh shift (♀)						
Mean ± S.D.	2.0 ± 0.7	4.3 ± 2.1	1.2 ± 1.6	0 (2)	53.8	0
Range (n)	1-3 (12)	2-6 (3)	0-5 (13)			
Eighth shift (♂)						
Mean ± S.D.	1.8 ± 0.9	3.5	1.1 ± 1.8	2.5	42.9	50
Range (n)	1-3 (12)	3-4 (2)	0-6 (14)	0-5 (2)		
Ninth shift (♀)						
Mean ± S.D.	2.3 ± 0.8	4.0	1.9 ± 2.5	1.0	58.3	100
Range (n)	1-4 (10)	3-5 (2)	0-7 (12)	(2)		
Tenth shift (♂)						
Mean ± S.D.	2.2 ± 1.0	3.0	2.5 ± 2.8	4 (1)	63.6	100
Range (n)	1-3 (9)	2-4 (2)	0-9 (11)			
Eleventh shift (♀)						
Mean ± S.D.	2.1 ± 0.9	3 (1)	1.0 ± 1.1	0 (1)	62.5	0
Range (n)	1-4 (10)		0-3 (8)			
Twelfth shift (♂)						
Mean ± S.D.	1.8 ± 1.1	2 (1)	1.6 ± 1.3	0 (1)	77.7	0
Range (n)	1-4 (9)		0-4 (9)			
Thirteenth shift (♀)						
Mean ± S.D.	1.6 ± 0.7	-	1.9 ± 1.6	-	77.7	-
Range (n)	1-3 (9)		0-4 (9)			
Fourteenth shift (♂)						
Mean ± S.D.	1.3 ± 0.7	-	1.0 ± 1.7	-	50.0	-
Range (n)	1-3 (9)		0-5 (8)			
Fifteenth shift (♀)						
Mean ± S.D.	2.0 ± 0.9	-	0.9 ± 1.2	-	50.0	-
Range (n)	1-3 (6)		0-3 (8)			
Sixteenth shift (♂)						
Mean ± S.D.	2.1 ± 0.7	-	1.2 ± 1.2	-	71.4	-
Range (n)	1-3 (7)		0-3 (7)			
Seventeenth shift (♀)						
Mean ± S.D.	1.5 ± 0.8	-	2.8 ± 1.3	-	100	-
Range (n)	1-3 (6)		1-4 (4)			
Eighteenth shift (♂)						
Mean ± S.D.	1.0	-	0.7 ± 0.6	-	66.7	-
Range (n)	(2)		0-1 (3)			
Nineteenth shift (♀)						
Mean	1.5	-	1.0	-	100	-
Range (n)	1-2 (2)		(2)			
Twentieth shift (♂)						
Mean	1.0	-	1	-	100	-
(n)	(2)		(1)			
Twenty-first shift (♀)						
Mean	2.5	-	1	-	100	-
Range (n)	2-3 (2)		(1)			
Twenty-second shift (♂)						
Mean	1	-	0	-	0	-
(n)	(1)		(1)			
Twenty-third shift (♀)						
Mean	1	-	0	-	0	-
(n)	(1)		(1)			

TABLE 26 — Incubation schedule in *Oceanites oceanicus* and *Fregetta tropica*

	O.oceanicus	F.tropica
INCUBATION		
Mean length of a shift (days)		
both sexes		
Mean ±S.D.	1.8 ±0.9	3.7 ±1.4
Range (n)	0.5-4(197)	1-7(37)
male		
Mean ±S.D.	1.9 ±1.0	3.7 ±1.4
Range (n)	1-4(94)	2-7(18)
female		
Mean ±S.D.	1.7 ±0.9	3.7 ±1.4
Range (n)	0.5-4(103)	1-6(19)
DESERTION		
Mean number of periods per nest		
Mean ±S.D.	8.5. ±5.1	7
Range (n)	3-18(6)	(1)
Total length per nest (days)		
Mean ±S.D.	14.0 ±7.0	22
Range (n)	6-26(6)	(1)
Mean length of a period (days)		
Mean ±S.D.	1.7 ±1.1	3.1 ±1.9
Range (n)	1-6(48)	1-8(20)
Frequency of nest-reliefs with desertion (per cent)		
Mean ±S.D.	52.4 ±20.4	70.3 ±19.4
Range (n)	26.7-85.7(6)	50.0-100.0(5)
STAYS AT SEA		
Mean length (days)		
both sexes		
Mean ±S.D.	3.9 ±2.8	7.7 ±2.3
Range (n)	1-17(152)	4-13(23)
male		
Mean ±S.D.	3.7 ±3.0	8.0 ±2.6
Range (n)	1-17(72)	4-13(11)
female		
Mean ±S.D.	4.0 ±2.3	7.4 ±1.9
Range (n)	1-11(80)	4-10(12)

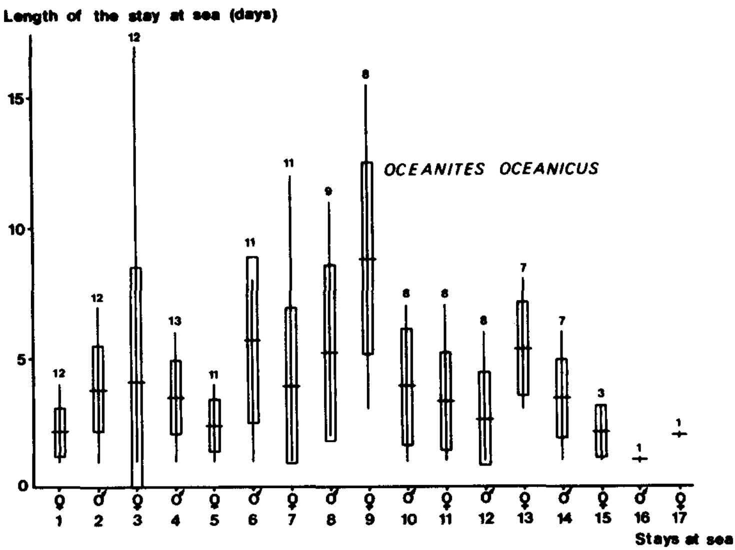

FIGURE 19 — Duration of sojourns at sea in *Oceanites oceanicus* throughout incubation. Mean ± standard deviation, range and sample size

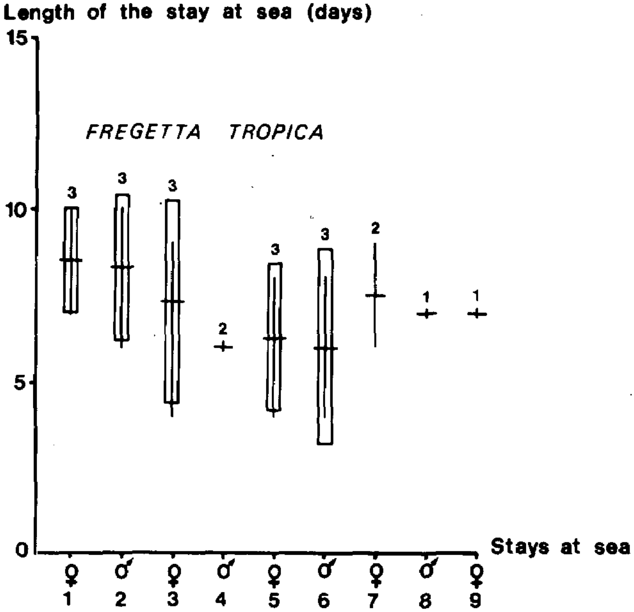

FIGURE 20 — Duration of sojourns at sea in *Fregetta tropica* throughout incubation. Mean ± standard deviation, range and sample size

between the length of these desertions and the apparent total incubation period (Fig. 21). For the Black-bellied Storm Petrel, the only total incubation period recorded lasted 61 days. After subtracting 22 days of desertions, we obtained an actual incubation length of 39 days, which is similar to those obtained in other localities (Beck & Brown 1971). We have no information for the Grey-backed Storm Petrel.

As with procellarids, the thermic emancipation of the chicks was rapid, by the age of 1.8 days (range 1-3 for 4 chicks) for Wilson's Storm Petrel, by 0.7 days (range 12-24 hours for 3 chicks) for the Black-bellied Storm Petrel, and by 24 hours at the latest for the Grey-backed Storm Petrel (Despin *et al.* 1972).

Chick growth

As the dates of our stay on East Island did not coincide with the whole breeding period, chick growth was only partly studied. The first half of growth after hatching was studied for one chick of *Garrodia nereis* in 1970-1971 (Despin *et al.* 1972) and the first month of growth in three chicks each of *Oceanites oceanicus* and *Fregetta tropica* in 1981-1982. Maximum weight was not determined for any of the chicks (Fig. 22-25). Growth was particularly rapid in the Grey-backed Storm Petrel chick. In the first half of its rearing period,

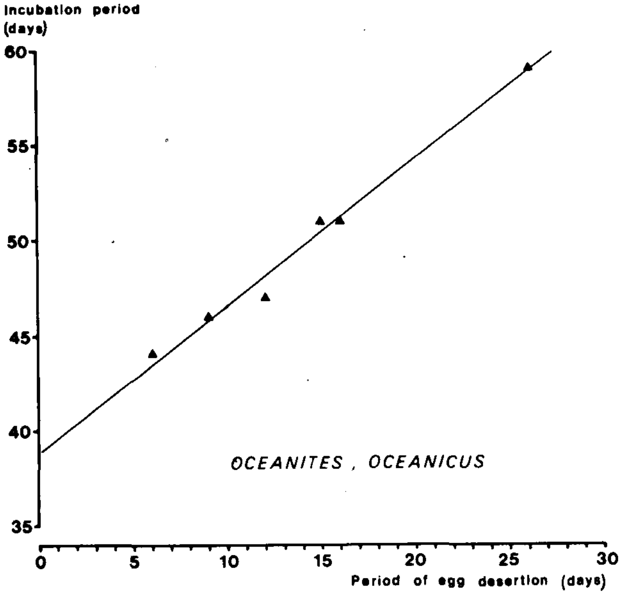

FIGURE 21 — Influence of egg desertions on the incubation period in *Oceanites oceanicus*. $y = 0.76x + 38.9$; $r = 0.99$; $n = 6$

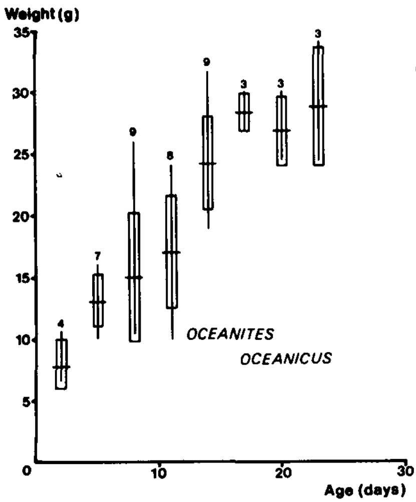

FIGURE 22 — Weight increase in *Oceanites oceanicus* chicks. Mean ± standard deviation, range and sample size

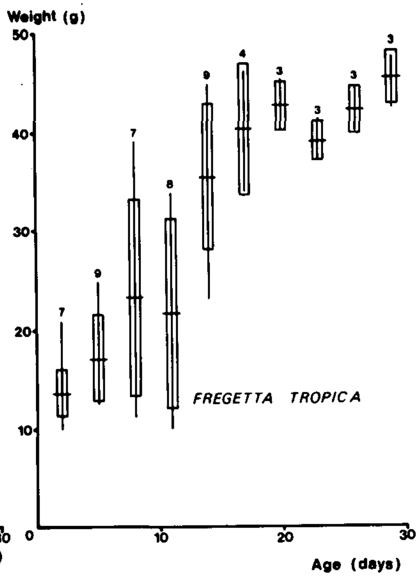

FIGURE 23 — Weight increase in *Fregetta tropica* chicks. Mean ± standard deviation, range and sample size

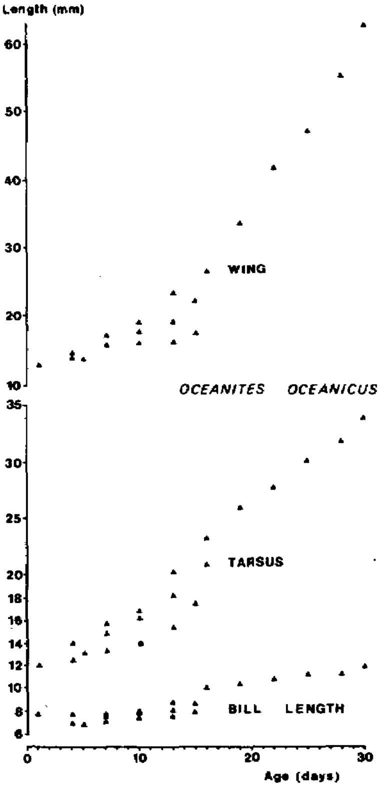

FIGURE 24 — Growth of wing, tarsus and bill length in *Oceanites oceanicus* chicks. Each point represents one measurement

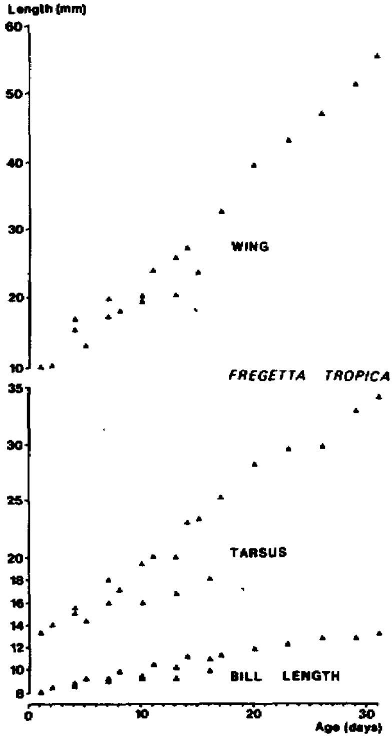

FIGURE 25 — Growth of wing, tarsus and bill length in *Fregetta tropica* chicks. Each point represents one measurement

its rate of weight gain in 3-day periods reached 39.1% compared with 30.9% in Wilson's Storm Petrel and 24.4% in the Black-bellied Storm Petrel. For this last species, weight gain was still very slow in the second 15 days after hatching, with an increase of only 2.2% compared with 19.6% during the same period for Wilson's Storm Petrel. As usual, the wing growth was slow at first, accelerating with the appearance of the vexilles of primaries. The culmen and tarsus grew rapidly during the first weeks of rearing.

Chick feeding was studied for Wilson's Storm Petrel and the Black-bellied Storm Petrel during the period of weight gain (Table 27). The average weight increase from day to day represented 19.4% of the chick weight of Wilson's Storm Petrel. The larger increase of 22.3% for the Black-bellied Storm Petrel corresponded with the proportionately and absolutely larger meals received by the chicks.

As during incubation, the Wilson's Storm Petrel spent shorter periods at sea (3.0 days) than the Black-bellied Storm Petrel (4.0 days), but they were more consistent in length during chick feeding. Both species returned to land more and more often during rearing, but especially the Black-bellied Storm Petrel. We have no equivalent data for the Grey-backed Storm Petrel.

DIVING PETRELS

Two species of diving petrels breed on the Crozet Islands, the South Georgian Diving Petrel *(Pelecanoides georgicus)* and the Common Diving Petrel *(P. urinator,* following the second edition of Peters' Check-list of Birds of the World — Jouanin & Mougin 1979). Table 28, which gives their measurements (partly from Prévost 1970, Despin *et al.* 1972), shows that the Common Diving Petrel is much larger than its relative, weighing 16.5% more, but its wing is only 2.5% longer and its culmen and tarsus are only 7.2% longer, although there is a considerable overlap of these measurements between the two species. The usual criteria for identification were tested (Table 29). The shape of the lower mandible appears highly unreliable. The coloration of the underwing coverts is a good criterion despite a small margin of error. Finally, the last criterion was found to be the most reliable: a black line on the back of the tarsus characterises *P. georgicus,* whereas black patches or a uniform blue coloration identifies *P. urinator,* as found on Kerguelen Islands (Milon & Jouanin 1953) and on South Georgia (Payne & Prince 1979).

Table 30 (partly from Despin *et al.* 1972, Derenne & Mougin 1976) shows the breeding cycle of these birds on Crozet archipelago. After totally deserting their colonies during the non-breeding season, diving petrels return to land at the end of winter, probably the end of August or the beginning of September for *P. urinator* and the end of September for *P. georgicus.* The breeding season lasts slightly longer than 5.5 months (170 days) for *P. urinator* and slightly less than 5 months (145 days) for *P. georgicus.* The difference of timing of the various stages of breeding between the two species becomes less as breeding progresses, and the well-synchronised fledging of chicks of both species occurs around mid-February (Fig. 26).

Reoccupation of burrows and pairing

A study of burrow visiting during pairing showed that *P. georgicus* is much less on land during the day than *P. urinator*. In the month before laying, an average of 3.6% of burrows were occupied by *P. georgicus* during the day, compared with 11.8% for *P. urinator*. In the Common Diving Petrel, the rate of burrow visiting was low until the 25th day before laying, when it increased progressively until the 6th day before laying (from 11.7 ± 16.2% to 18.1 ± 11.7% in 5-day periods). It then decreased suddenly in the last five days of pairing (7.8 ± 5.3%), corresponding to the prelaying exodus of at least one sex. Burrows were rarely occupied at this stage, and by only one bird.

No laying occurred in 20% of the 25 monitored burrows of *P. georgicus* and in 12% of the 41 of *P. urinator*. Each burrow of *P. georgicus* was visited by an average of 2.2 ± 0.7 birds (range 2-4 for 18 burrows) and each burrow of *P. urinator* by an average of 2.3 ± 0.7 birds (range 2-4 for 21 burrows). At the end of the prelaying exodus, the females of both species usually returned to land on the night before laying.

TABLE 27 — Chick-feeding pattern in *Oceanites oceanicus* and *Fregetta tropica*

		O.oceanicus	F.tropica
Period of increase in weight			
Number of chicks weighed		3	3
Number of weighings		45	51
Number of nights with visits (percent of total number of nights studied)	Mean ±S.D.	55.8 ±2.2	44.1 ±8.5
	Range	54.6-58.3	38.5-53.9
Interval between meals (days)	Mean ±S.D.	1.49 ±0.07	2.03 ±0.41
	Range	1.41-1.53	1.56-2.32
Weight increase per 24 hours when the chick is fed (g)	Mean ±S.D.	4.4 ±2.8	6.6 ±3.6
	Range (n)	0-11(25)	1-16.5(22)

TABLE 28 — Weights (g) and measurements (mm) of diving petrels

		P.georgicus	P.urinator
Weight	Mean ±S.D.	121 ±13	141 ±13
	Range (n)	90-150(71)	105-165(52)
Wing length	Mean ±S.D.	119 ±5	122 ±4
	Range (n)	106-129(35)	114-129(54)
Culmen length	Mean ±S.D.	15.3 ±0.8	16.4 ±0.7
	Range (n)	13.8-16.8(35)	14.0-18.0(54)
Culmen width	Mean ±S.D.	9.3 ±0.5	9.3 ±0.6
	Range (n)	8.5-10.5(23)	8.5-10.5(33)
Tarsus length	Mean ±S.D.	25.0 ±0.9	26.8 ±1.0
	Range (n)	23.0-26.5(35)	25.3-29.0(54)

TABLE 29 — Identification criteria for *Pelecanoides georgicus* and *P. urinator*

	P.georgicus	P.urinator
Lower mandible		
Number of birds studied	23	37
Rami parallel (percent)	0	43.2
Rami converging (percent)	100	56.8
Underwing coverts		
Number of birds studied	23	42
Grey (percent)	4.3	100
White (percent)	95.7	0
Posterior part of tarsus		
Number of birds studied	23	36
Black line (percent)	100	0
Black spot (percent)	0	58.3
No black (percent)	0	41.7

TABLE 30 — Timing and duration of events during the breeding cycle of the diving petrels

	P.georgicus	P.urinator
First returns on land	22 sep 81	before 19 sep 81
Length of pariad (days)	60	>40
Laying period		
Mean ±S.D.	18 nov 81 ±11	27 oct 81 ±12
Range (n)	29 oct -8dec (18)	5 oct -24 nov (33)
Period from laying to hatching (days)		
Mean ±S.D.	47.1 ±3.0	55.5 ±3.6
Range (n)	44-52(7)	49-63(16)
Real incubation period (days)	46	50-51
Hatching period		
Mean ±S.D.	25 dec 70-20 jan 71 30 dec 81 ± 11	20 dec 81 ±11
Range (n)	14 dec - 15 jan (11)	30 nov -11 jan (24)
Fledging period (days)		
Mean ±S.D.	50.3 ±2.7	53.6 ±3.9
Range (n)	47-54(8)	47-59(10)
Departure of fledglings from the colony	16-17 feb 71 (2) 17 feb -22 mar 74	
Mean ±S.D.	12 feb 82 ± 11	7 feb 82 ±10
Range (n)	31 jan - 3 mar (6)	25 jan -2 mar (11)

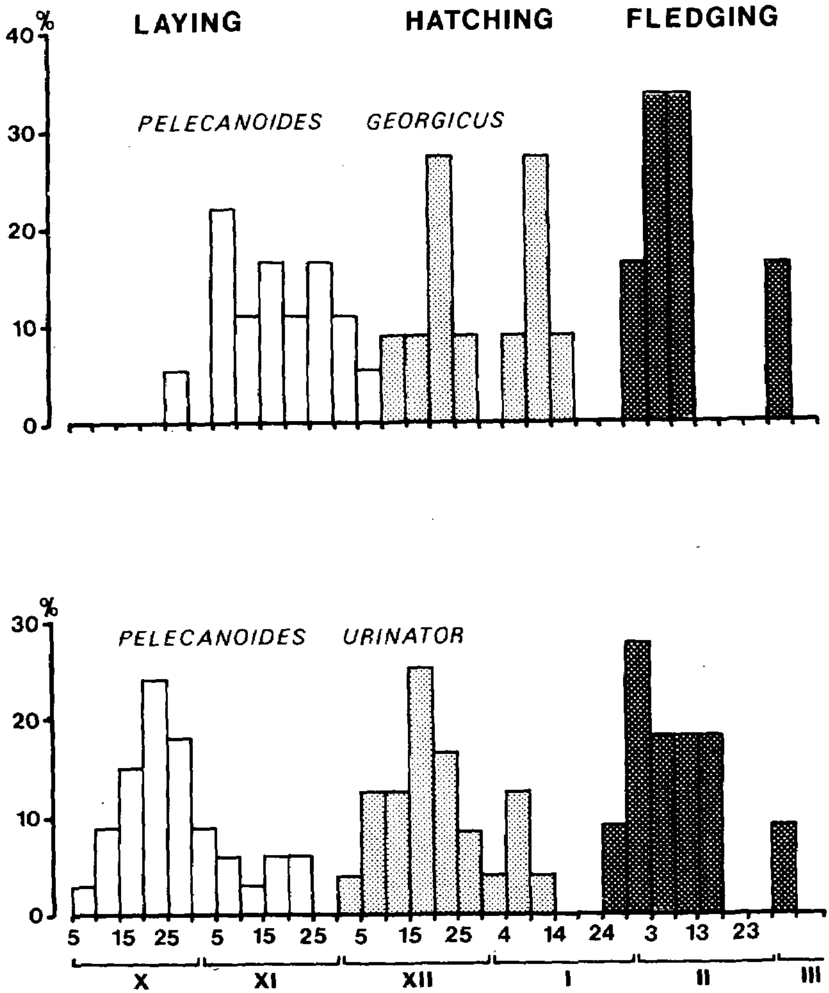

FIGURE 26 — Timing of events during the breeding cycle of *Pelecanoides georgicus* compared with *Pelecanoides urinator*

Laying

Common Diving Petrels laid, on average, 22 days before South Georgian Diving Petrels (Table 29 and Fig. 26). This was a significant difference ($t = 6.43$, $p < 0.001$) in spite of an overlap of 27 days. The laying period was long for both species (51 days for *P. urinator* and 41 days for *P. georgicus*). The laying date did not seem to influence the success of the egg in *P. georgicus*. In this species, 11 eggs that were abandoned were laid on 18 November ± 13 days (29 October-8 December) at the same date — 18 November ± 9 days (7-26 November) — as 7 eggs which were due to hatch.

The egg measurements for the two species (partly from Despin *et al.* 1972) did not differ significantly (Table 31). Thus, the ratio of egg weight to adult weight was smaller for the bigger *P. urinator* (15.7%) than for the lighter *P. georgicus* (17.4%). In both cases, however, the values were relatively low for burrowing Procellariiformes of such a small size.

Incubation

The incubation shifts were very different between the two species, being much shorter and more numerous ($t = 11.6$, $p < 0.001$) in *P. urinator* than in *P. georgicus*. The length of the shifts remained the same during all incubation, and in both species the sexes shared the duties equally. Temporary egg desertions were not common and were fewer in *P. georgicus* than in *P. urinator* (Table 32). Thus, the changing of partners on the egg was well synchronised.

Table 30 shows the hatching dates of the two diving petrels of Crozet archipelago. Hatching was more synchronised between the species than laying, only 10 days separating the average dates of hatching. For both species the hatching period was rather long, 33 days for *P. georgicus* and 43 days for *P. urinator*, with a considerable overlap of 29 days between the two species. As with laying, hatching was evenly distributed over the whole period with slightly more hatchings taking place in the early stages. The date of hatching appeared to have a large influence on the subsequent fate of the chicks, in contrast with the date of laying. *P. georgicus* chicks which eventually fledged hatched on average 14 days before those that did not — on 24 December ± 9 days (from 14 December to 10 January for 6 birds) compared with 7 January ± 9 days (from 21 December to 15 January for 5 birds). This was also true for *P. urinator*, where the interval measured 12 days, from 14 December ± 6 days (from 30 November to 21 December for 11 chicks) to 26 December ± 12 days (from 7 December to 11 January for 13 chicks).

The average total apparent incubation periods for the two species (47.1 days for *P. georgicus* and 55.5 days for *P. urinator*) were significantly different ($t = 5.39$, $p < 0.001$), although the actual incubation periods were similar. Desertions making up approximately 2.1% of the total apparent incubation period for the South Georgian Diving Petrel and 7.6-10.5% for the Common Diving Petrel, the actual incubation periods lasted about 46 days for the first species and 50-51 days for the second.

These species differed from the procellarids and storm petrels in that the thermic emancipation of their chicks was late, being 6.3 ± 2.0 days after hatching (range 3-9 days for 12 chicks) for *P. georgicus* and 11.6 ± 1.3 days after hatching (range 8-13 days for 17 chicks) for *P. urinator*. As they did during incubation, the adults took alternate shifts on the nest for an average

TABLE 31 — Weights (g) and measurements (mm) of diving petrel eggs

		P.georgicus	P.urinator
Weight	Mean ±S.D.	21.1 ±1.7	22.1 ±2.0
	Range (n)	19-24(19)	19-26(19)
Length	Mean ±S.D.	38.8 ±1.5	40.0 ±1.6
	Range (n)	36.2-41.7(32)	37.6-45.2(31)
Breadth	Mean ±S.D.	31.6 ±1.0	31.6 ±1.0
	Range (n)	29.0-33.0(32)	29.3-34.0(31)

TABLE 32 — Incubation schedule in *Pelecanoides georgicus* and *P. urinator*

	P.georgicus	P.urinator
INCUBATION		
Mean length of a shift (days)		
both sexes		
Mean ±S.D.	2.4 ±0.7	1.3 ±0.5
Range (n)	1-4(107)	1-3(165)
male		
Mean ±S.D.	2.3 ±0.9	1.5 ±0.6
Range (n)	1-4(21)	1-3(38)
female		
Mean ±S.D.	2.1 ±0.6	1.3 ±0.5
Range (n)	1-3(22)	1-3(38)
DESERTION		
Mean number of periods per nest		
Mean ±S.D.	1	3.0 ±1.7
Range (n)	(2)	1-4(3)
Total length per nest (days)		
Mean ±S.D.	1	4.3 ±3.5
Range (n)	(2)	1-8(3)
Mean length of a period (days)		
Mean ±S.D.	1	1.4 ±1.0
Range (n	(2)	1-4(9)
Frequency of nest-reliefs with desertion (per cent)		
Mean	4.9	6.2
Range (n)	4.5-5.3(2)	3.4-8.9(2)
STAYS AT SEA		
Mean length (days)		
both sexes		
Mean ±S.D.	2.3 ±0.7	1.6 ±0.6
Range (n)	1-4(43)	1-5(76)
male		
Mean ±S.D.	2.2 ±0.6	1.5 ±0.7
Range (n)	1-3(22)	1-4(38)
female		
Mean ±S.D.	2.4 ±0.8	1.7 ±0.6
Range (n)	1-4(21)	1-5(38)

length of 1.1 ± 0.3 days (range 1-3 days for 64 shifts on 6 nests) for *P. urinator* and 1.5 ± 0.8 days (range 1-3 days for 13 shifts on 4 nests) for *P. georgicus*. The periods of time spent on land, which were shorter than during incubation, did not differ significantly between the two species.

Chick growth

The weight increases shown in Table 33 and in Figures 27 and 28 result from a study of 8 *P. georgicus* and 11 *P. urinator* chicks. The rates of increase in 3-day periods were 23.4 ± 19.6% for *P. georgicus* and 19.2 ± 17.0% for *P. urinator*. The chicks of both species reached the same maximum weight, 20% more than the adult weight for *P. georgicus* and 4% more for *P. urinator*, by the time they were three-quarters fledged for the first species and less than two-thirds fledged for the second. The subsequent loss of weight (29% of the maximum for *P. georgicus* and 22% for *P. urinator*) corresponds to a rate of decrease in 3-day periods of 3.0 ± 4.1% for *P. georgicus* and 3.1 ± 0.8% for *P. urinator*. The weight at fledging as a percentage of adult weight was the same for both species (82-86%). The growth of the wing (Fig. 29) was slow before the appearance of the primaries, then became more rapid, but adult measurements were not reached at fledging. The length increase, in periods of three days for the whole time on the nest, was approximately 13.2 ± 6.6% for *P. georgicus* and 11.8 ± 6.7% for *P. urinator*. The culmen and tarsus (Fig. 29) grew rapidly at the beginning of rearing and then slowed down until reaching adult size at fledging.

Table 34 gives the results of a chick-feeding study between hatching and fledging. For these chicks, the weight gains before and after thermic emancipation were separated. The chicks of both species were fed in a similar manner between hatching and emancipation. Between the emancipation of chicks and their reaching maximum weight, adults of both species returned to land less often but the meals were larger — the chicks of *P. georgicus* being fed less often than those of *P. urinator* but the size of their feeds being larger. Finally, during the period of weight loss, the adults returned to land even less often than before and decreased the size of the feeds. At this stage, each *P. georgicus* parent returned to land every 4.9 days and each *P. urinator* parent every 4.3 days.

Fledging

Table 30 and Figure 26 show the dates of fledging. Synchrony in breeding continued to improve between the two species until only 5 days separated the average fledging dates. But, as with laying and hatching, the dates of fledging were spread out, lasting 32 days for *P. georgicus* and 37 for *P. urinator*, with a considerable overlap of 31 days, these long periods appearing to be caused by a few late-fledging chicks. The total fledging period for both species was very similar (Table 30), approximately 50 days for *P. georgicus* and 54 days for *P. urinator*. Payne & Prince (1979), comparing their data with that of Despin *et al.* (1972), noticed rather large differences between the length of the fledging periods of *P. georgicus* on South Georgia and Crozet archipelago. Although such variability could be interpreted as different responses of populations exposed to different marine and climatic environments, these authors suggested that the data from Crozet were "atypical" or "based on a misidentification". However, the 1980-1981 data confirm the findings of Despin *et al.* (1972).

TABLE 33 — Weight growth in diving petrel chicks

		P. georgicus	*P. urinator*
Weight at birth			
Weight (g)	Mean ± S.D.	14.8 ± 0.8	15.5 ± 1.0
	Range (n)	14.0-16.0 (5)	14.0-17.0 (9)
Percent adult weight		12.2	11.0
Maximum weight			
Weight (g)	Mean ± S.D.	145.4 ± 21.7	146.9 ± 21.7
	Range (n)	122-175 (8)	122-184 (11)
Percent adult weight		120.2	104.2
Age at peak weight (days)	Mean ± S.D.	37.9 ± 5.4	33.7 ± 4.9
	Range (n)	30-47 (8)	28-42 (11)
Weight at fledging			
Weight (g)	Mean ± S.D.	103.5 ± 23.5	115.0 ± 23.1
	Range (n)	82-155 (8)	86-148 (11)
Percent adult weight		85.5	81.6

TABLE 34 — Chick-feeding pattern in diving petrels

Period of increase in weight		*P. georgicus*	*P. urinator*
-Before emancipation			
Number of chicks weighed		8	11
Number of weighings		38	105
Number of nights with visits (percent of total number of nights studied)	Mean ± S.D.	85.6 ± 17.4	80.3 ± 10.9
	Range	57.1-100.0	58.3-100.0
Interval between meals (days)	Mean ± S.D.	0.80 ± 0.37	0.91 ± 0.23
	Range	0.50-1.45	0.50-1.41
Weight increase per 24 hours when the chick is fed (g)	Mean ± S.D.	4.8 ± 4.5	5.3 ± 4.8
	Range (n)	0-20 (31)	0-32 (84)
-After emancipation			
Number of chicks weighed		6	11
Number of weighings		167	249
Number of nights with visits (percent of total number of nights studied)	Mean ± S.D.	61.5 ± 5.5	68.6 ± 4.9
	Range	54.6-70.4	60.0-75.0
Interval between meals (days)	Mean ± S.D.	1.33 ± 0.15	1.14 ± 0.11
	Range	1.10-1.53	1.00-1.36
Weight increase per 24 hours when the chick is fed (g)	Mean ± S.D.	11.2 ± 8.7	8.9 ± 6.7
	Range (n)	0-39 (102)	0-29 (170)
Period of decrease in weight			
Number of chicks weighed		5	11
Number of weighings		61	210
Number of nights with visits (percent of total number of nights studied)	Mean ± S.D.	37.3 ± 5.5	41.7 ± 6.9
	Range	33.3-44.4	31.3-52.0
Interval between meals (days)	Mean ± S.D.	2.44 ± 0.38	2.17 ± 0.42
	Range	1.96-2.72	1.63-2.93
Weight increase per 24 hours when the chick is fed (g)	Mean ± S.D.	10.1 ± 9.9	4.4 ± 4.2
	Range (n)	0-31 (23)	0-20 (89)
Total growth period			
Number of chicks weighed		5	11
Number of weighings		225	564
Number of nights with visits (percent of total number of nights studied)	Mean ± S.D.	57.4 ± 2.4	60.7 ± 3.1
	Range	54.2-60.0	56.5-64.6
Interval between meals (days)	Mean ± S.D.	1.44 ± 0.08	1.34 ± 0.09
	Range	1.36-1.55	1.23-1.47
Weight increase per 24 hours when the chick is fed (g)	Mean ± S.D.	9.9 ± 8.5	6.9 ± 6.0
	Range (n)	0-39 (156)	0-29 (343)
Last meal (nights before fledging)	Mean ± S.D.	2.2 ± 0.8	3.9 ± 1.5
	Range (n)	1-3 (5)	1-5 (8)

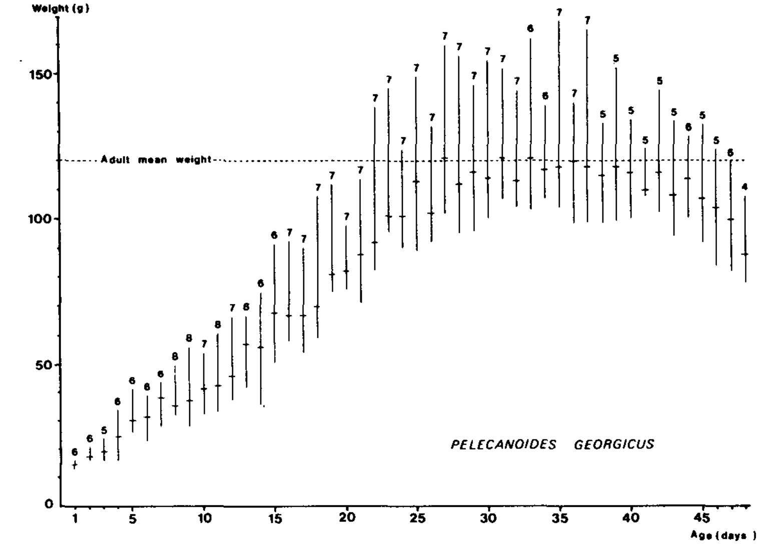

FIGURE 27 — Weight increase in *Pelecanoides georgicus* chicks. Mean, range and sample size

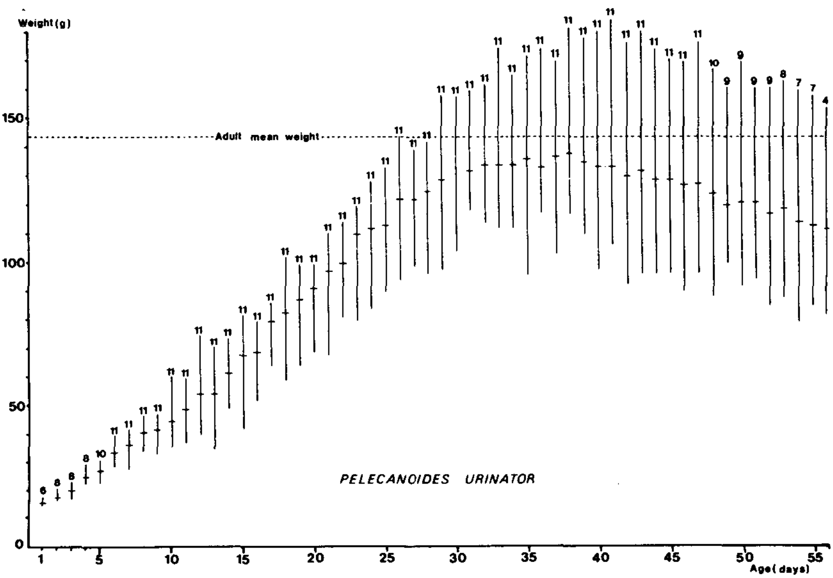

FIGURE 28 — Weight increase in *Pelecanoides urinator* chicks. Mean, range and sample size

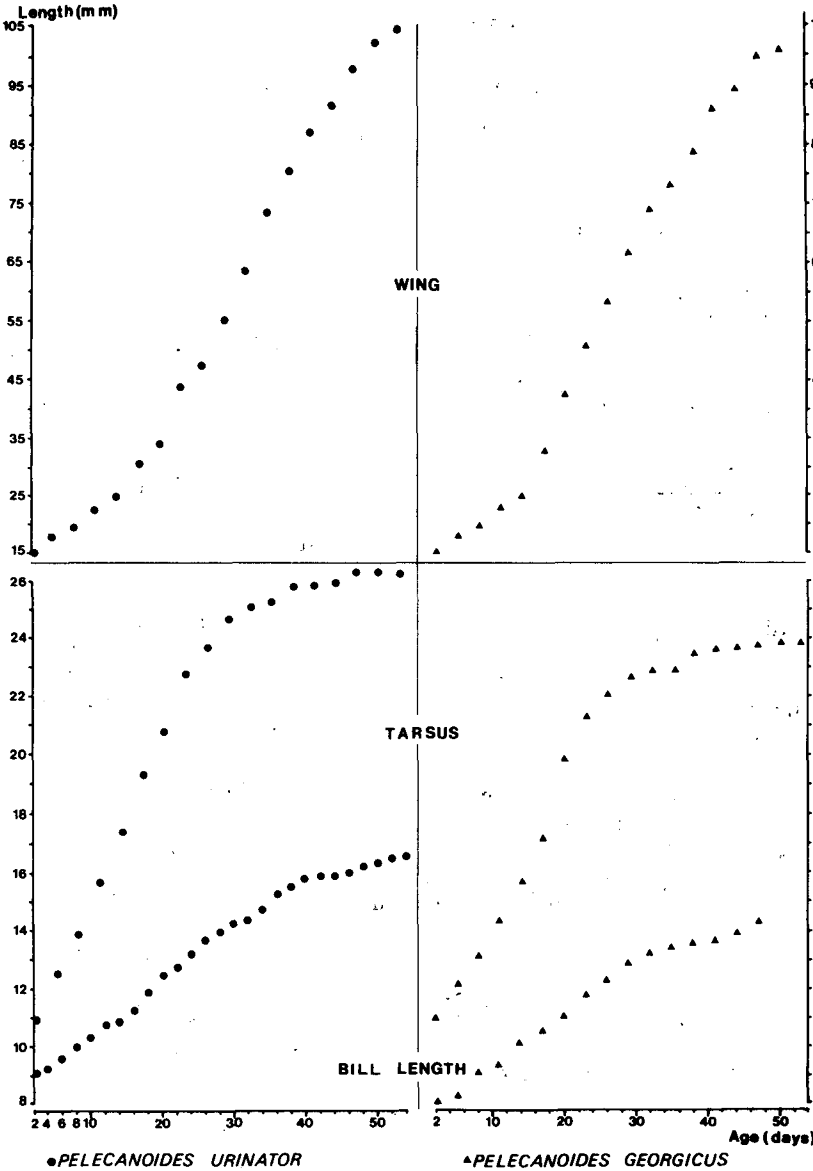

FIGURE 29 — Growth of wing, tarsus and bill length in *Pelecanoides georgicus* and *P. urinator* chicks. Mean points

DISCUSSION

Among the many points highlighted by these data, we have chosen five for discussion.

Abundance cycles in the colonies during pairing

Daily inspection of burrows showed that, during nest reoccupation, the return to land of certain petrels was cyclic. These rhythmic visits were particularly marked for Salvin's Prion, the Black-bellied Storm Petrel and the Grey-backed Storm Petrel, where two abundance peaks were separated by an average interval of 7.4 days, 15.5 days and 16.5 days respectively. The White-chinned Petrel had a similar but less marked abundance pattern. For the other species studied, the numbers observed every night were rather constant.

In these colonies, we made daily 10-minute point counts one hour after sunset, by which time all species were present on land. In each point count (always from the same place) we assessed how many birds of each species were calling. These two methods — inspection of burrows and point counts — used together showed that bird numbers in burrows and vocal activity in the colonies were closely linked. The point count results, partly shown in Figure 30, confirm a cyclic activity for certain species.

Why do these species return to land in such a synchronised way? Do environmental factors influence them? A clear night with a full moon could, for example, stimulate them to return to land by making the colonies or burrows easier to see or, on the contrary, could discourage them by allowing greater skua activity in the colonies. In fact, the returns to land did not correlate with moon or clouds. They did not correlate with weather conditions either: the petrels returned to land independently of wind, rain or fog. Bartle (1968) came to the same conclusions when working on *Pterodroma pycrofti* in New Zealand.

The species that returned cyclically seemed to follow a precise rhythm, perhaps induced by physiological factors. It is hard to believe that birds from the same colony satisfy their hunger simultaneously and return to the colony together or that they stay together at sea in groups. For *Fregetta tropica* the frequency of these rhythms increased during pairing and gradually matched their rhythms of incubation shifts.

We know the importance of physiological and social factors in these birds' breeding biology (Craig 1911, 1913, Darling 1938) and so it is possible that certain species begin to synchronise their shift cycles even before laying. These return-to-land rhythms may be part of a developing synchrony in their social life which facilitates the meeting of adult pairs and pairing of young birds.

Temporary egg desertion

Temporary egg desertions during incubation in many species of procellariiformes are known to occur between the departure of one incubating parent at the end of a shift and the return to land of its partner (for references, see Boersma & Wheelwright 1979), and the embryo survival, even at low temperatures, is a remarkable physiological adaptation. Most of the petrels

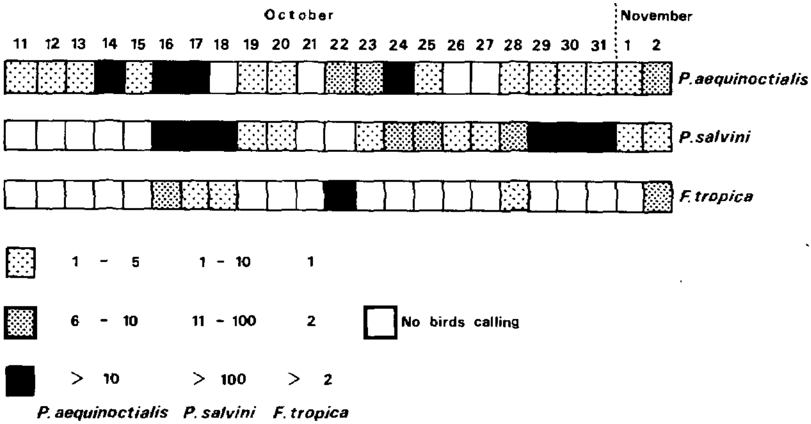

FIGURE 30 — Ten-minute point count results from a mixed petrel colony on East Island (mid-October to beginning of November). Classes represent the number of calling individuals

breeding on the Crozet Islands have this characteristic because the climate is relatively mild and, in fact, these temporary desertions are more limited in the more severe climates, as shown by the example of Wilson's Storm Petrel: 14 days on the Crozet Islands (45°S), 4.1 days on Signy Island (60°S, Beck & Brown 1972) and 1.4 days in Adélie Land (68°S, Lacan 1971).

The cumulated length of the desertions during incubation did not seem to influence hatching success. On the contrary, the embryo survival depends on the timing of the desertions — well-developed embryos suffer more than newly laid eggs from the absence of incubating birds — and on the length of the individual periods — on the Crozet Islands 11 days of desertion early in incubation did not prevent hatching for *Pterodroma brevirostris,* but it is the longest egg desertion known for procellariformes.

Boersma & Wheelwright (1979) have reviewed different aspects of the meaning of egg desertion in procellariiformes. From our Crozet data, we can compare the frequency of shifts with egg desertions and the frequency of egg desertions during two breeding seasons for nine species of burrowing petrels (Table 35). These comparisons show that we have to allow for such factors as the size of the bird and its flying capacity when we consider egg desertion in petrels.

Among the species of Table 35, the only ones seen flying during gales in the southern oceans are the diving petrels. They are birds of coastal and continental waters with a powerful and linear flight pattern, and they rarely desert their eggs. Except for the diving petrels, small petrels are more likely than larger ones to desert their eggs during incubation. They are also more likely to be prevented from returning to their colonies by storms and, especially because of their size, less capable of prolonged fasts when incubating. In contrast, *Procellaria aequinoctialis,* one of the largest burrowing procellariiformes, never deserts its egg. Probably because of its large size, the incubating bird can fast for a long period when the return of its partner is delayed. Finally in *Pterodroma brevirostris,* which is one-third smaller than *P. aequinoctialis,* egg desertion varies from year to year: it occurred often in 1981-1982 but not at all in 1968-1969. The weather records during incubation were average for both years, suggesting that the difference between the two cycles was caused by foraging difficulties and not by weather. Because of these difficulties in 1981-1982, the Kerguelen Petrels spent more time at sea and they could do this by means of egg desertion between shifts rather than by lengthening the incubation shifts. Temporary egg desertions can allow for lengthy sojourns at sea which may permit longer foraging times. In fact, they play the part of a "safety device" useful when the foraging birds are unsuccessful or prevented from coming back to land by bad weather, and when the incubating birds, unable to fast any longer, are obliged to leave the nest.

Competition for burrows

Some petrels studied on the Crozet Islands did not breed in haphazardly chosen burrows but, during the prelaying stage, showed preferences for certain burrows. As a result, favoured burrows in which an egg was ultimately laid often attracted more birds than those in which no egg was laid (Table 36). This attraction for certain burrows suggests competition for the breeding sites. Two or more successive layings were noted in some burrows, each taking place after the eviction of the former egg and sometimes of the incubating adults as well.

TABLE 35 — Egg-desertion frequences and schedules in burrowing procellariiformes

	Frequency of shifts with egg desertion (%)	Mean cumulative egg desertion period (days)	Mean duration of a single egg desertion (days)	Maximum length of an egg desertion (with hatching success) (days)
P. brevirostris				
1968-1969	0	0	0	0
1981-1982	46.7	9.0	4.5	11
P. mollis	11.7	1.8	3.7	4
H. caerulea	43.3	5.6	2.9	5
P. salvini	41.2	4.8	1.9	5
P. aequinoctialis	0	0	0	0
O. oceanicus	52.4	14.0	1.7	6
F. tropica	70.3	22.0	3.1	8
P. georgicus	4.9	1.0	1.0	1
P. urinator	6.2	4.3	1.4	4

TABLE 36 — Nest reoccupation and nest selection in burrowing procellariiformes

	Number of birds visiting nests with subsequent laying	Number of birds visiting nests without subsequent laying	Number of nests visited without subsequent laying (%)	Number of nests visited with 2 successive layings (%)	Number of nests visited with 3 successive layings (%)
P. mollis	3.71 ± 1.53 (17)	2.07 ± 1.33 (15)	46.9 (32)	5.9 (17)	0
P. brevirostris	-	-	23.5 (34)	0	0
P. salvini	4.32 ± 2.01 (38)	3.00 ± 1.75 (20)	34.5 (58)	5.7 (53)	5.7 (53)
P. aequinoctialis	3.06 ± 2.01 (18)	3.29 ± 1.94 (13)	42.0 (31)	5.6 (18)	0
O. oceanicus	-	-	16.0 (25)	0	0
F. tropica	-	-	82.0 (17)	0	0

Comparison with other localities

Little has been published on the breeding biology of the burrowing petrels of the Crozet archipelago in other localities. However, a different subspecies of the Great-winged Petrel, *Pterodroma macroptera gouldi,* was studied in New Zealand (Imber 1976) where, despite breeding in the subtropical zone, laying occurs 6 weeks later than on the Crozet Islands. Feeding frequency of chicks is lower in New Zealand — 3.9 days compared with 3.25 days — but, despite this, fledging weight is higher (540 g versus 460 g). Results of the studies on the Black-bellied Storm Petrel *(Fregetta tropica)* and the Wilson's Storm Petrel *(Oceanites oceanicus exasperatus)* were reported by Beck & Brown (1971, 1972) from Signy Island, South Orkney Islands. For Wilson's Storm Petrel, even though our study was again of a different subspecies *(O. o. oceanicus),* no differences in breeding could be detected. In Adélie Land, Antarctica, where *O. o. exasperatus* also breeds, the breeding occurs a month earlier and the incubation shifts are half as long as on the Crozet or Signy Islands.

The diving petrels show important differences between the Crozet Islands and the other breeding localities. Prince & Payne (1979), comparing their South Georgian results for *P. urinator* and *P. georgicus* with preliminary studies made on the Crozet Islands, showed that the first one lays its egg at about the same time in both localities whereas the second is almost a month later in South Georgia than in the Crozet archipelago. In the colder locality, there is a very strong synchronisation of laying, especially with the first species. It seems that a more climatically severe nesting habitat causes the delay in the breeding cycle of one of the species. On both Crozet Islands and South Georgia, *P. urinator* nests on steep slopes near the sea whereas *P. georgicus* nests on the higher slopes. Thus, when this species' laying season starts on the Crozet Islands, in November, the colonies are still covered with snow in South Georgia. Thus, specific breeding habitat requirements determine the differences in breeding in this species, rather than food supply.

FIGURE 31 — A Kerguelen Petrel at the entrance of its burrow in a marshy area (Possession Island).
Photo: H. Weimerskirch

FIGURE 32 — A Grey Petrel at the entrance of its burrow among *Poa cookii* (Possession Island). Photo: H. Weimerskirch

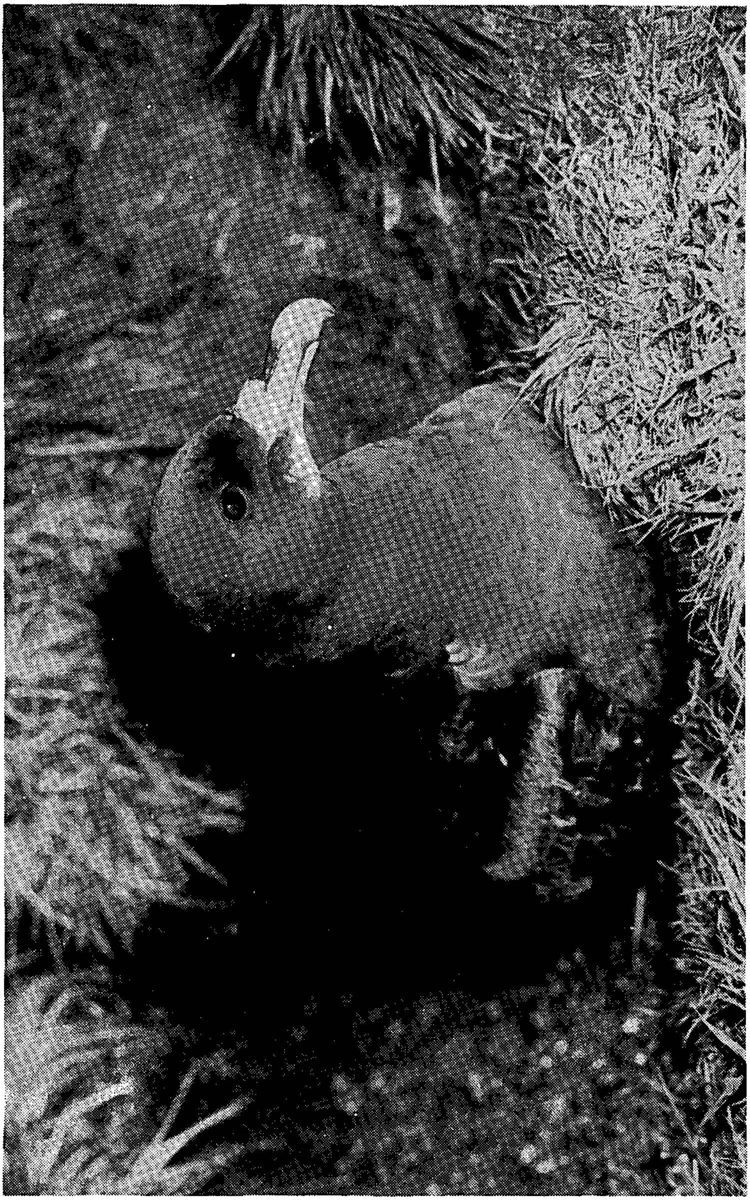

Photo: H. Weimerskirch

FIGURE 33 — A White-chinned Petrel at Possession Island.

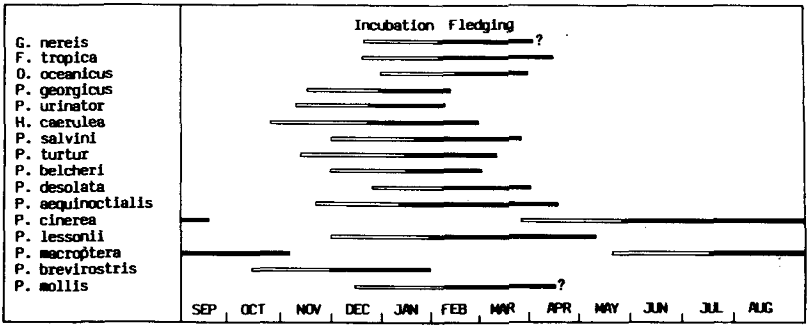

FIGURE 35 — Timing of the breeding season for the 16 burrowing procellariiformes of the Crozet Islands

around the Crozet Islands. Their food ranges therefore overlap broadly (Ridoux, unpubl.). At the present time, the only known feeding-related differences between the two species consist of the filtering device on the bill and the less pelagic sea distribution of *P. salvini.*

The three storm petrels breed at the same time of the year but have different breeding habitats and diets. *Garrodia nereis* is narrowly specialised for prospecting for floating algae on the Crozet shelf. *Fregetta tropica* concentrates over the continental slope, whereas *Oceanites oceanicus* is limited to the shelf (Stahl, unpubl.). This difference in habitat and diet is reflected in that the incubation shifts (Table 26) and the time between successive feeds to chicks (Table 27) are longest for the species which feeds furthest from the nesting grounds. The diets of the two larger storm petrels overlap slightly, but *F. tropica* feeds on larger prey than *O. oceanicus* (Ridoux, unpubl.).

Finally, although the two diving petrels breed at the same time, their incubation shifts and their feeding frequencies are very different (Tables 32 and 34). Observations at sea around the Crozet Islands show that *Pelecanoides georgicus* feeds further offshore than *P. urinator* because the first is observed mostly over the continental slope and the second mostly over the continental shelf. So, *P. georgicus* displays the longest feeding trips. In South Georgia the two species do not breed at the same time. This, as we have seen, may be due to nesting habitat segregation with snow covering the higher burrows of *P. georgicus*. Little information is available on where the diving petrels feed around South Georgia. If, taking advantage of the local temporal segregation, both species feed near the coast, that would explain why the chicks of *P. georgicus* grow faster in South Georgia than in the Crozet archipelago (45.5 days compared with 50.3 days). These results are in opposition with the conclusions of Payne & Prince (1979) and show that data from one locality cannot necessarily be applied to another.

Preliminary data about the diet of the petrels of the Crozet Islands (unpubl.) show on one hand that an important overlap exists for closely related species and on the other that the same species may change diet from one island to another. Thus generally it appears that the spatio-temporal factors are at least as important as diet. Indeed food seems mainly implicated indirectly (through latitude, temperature, salinity, i.e. the masses of water). Ecological segregation in seabirds is not the result of a single factor but usually reflects several factors working together.

ACKNOWLEDGEMENTS

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SHORT NOTE

A Cattle Egret

On May 1985, I picked up a Cattle Egret on the Drake Flats, Waiatoto Valley, South Westland, which appeared to have been recently taken by a Falcon. The whole neck and body were plucked, the feathering remaining only on the head and wings. All the plumage was white.

The bill was horn yellow at the tip, shading to deep yellow at the base; the iris was clear yellow; the legs were grey-green around the metatarsal joint, shading to charcoal lower down; top of toes blackish, undersides pale sage-green; claws blackish. Although this was about 22 km in a direct line from the sea coast and where Hereford cattle were grazed, three other egrets were feeding 7 km further up the valley (at the Donald Flats), where there were no stock.

PETER CHILD, *10 Royal Terrace, Alexandra*