THE ANNUAL CYCLE OF THE SOOTY SHEARWATER *Puffinus griseus* AT THE SNARES ISLANDS, NEW ZEALAND[1]

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ABSTRACT

A study of the Sooty Shearwater was made at the Snares Islands during four summers. The work is based partly on the activities of 31-45 marked pairs in burrows and partly on more general observations. These large, powerful shearwaters (weight 819 g) return in late September and, after a 'scratching-out' period of about a month, part of the population leaves on a prelaying exodus which lasts about two weeks. Laying reaches a peak from 20 to 24 November and incubation takes 53 days, most eggs hatching from 11 to 16 January. No precise nestling periods were obtained, but adults depart on migration from the end of March and most leave by the third week of April. Most chicks leave during the last weeks of April and the first week of May.

Surface-laid eggs are plentiful. They tend to be smaller and narrower than burrow-laid ones and, on average, are laid three days later than those underground. During incubation the male takes the first stint on the egg after the female's brief initial one. Thereafter the stints are of similar length, averaging about 9.4 days for both sexes. Samples of chick weights for their first 40 days are given as well as weights of 500 chicks at the time of banding just before their first flights. Flooding of burrows is the chief overt cause of chick mortality. Differences in timing of breeding at Whero Island and The Snares are discussed. In general, the timing seems to be similar throughout the birds' range from Australasia to the Falklands and Tierra del Fuego, but precise information is very sparse.

INTRODUCTION

The Sooty Shearwater or New Zealand Muttonbird *(Puffinus griseus)* breeds from the Three Kings Islands at 34°S, 172°E to Macquarie Island at 55°S, 159°E. Some still try to breed on headlands of mainland New Zealand despite the attentions of feral cats, stoats and other predators. The chief breeding places, however, are the many islands around Stewart Island and on the Snares Islands. Sooty Shearwaters also nest in small numbers on eight islands off New South Wales and three around Tasmania (Lane & White, in press), often

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in association with Short-tailed and/or Wedge-tailed Shearwaters, *P. tenuirostris* and *P. pacificus.* There are also important, though little known, breeding places in southern South America and some also nest at the Falkland Islands.

These are powerful petrels about 500 mm long, wingspan c. 1050 mm, and weighing 819.1 $\pm$ 76 g (n = 299) at the Snares Islands — bills and claws and, if hand-held, struggle persistently and on release often desert their egg permanently. They are highly sociable often desert their egg often permanently. They are highly sociable summer breeders, laying one egg in a chamber dug at the end of a tunnel in the ground, less often in a rock crevice. As with other petrels, pair-bonds and burrows tend to be retained from year to year.

Sooty Shearwaters are notable transequatorial migrants, and most spend the southern winter in the cool offshore waters of the North Atlantic and North Pacific Oceans.

Detailed biological work on the species was carried out by L. E. Richdale on Whero Islet off the north-east corner of Stewart Island at 47°S, 168°E between 1940 and 1957. His classic account (Richdale 1963) was based on observations of about 500 banded adults and dealt mainly with the post-egg stage of the annual cycle.

Our work at The Snares (48°S, 166°E) was undertaken during four expeditions — 17 January to 13 February 1967, 14 November 1968 to 23 February 1969, 20 November 1969 to 19 February 1970, and 18 November 1970 to 11 March 1971. Further information was collected for us during the 1971/73, 1974/75 and 1976/77 expeditions, particularly by D. S. and C. J. Horning, and these have helped to fill some of the gaps in our observations. Our study covered mainly the early part of the breeding cycle and so largely complements that of Richdale.

METHODS

The shearwater tunnels may be 2-3 metres long, often twisting to avoid tree roots. The occupants are seldom visible from outside and many cannot be reached with the aid of a bent wire. Furthermore, fitting of observation panels to nests (Warham 1966: 193-200) is usually impracticable because of the depths of the chambers and the thick roots. To facilitate inspections, the shorter straighter burrows were selected, and so in this respect ours was a biased sample. Numbered pegs identified the 31-45 burrows in the study.

Study birds were marked with stainless steel leg bands, as were others banded in the hope of recovery overseas. Temporary paint marks on foreheads allowed some individual birds to be identified without handling — their legs were seldom visible. We have no evidence of band loss. Attentiveness at nests was gauged by direct observation of the marked birds and from displacements of fine wire fences set across burrow entrances.

FIGURE 1 — Sooty Shearwater carrying nesting material into burrow.
Photo: John Warham

The shearwaters were sexed by cloacal examination around the time of laying (Serventy 1956) and sometimes by palpating shelled eggs in females but, to reduce nesting failure, examinations and handling were kept to a minimum. Measurements were made with vernier calipers and weights with spring balances, those below 200 g being accurate to ±1 g, those above 200 g to ±10 g. Where appropriate, measurements are given ± 1 standard deviation.

THE HABITAT

The Snares consist of Main or North East Island (280 ha) and Broughton Island (48 ha), both with many offlying stacks and islets, and a group of large almost unvegetated rocks known as the Western Chain — for maps see Warham (1967) or Fineran (1969). Main and Broughton Islands are granitic, mostly covered in deep peat and well vegetated. There are no man-introduced vertebrates.

These islands lie in the west-wind zone and experience frequent gales, rain and mists. Only for 1972 do our meteorological data cover a complete year. The 1481 mm of rain that then fell was fairly evenly distributed throughout that year while the mean monthly temperatures ranged from 6.9 °C in June to 13.5 °C in February.

Main and Broughton Islands are largely covered with a forest of *Olearia lyallii* with some admixture, particularly on Broughton, of the tree *Senecio stewartiae.* Both produce almost closed canopies at about 6 m. Outside the tree zone the peat supports lush meadows of tussock grasses, notably the broad-leaved *Poa tennantiana.* Mostly peripheral to these meadows, but interdigitating with them to some extent, are meadows of a narrow-leaved grass *Poa astonii,* which tends to grow in larger stools to 1.5 m high. Another important floral element is *Hebe elliptica,* a tough-stemmed salt-resistant bush growing to about 3 m high and forming dense thickets in some places outside the forest zone. The Snares Islands flora has been described by Fineran (1964, 1969); its geology and soils by Fleming *et al.* (1953), and its birds by Warham (1967) and Horning & Horning (1974).

The Sooty Shearwater is by far the most numerous vertebrate on these islands in the summer. We estimated that they had nearly 3 600 000 burrows on Main and Broughton Islands, which, at an occupation rate of 75%, represents a population of about 2 750 000 pairs (Warham & Wilson 1982).

The birds' effects on the vegetation are very marked. The extensive burrowing honeycombs the peat and undermines the vegetation so that the trees are predisposed to uprooting. Trees with an initial lean become progressively inclined over the years and during severe gales many fall, opening the canopy. Particularly widespread wind-blows occurred twice between 1967 and 1973.

Petrel trampling deters seedlings from becoming established in the forest: they survive mainly where burrow densities are low or where young plants are protected by logs. The forest floor is bared of dead leaves and small twigs because these are carried underground to line the nest chambers (Fig. 1) and the forest floor comes to 'resemble an extensive poultry run' (Fineran 1964). Among the tussocks these effects are less obvious, though here too there is little leaf litter and the tussock pedestals tend to become unstable owing to the burrowing. Other petrels, e.g. *Pterodroma inexpectata* are also involved, particularly among *Poa astonii.*

Active cropping of the ground vegetation by the shearwaters, which tear off beakfuls of leaves for nest linings, also inhibits plant growth. Presumably seedling trees receive similar treatment.

THE ANNUAL CYCLE

The annual cycle of a typical breeding pair is summarised in Fig. 2. The records of the 1971/73 expedition show that the bulk of the shearwaters returned in the last two weeks of September (Horning & Horning 1974). There was a decline in numbers ashore from late October to mid-November, marking an exodus lasting about 14 days, followed immediately by egg laying. Between 1968 and 1970, two-thirds of the eggs appeared between 20 and 24 November. Incubation took 53 days and two-thirds of the eggs hatched between 11 and 16 January, mean date 13 January. Chick rearing continued until about the third week of April in 1972, by which time the adults had left. Most chicks departed between the last week of April and the first week of May.

From late April to mid-September these shearwaters are mostly absent from New Zealand seas while undertaking their contra-nuptial migrations to the North Pacific Ocean, crossing the Equator in both directions in high-speed flights. They moult on their wintering grounds in the northern summer.

Two recoveries show that Snares Island birds participate in this movement. Z-5609, a male banded on 25 November 1968 and whose partner laid an egg in one of our burrows that summer, which they failed to hatch, died on a Japanese fishing line on 30 March 1970 at 49°09'N, 175°50'W. It had not been recorded ashore in the 1969/70 season, although it could easily have been overlooked that year and have left early, perhaps once again as a failed breeder. Z-6848, an adult of unknown status, banded on 13 January 1969, died in a Japanese net on 23 August 1969 at 48°45'N, 175°50'W. Both recoveries were south of the central sector of the Aleutian Chain, an area well known for its concentrations of shearwaters (Shuntov 1974).

The prebreeding component of the shearwater population is omitted from Fig. 2. We learnt little about these birds as it was not until 1972 that any chicks were banded. Of 500 fledglings marked that year, at least one was ashore at 3 years old and 13 were resighted in the 1976/77 summer, when 5 years old. None was known to be breeding. Richdale (1963: 76) found one 9-year-old nesting, not necessarily for the first time. With the better known Short-tailed Shearwater, a few 2-year-olds appear on land for about a month, more 3-year-olds stay for about two months, many 4-year-olds for three months (from egg laying onwards) and the prebreeders 5 to 8 years old arrive with the breeders but leave about a month before them (Serventy *et al.* 1971). By analogy, we would have expected a steady increase in the numbers of prebreeding Sooty Shearwaters until about the end of February with a considerable decline in March as they left on their northwards migration.

We have no information on failed breeders but Richdale (1936: 106) found that these birds usually stopped coming ashore soon after their egg or chick was lost.

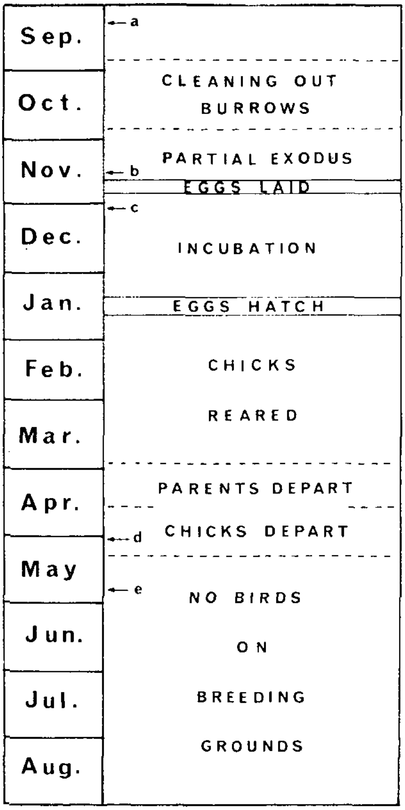

FIGURE 2 — The annual cycle of breeding Sooty Shearwaters at The Snares. a — first birds return (8 Sep.); b — first egg laid (16 Nov.); c — last egg laid (2 Dec.); d — last adult seen (1 May); e — last chick seen (25 May)

THE PRELAYING PERIOD

Our information suggests that for most breeding birds approximately eight weeks elapse between arrival about 25 September and the appearance of the egg about 23 November.

The re-occupation was followed in 1972. On 8 September some burrows were found to have been scratched out. On the evening of 11 September a group of about 50 shearwaters was seen overhead; none was seen on the 12th but 'hundreds' on the 15th and 'thousands' on 18 and 19 September, although none had yet been sighted on the ground. By 22 September about 10% of the burrows had been excavated and by the next day most of those on the east coast south of the Biological Station had been dug out. By 28 September the Hornings estimated that only about 1% of the burrows showed no sign of use.

During this re-occupation period many birds stayed in their burrows by day, when some sang briefly. Others could be stimulated to do so by a footfall, but many returned to sea before dawn and the departure chorus was 'deafening.'

A pre-egg stage of nearly two months (Fig. 2) is much longer than the one month estimated by Richdale (1963: 14) but very similar to the length of this stage in *P. tenuirostris,* another transequatorial migrant which makes its first landfall in the last week of September and has a peak of laying from 19 to 21 November (Serventy *et al.* 1971).

Sooty Shearwater activity, as gauged by numbers overhead in the evenings and by singing volume, declined around the beginning of November, although birds were suddenly very numerous on the dark night of 6 November 1972, three days before a new moon. On 14 November that year the Hornings recorded that the muttonbirds had been strangely silent for about two weeks. On the 17th they were back in strength, landing early in the evening, and by the 23rd the Hornings collected 11 surface-laid eggs from a limited area of ground.

Likewise in 1968 we noted a low level of calling and activity on 15 November, a little more on the 16th, a marked increase on the 17th and still more on the 18th when the first egg for that year was found.

Such prelaying exoduses have been reported for a wide range of procellariiforms (Warham 1964). Often the males tend to remain behind but with some species, of which the Short-tailed Shearwater is the best known example, both breeders and prebreeders dramatically desert the nesting islands to return equally abruptly about three weeks later to lay immediately (Serventy *et al.* 1971).

EGG LAYING

Females carrying eggs and with swollen cloacae were handled on the night of 15 November 1968 but the earliest egg seen was on

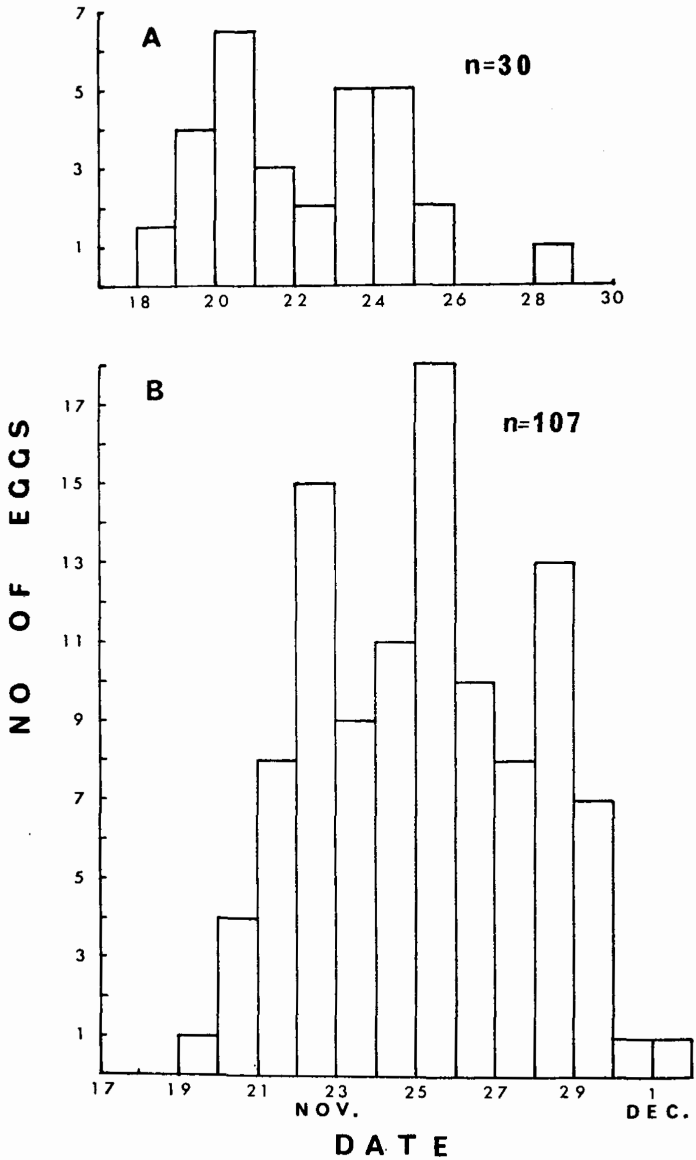

FIGURE 3 — Progress of laying of Sooty Shearwater eggs; A, in burrows; B, on the surface, in 1969 and 1970

17 November 1972. As the last-known laying date was the night of 1/2 December, eggs appeared over at least 18 days. Doubtless there were some earlier and later layings and one bird with a palpable egg was caught on the night of 9 December 1968.

Figure 3A shows the dates of laying of 30 eggs in study nests in 1969 and 1970. In 1969, four burrows already held eggs when we arrived, and their dates of laying have been calculated by subtracting 52.7 days of incubation from their hatching dates (see below). To reduce desertion the nests were examined only once daily, in the morning, and it was assumed that the eggs were laid the previous midnight. The 13 eggs in 1969 were laid on a mean date of 22.7 November and the 17 in 1970 on 21.9 November. The mean date for the whole sample is 22.3 ± 2.4 November, with 66% being laid between 20 and 25 November.

Many eggs were laid on the surface and abandoned and could remain untouched for days before being discovered by gulls or buried by other shearwaters. Such eggs were very obvious on the bare floor of the forest. Fig. 3B shows the dates of laying of 107 surface eggs collected in 1970. They were laid in a 3160 m^2 low-density area (73 burrows/m^2) and in a 2860 m^2 high-density area (106 burrows/m^2), both being within the *Olearia* forest.

The mean dates of laying in the areas of low (25.1 November) and high burrow density (25.3 November) were almost identical, and the mean for the whole sample of 25.23 ± 2.80 November was nearly three days later than the mean for the 30 burrow-laid eggs in 1969 and 1970 of 22.27 ± 2.39 November. The difference is highly significant (t = 4.870 and $P < 0.001$), suggesting that birds that laid on the surface did so later than those laying in burrows.

We found no surface eggs in the few areas where the soil was waterlogged or shallow and unburrowed: the birds laid on the surface only where there were occupied burrows. On the other hand we found that such birds were not attracted preferentially to places where nests were most concentrated because in the low-density area 1.84 eggs/m^2 appeared and in the high-density area 1.92/m^2 — an insignificant difference of only 4% as against a 45% increase in burrow density.

If the areas we sampled were typical of the 147 ha of forest on Main Island, then some 27 000 eggs were surface-laid there in 1970. Surface eggs were also laid among the tussock but were difficult to find and we did not count them. There is little information on surface-egg numbers for other shearwaters populations. Richdale (1963) recorded the phenomenon in *P. griseus* at Whero Island, but not its extent. Warham (1960) collected 14 eggs of *P. tenuirostris* from 2508 m^2 of tussock (0.56/100 m^2) burrowed at a similar density to our low density area at The Snares.

We believe that some of these surface eggs of *P. griseus* were viable as four out of five showed signs of development after artificial incubation for 72 hours by Snares Crested Penguins *(Eudyptes robustus)*. However, in the only other study we know of to check the viability of surface eggs, Naarding (1980) found that those of *P. tenuirostris* were sterile, whether incubated in an incubator or when exchanged for burrow eggs and incubated naturally. Only on two occasions did we see adult shearwaters incubating surface eggs by day and both soon deserted.

Richdale (1963: 17) calculated that the peak of laying at Taieri Island, Otago, occurred about 29 November in 1943 and, assuming an incubation period of 56 days, found that this agreed with his hatching dates from Whero Island. Using our more precise figure of 53 days' incubation, the mean laying date for Whero Island would be 26 November, some four days later than burrow-laid eggs at The Snares.

EGG SIZE AND SHAPE

In Table 1 the dimensions and shapes of freshly-laid Sooty Shearwater eggs measured at The Snares are summarised. Figures for the statistic length $\times$ breadth squared (both measured in cm) are also given because these provide a useful check on egg size because weight $= k\ LB^2$, where k is a constant for the species. In the three samples weighed the mean values of k were 0.548, 0.548 and 0.551. Also listed is the mean shape index, B/L $\times$ 100, a measure of the roundness of the egg, a sphere having an index of 100. *P* values are from standard error tests. The eggs were collected throughout the laying period but the burrow eggs did not come from the same nests in 1968/69 and 1969/70 nor was sampling restricted to particular areas.

The table also includes Richdale's figures for Whero Island (Richdale 1963: 19), where few eggs were laid on the surface. He pointed out that if their mean breadth was significantly narrower than those of eggs from burrows, surface layers were probably young birds. Serventy (1967) showed that eggs of Short-tailed Shearwaters breeding for the first time were longer and narrower than those laid by older birds, that mean breadth increased up to the sixth or seventh breeding season and that, in a sample of 52 surface eggs, the mean breadth was significantly less than the mean of a random sample from the burrows. He concluded that the surface eggs were very probably laid by young inexperienced birds.

Our figures for 1968/69 did not fit this pattern, neither mean lengths nor mean breadths being significantly different in the two samples. Rather, the surface eggs averaged slightly larger (higher LB^2). although they were a little longer (lower shape index).

The 1969/70 data conformed with Serventy's findings. The burrow eggs were on average significantly broader, larger and heavier than those from the surface, suggesting that the average breeding experience of those laying on the surface that year was less than that of those with burrows. Maybe the difference between the 1968/69 and 1969/70 samples reflected a changed age-composition in the surface-

TABLE 1 — Dimensions of surface and burrow laid Sooty Shearwater eggs. (coefficients of variation in parentheses)
P values show results of tests for differences between means for surface and burrow eggs.

Year	Where laid	n	Length ± 1 S.D. (cm)	Breadth ± 1 S.D. (cm)	LB^2 ± 1 S.D.	n	Weight ± 1 S.D. (g)	Mean Shape Index
1968/69	Surface	50	7.69 ± 0.30 (3.94)	4.91 ± 0.17 (3.42)	185.7 ± 14.3 (7.69)	50	101.76 ± 7.99 (7.85)	63.90
	Burrow	53	7.60 ± 0.39 (5.18)	4.92 ± 0.17 (3.42)	184.1 ± 17.2 (9.33)	-	-	64.68
	P		n.s.	n.s.	n.s.			-
1969/70	Surface	81	7.68 ± 0.30 (3.91)	4.88 ± 0.17 (3.48)	183.2 ± 14.8 (8.10)	74	100.38 ± 7.80 (7.77)	63.50
	Burrow	77	7.70 ± 0.29 (3.83)	5.00 ± 0.13 (2.52)	192.3 ± 12.7 (6.63)	32	105.88 ± 7.40 (6.99)	64.92
	P		n.s.	<0.001	<0.001		<0.001	
1972	Surface	100	7.62 ± 0.28 (3.72)	4.93 ± 0.31 (6.33)	185.9 ± 28.4 (15.30)	-	-	64.68
Richdale (1963: 19)	Burrow	72	7.74 ± 0.29 (3.75)	4.83 ± 0.18 (3.73)	180.57	25	95	62.40

layers sampled in those years, the 1969/70 eggs being significantly broader ($P < 0.001$) and bigger ($P < 0.001$), which may mean that there were more old birds or better food in the 1969/70 season.

The mean dimensions of the three samples of surface eggs are not statistically different, but the 1972 eggs were rather variable in breadth. This was unexpected as all were laid before 27 November and the youngest birds, the most likely group to lay very narrow eggs, would be expected to be among the last to lay.

Eggs measured by Richdale were smaller (low LB^2) and more elongated (low shape index) than ours. His mean weight of 95 g also seems low but it was based on 25 fresh eggs, not those of his larger sample of 72. If we applied a k value of 0.549, an egg of his mean dimensions would weigh 99 g.

INCUBATION

The roles of the sexes during incubation were difficult to unravel owing to the bird's sensitivity to disturbance. To reduce desertions we examined study burrows every other day and so our data are few and rather imprecise.

Some females left before dawn on the night they laid but others spent one or even two days with their egg before leaving the male to incubate. From 10 nests inspected every two days in 1968/69 the mean length of 32 incubation spans was found to be 9.4 days. Only two of these (3 ± 1 and 4 ± 1 days respectively) were less than eight days long. While some changeovers may have been missed by not making daily inspections, the lack of any two-day stints implies that unrecorded short spells did not occur. Eleven stints by banded males averaged 9.45 ± 1.3 days and 12 by banded females 9.58 ± 2.7 days, and so the lengths of stint by the partners were similar. Changeovers took place at night and only twice were two birds together by day.

We saw little temporary desertion. Eggs left uncovered usually failed to hatch. Several incubating birds fled their burrows during daytime checks. Their partners often resumed incubation one or two nights later, and it seemed that desertion was most likely when the on-duty partner's relief was overdue. Only one temporarily deserted egg hatched: the desertion occurred one week before hatching and lasted one day only. It should not be concluded that Sooty Shearwater eggs are not resistant to chilling: failure to hatch re-incubated eggs seemed to be largely due to the reluctance of the deserting partner to resume duty.

Our meagre data suggest that a typical female put in two, and her mate three long stints, with either in charge of the egg at hatching.

During the 1969/70 and 1970/71 seasons the time between laying and hatching at nine nests, determined to within one day, was 51.5 days for one egg, 52.5 days for five eggs, 53 days for two eggs and 54.5 days for one egg. The mean incubation period was 52.7 days.

HATCHING

Hatching success in the study burrows was low. In 1970 checks were made once daily and 58% of the 19 eggs laid hatched, but in 1971 when checks were made twice daily to get more precise information, only 33% of the 18 eggs laid hatched. These losses were certainly abnormal, a consequence of the disturbance necessary to establish that hatching had occurred. Without better techniques such losses seem inevitable and the effects of disturbance have also been experienced with supposedly insensitive petrels: in the Manx Shearwater *(P. puffinus)*, Harris (1966) found that hatching success fell from 78% to 59% owing to handling.

In 1971 the mean date of hatching for seven eggs whose laying dates were known to within eight hours was 14.4 January and the mean date of hatching of 28 eggs laid in 1967, 1970, 1971 and 1972, most of whose dates of laying were known only ± 1 day, was 12.9 January, range 7 - 18 January. Some eggs doubtless hatched before and after these dates.

We had no evidence that the spread of hatching varied between years, nor did Richdale (1963: 24) find differences between seasons from 257 hatching dates collected over five years. Yet his mean date of hatching was 24.1 January ± 4.2 days, range 16 January to 4 February, some 11 days later than we found at the Snares Islands only some 175 km to the south. This difference is greater than the apparent 4-6 day difference in laying dates between the Snares birds and those calculated for Taieri and Whero Islands. Richdale also thought that a Sooty Shearwater chick he found at The Snares on 13 January 1948 was an early hatchling, whereas it was born at the peak of the hatching period found by us.

Seven eggs were closely followed from the time the first crack in the shell appeared. After this, one chick took 5 days, three took 4 days and three took 3 days to break free, the mean time being 3.7 days. From a sample of ten chicks the time elapsing between hatching and loss of egg tooth varied from 5 to 23 days with a mean of 16 days.

THE CHICK

We were unable to follow growth in detail for comparison with the very full particulars provided by Richdale (1963: 26-55) but some new information on the early stages was obtained, partly because we could sex our parent birds, which Richdale did not do.

In 1969 nine chicks were weighed daily from the day they hatched until late February. Table 2 shows the attentiveness of parents for the first 15 days for comparison with Richdale's Table 24 (1963: 47). Our birds showed a greater tendency to stay with their chick by day than his did, for his parents were rarely present after the third day. A parent was with most of our chicks up to their fifth day and lone parents even stayed ashore with 16- and 21-day-old chicks.

Table 2 also shows the frequency with which the nine chicks were fed. Presumably they had also been given a meal before our first weighing, as found by Richdale. All were fed almost nightly during their first five days and after day 1 received meals, on average, on at least eight of their first 14 days. The incidence of fasting increased as they grew. (The longest time that a chick went without food was seven days.)

The six chicks still alive when weighing ceased at 40 days had not reached the weight plateau that Richdale reported in about the 7th week. Nevertheless, four were above the mean adult weight of 819 g by the time they were 38 days old.

As Richdale found, some 20-30-day-old chicks received gargantuan

TABLE 2 — Attentiveness of Sooty Shearwater parents with chicks 1-15 days old*

Age of chick (days)	Nest no. 1	2	3	4	5	6	7	8	9
1	A	A	A	A	A	A	A	A	A
2	NF	F A	F A	F A	F A	F	F A	F	F A
3	F	F A	F A	F A	F	F	?	?A	F A
4	F A	F A	NF	NF	?A	F	F A	F A	F A
5	F A	F A	F A	F A	F A	F A	NF	F	F
6	?A	F	?	NF	F	NF	F A	NF	NF
7	F A	NF	?	F	?	NF	NF	F A	F
8	NF	F	?	F	F A	F A	NF	NF A	F
9	F	NF	F A	NF	NF	NF	F	F	NF
10	F	NF	NF	F	F	NF	NF	F A	NF
11	F	F	?	F	?	F	F	F A	F A
12	F	F	F A	NF	NF	NF	NF	F	NF
13	F	NF	NF A	?	NF	NF	F	F	F A
14	NF	NF	F	?	F	F	F	NF	NF
15	NF	F	NF	?	NF	F	NF	F	F

* c.f. Richdale 1963, Table 24: 47.

F = chick fed since previous day. NF = chick not fed since previous day.
A = adult present by day. ? = not determined if chick fed.

TABLE 3 — Weights of Sooty Shearwater chicks at weekly intervals according to age.

Age (days)	Richdale's 'heavy' chicks[1]			The Snares 1969		
	n	Mean wt (g)	Range (g)	n	Mean wt (g)	Range (g)
1st to 7th	50	113	70-187	42	128	55-240
8th to 14th	54	202	95-321	42	247	130-445
15th to 21st	215	367	147-670	41	380	220-555
22nd to 28th	231	561	245-915	42	513	260-750
29th to 35th	231	617	310-915	39	645	380-880

[1] From Richdale 1963, Table 12.

meals, almost doubling their weight overnight. One 26-day-old chick increased from 460 to 705 g overnight and a 29-day-old from 360 to 715 g. Our chicks grew rather faster during their first 40 days than Richdale's 'heavy' chicks at Whero Island — Table 3.

Table 4 shows the results of day and night inspections of two nests for the chicks' first 36 days of life. At both nests the male was on duty with the newly hatched chick. Thereafter, although either parent came in after dark, there was a tendency for the same bird to visit for two nights in succession. The female at nest 8 was present by day on days 3 and 4 and by night from day 2 to day 6 inclusive. Here and at some other nests the alternate-shift system of incubation seemed to be carried over into the early part of chick rearing, as suggested for *P. tenuirostris* (Serventy 1967: 171). At nest 8 there was some overlapping of parental visits on the night of day 9. Nearly all visits occurred before midnight.

ADULT DEPARTURE

Richdale (1963: 51) established that adult Sooty Shearwaters leave the nesting colonies before their chicks. On average, 58 'heavy' chicks, the only ones that he thought likely to survive, were deserted for 11.9 days, 25 'light' chicks for 21.0 days, the total range being 0-27 days.

We were unable to follow marked chicks but the Hornings' notes for 1972 suggest that by 10 April most adults had left; on that date only about 200 birds took off from a rock used nightly by many thousands earlier in the season. After 29 April no shearwaters were seen overhead at dusk and on 30 April the take-off rocks were almost deserted. The last adult identified that season was seen on 1 May (not 17 May as stated in Horning & Horning, 1974). This was a bird banded on 17 January 1967.

CHICK DEPARTURE

In 1972 chicks with wisps of down were first seen on the ground on 21 April and such sightings soon became common at night. Chick weighing started on 15 April with birds still in burrows and continued until 7 May with mostly birds from the surface — Table 5. On that date the last 14 chicks were banded after much searching and it appeared that most chicks had gone. Yet some still remained, for many

TABLE 4 — Roles of the sexes in early care of the Sooty Shearwater chick.

Chick's age (days)	Nest 6		Nest 8		Chick's age (days)	Nest 6		Nest 8	
	Day	Night	Day	Night		Day	Night	Day	Night
1	♂	♂	♂	?	19	-	-	-	-
2	-	-*	-	♀	20	-	-	-	♂
3	-	-*	♀	♀	21	-	-	-	♀
4	-	♀	♀	♀	22	-	-*	-	-
5	♀	♀	-	♀	23	-	-	-	-
6	-	-	-	♀	24	-	♀	-	-*
7	-	♀	♀	?	25	-	-*	-	-
8	♀	♀	♀	?*	26	-	-	-	-
9	-	-	-	♂	27	-	-*	-	-
10	-	?	♀	♂	28	-	-	-	-
11	-	?*	♂	?*	29	-	♂	-	-
12	-	-	-	-*	30	-	-	-	-
13	-	♂	-	-	31	-	?*	-	-
14	-	♂	-	♂	32	-	-*	-	♀
15	-	-*	-	-	33	-	♂	-	-*
16	-	-	-	-	34	-	♂	-	-
17	-	♂	-	♀	35	-	-	-	-
18	-	-*	-	-*	36	-	-	-	-*

♂ = male parent with chick; ♀ = female parent with chick; - = no parent with chick; ? = nest not inspected; * = chick fed but no parent seen.

were dead on the ground on 13 May after a heavy rain storm. The last chick seen on 25 May was fat and healthy.

We were unable to follow marked chicks from birth and so gained no precise data on nestling periods. Richdale (1963: 53) gave a mean nestling period of 97 days, range 86-106 days. That period added to our mean hatching date of 14 January gives a mean fledging date of 21 April, range 10 to 30 April. Our chicks seem to have left later than this, perhaps at dates comparable to those at Whero where chick departure peaked on 2 May, range 19 April to 12 May, but our information is not good enough for certainty.

Departure was a gradual process, unlike the hectic pre-dawn exoduses of the adults at the height of the breeding season. Sometimes, in the early morning before dawn, quite large numbers of chicks were spread out across the tussock slopes beating their wings. There was little jostling for position and departure was orderly and rather cryptic. Occasionally chicks still with down on their bodies were seen to land and so not all fledglings got away on their first flight.

Each of the 500 chicks banded at the end of 1972 season was weighed — Table 5. The April chicks were identified by their residual down. Some were caught on the surface, but the earlier samples were mainly of birds from burrows and probably not yet ready to leave and hence weighing more than they would at departure. The samples in May, whose mean weights varied little from night to night, probably included few birds not within two or three days of leaving. Most were now down-free and so a few late adults could have been included in error, although the last known adult was identified on 1 May.

The grand mean for the 500 chicks was 746 $\pm$ 176 g, about 91% of the adult mean weight of 819 g. Both weights and proportions are greater than those for Richdale's 'heavy' chicks taken from their burrows the morning before their departure. These averaged 622 $\pm$ 100 g. Our samples were more mixed in that many of the chicks would not have left for several days, during which time they would have lost about 30 g daily (Richdale 1963: 52). Similarly, our sample of adult weights, unlike his, were not all known to be of breeding birds. Hence the differences may be more apparent than real.

Another complication is Richdale's finding that the mean weights of departing fledglings varied from year to year owing, he suggested, to variations in the food available to the parents. Stonehouse (1964), in reporting a 'wreck' of young birds in May 1961, also hypothesised that these had fledged underweight as a consequence of food shortage. Lack (1968) wondered whether the sensitive parents could have been put off feeding their young by Richdale's activities, and so weighed less.

The figures in Table 5 do not suggest any decline in fledgling weight towards the end of the season, but the declining proportion of chicks less than 500 g with time suggests either that lightweight nestlings left early and/or that most such had died in their burrows and were not included in the later samples. Partly as a consequence of the decrease of lighter chicks the variability of the later samples was less.

MORTALITY

We have no precise information on the proportion of chicks that died in their burrows of starvation and other factors. Otherwise, bad weather was the only major cause of mortality on land and this affected chicks only.

Thus on 26 January 1970, after 74 mm of rain overnight, many chicks were on the surface beside flooded burrows. Those alive were cold, wet and almost immobile, although capable of reviving when dried out indoors. The mortality in the areas affected was quite high but no precise counts were made. On 13 May 1972 after 51 mm of rain, dead chicks were again plentiful on the ground. Most were now well feathered and evidently deserted by their parents: again, many succumbed.

Some of the chicks exposed in this way were finally despatched by Southern Skuas *(Stercorarius skua)*, particularly during the 1970 flooding, when for the first time significant numbers of skuas were seen below the forest canopy. Far more chicks died of exposure, however, than from skua attack.

TABLE 5 — Mean weights of 500 Sooty Shearwater chicks when banded in 1972.

Date	n	Mean Wt. 1 S.D. (g)	Coeff. of Varn.	Range	% weighing < 500 g
pm 15 April	11	852 ± 216	25.4	494 - 1090	18
pm 21 April	31	707 ± 245	34.7	224 - 1415	16
am 23 April	48	709 ± 165	23.3	266 - 990	8
pm 23 April	29	610 ± 122	20.0	351 - 905	14
am 29 April	51	728 ± 168	23.1	422 - 1018	12
pm 29 April	7	704 ± 219	31.1	394 - 1018	29
am 1 May	24	774 ± 211	27.3	468 - 1178	17
pm 3 May	10	761 ± 155	20.4	506 - 921	0
pm 4 May	41	751 ± 151	20.1	402 - 1112	2
pm 5 May	110	781 ± 158	20.2	446 - 1183	3
pm 6 May	124	756 ± 134	17.7	469 - 1122	2
pm 7 May	14	765 ± 111	14.5	583 - 951	0

am = early morning before dawn; pm = after dark but before midnight.

Adult shearwater carcasses were common in skua middens, particularly on the west coast of Main Island, but we do not know if this was from predation or scavenging. We believe that deaths due to skuas were unimportant, as is indicated by the shearwaters' readiness to land in daylight and to leave after dawn despite skuas flying nearby. No skua:shearwater reactions were seen by us. Red-billed Gulls *(Larus novaehollandiae)* also got some eggs and small chicks from shallow burrows around the Boat Harbour where the gulls nest.

A small but steady source of mortality was the Sinkhole, a collapsed cave about 90 m by 30 m and some 30 m deep. Petrels commonly get trapped here and shearwaters were the commonest victims, their high wing-loadings preventing their flying out. On 30 January 1967 six exhausted shearwaters were rescued but 12 newly dead, one weighing 1030 g, were also collected. The total effect of such accidents must be quite minor, and even less important were the few occasions when adults died after being trapped in the branches of trees while trying to land.

Ectoparasites were not known to have caused deaths. About half of the chicks on the surface after the rains of 25 January 1970 carried one or more examples of the large blood-sucking leech *Ornithobdella eduntula,* whose activities could have contributed to the chicks' deaths. This leech was usually attached to the feet and webs, occasionally to the neck. In 1969 ticks were noted on the chicks' feet at about 14 days old, up to five being attached to the webs of one foot. The numbers generally declined as the chick grew. Such infestations varied from year to year and none was found on chicks in the 1971/72 and 1972/73 seasons during careful checks for ectoparasites. The only tick identified from the islands is *Ixodes auritulus zealandicus* Dumbleton.

DISCUSSION

That the Sooty Shearwater deserts its chicks for about 12 days implies that it is under some pressure to begin its long migration. At the end of this it undergoes its post-nuptial moult. Nonetheless, the breeders spend a long time at or around the nesting places. At The Snares the time between the first arriving adult and the last departing chick (8 September to 25 May) spans some 260 days but a typical breeder arriving on 25 September and leaving on 10 April will have spent about 6½ months in the area.

The breeding Short-tailed Shearwater, another migrant to the North Pacific, has a timetable closely paralleling that of the New Zealand bird, typically arriving about 28 September and leaving about 10 April (Serventy 1967).

In comparing the birds at Whero and The Snares, it will be noted that the former were smaller birds and laid smaller eggs. One of several explanations for this could be that the Whero colony included a higher proportion of young birds, which would be expected to lay smaller eggs and at later dates. Their food supply too may have been less reliable or accessible, and in any case the Whero colony seems not to have been well established and in due course the whole colony was eliminated by Stewart Island Shags *Phalacrocorax carunculatus* (Richdale 1963: 72).

Our information on the timing of the breeding cycle compared with that of Richdale suggests that laying was about four days earlier at The Snares than at Taieri Island and hatching was some 11 days earlier than at Whero, and yet The Snares' chicks appear to have fledged later. As Richdale had no precise dates of laying and we have no precise dates of fledging, the apparent differences may not be real: nevertheless, mean hatching dates do seem to be significantly different. Note that the range of dates for our small sample (7-18 January) lies almost completely outside that of his 257 hatchings (16 January - 4 February). Because it is unlikely that there were differences in the incubation periods at the two sites and no indication that the Whero birds incubated intermittently, it seems probable that they did lay appreciably later than ours at The Snares. Also there are vast high-density colonies there, whereas the Whero colony was small. It could have contained a higher proportion of inexperienced breeders than ours. The small, rather narrow eggs laid on Whero (Table 1) may also be the result of a younger population. Perhaps with less competition for nest sites, and thus less selective pressure to lay early, later laying at Whero would be expected.

Information on the Sooty Shearwater's breeding timetable elsewhere in New Zealand is meagre. Oliver (1955) averred that the patterns are the same throughout the country, apparently following Falla (1934).

We can find very little data for the more northerly populations. According to Sandager (1890), eggs were laid at Mokohinau Island (36°S) from the beginning of December to mid-January, the young left in mid-April and all had gone by the end of May. His laying dates seem very imprecise. A November to early December laying period was deduced for the Alderman Islands' population at 37°S by Sladden & Falla (1927). Eggs were being laid at Hen Island on 28 November 1962 (P. C. Harper, pers. comm.). Further south in Cook Strait, New Zealand Banding Scheme records show that adults were ashore on The Trios by 3 October in 1963 and on Stewart Island (French Pass) by 9 October, with a bird banded on Stephens Island on 1 October that year being recovered off California on 26 August 1965 (Robertson 1972).

At Mangere Island in the Chathams Group (44°S), ten adults were banded on 8 and 10 October 1973, while hatching had been first recorded on 15 January in 1923 (Archey & Lindsay 1924). Elsewhere in the Chathams fresh eggs were being incubated on 1 December 1937, none had hatched that year on 31 December, and the chicks were traditionally harvested in March and April (Fleming 1939).

Further south in Foveaux Strait on Herekopere Island during 1911 and 1912 Guthrie-Smith (1914) found no eggs on 22 September or on 2 October, although on the latter date the birds were calling ' perhaps in hundreds.' This author noted that the Stewart Island mutton-birders believed that all the eggs were laid on 25 November each year. At Cundy Island, also in Foveaux Strait, some eggs were laid by 3 December in 1931, and further south on Solomon Island, the first was found on the night of 28/29 November that year (Wilson 1959).

Filhol (*in* Westerskov 1960) found birds on fresh eggs at Campbell Island (52°S) on 15 November 1874. Sorensen, at the same island, noted birds ashore on 16 October 1959, cleaned-out burrows on 18 October 1942, cleaned-out empty burrows on 30 October 1942 (perhaps during the prelaying exodus?), birds in burrows without eggs on 26 November 1943 and birds incubating on 7 December 1942 (Bailey & Sorensen 1962).

At the most southerly station in the New Zealand region, Macquarie Island (55°S), where the species is not common, our earliest definite record is of a bird in a burrow on 8 October 1960. It lacked a brood patch. On the previous day displacements of fenced entrances to Sooty Shearwater burrows and red faecal splashes nearby showed that the birds had recently arrived (Warham, pers. obs.). As far as it goes this information tends to support Falla's statement that breeding dates at Macquarie Island do not differ from those at places nearer New Zealand, and overall, the information summarised above does suggest that there are no major differences in the timetables of this species around the country despite the small variation between The Snares and Whero Island.

Precise information on the breeding season in Australia is also not available. Rohu (1914) took a bird and egg from a burrow on Broughton Island, NSW, on 29 December 1912. An adult and small chick (43 g) were found in a burrow on Lion Island, NSW, on 2 February 1947 (Keast & McGill 1948). Fullagar (1976) stated that the birds were present at Cabbage Tree Island, NSW (33°S), 'from September' and Lane (1965) and Robinson (1964) found eggs on Bird Island, NSW, and Courts Island, Tasmania, on 12 December 1963 and 28 November 1961 respectively. None of this information suggests any marked deviation in timing from that of the New Zealand populations.

The earliest date for the South American populations appears to be R. H. Beck's record of an irregular but steady southwards flight of Sooty Shearwaters off Cape San Diego (55°S) as early as 6 August 1915 (Humphrey *et al.* 1970) — compare sightings of this shearwater off Bald Head, south-western Australia on 9 August 1973 (Fullagar & van Tets 1976). Beck found well-incubated eggs at Wollaston and Deceit Islands on 28 December 1914 and early January 1915 and 'very hard set' eggs were collected on 22 December at Bayly and Wollaston Islands (Murphy 1936: 670).

Better information is available from the Falkland Islands, to which the birds return by the end of October (Cawkell & Hamilton 1961). Fresh eggs were found on 24 November 1961, adults had gone by 8 April 1961, fully feathered nestlings were in burrows on 16 April 1962 and the last chick was seen on 3 May 1962 (Woods 1975). Woods concluded that the breeders arrive in mid to late October and leave towards the end of March, the fledglings following in the first week of April.

Taken as a whole, therefore, the evidence suggests that the timetables of all these populations are rather similar despite being spread over 23 degrees of latitude and 147 degrees of longitude. The birds too are alike; no subspecies is recognised and it is not possible to separate a South American Sooty Shearwater from an Australasian one on external morphological characters. For example, a sample of 28 live birds measured in the North Atlantic by Brown *et al.* (1981), and presumably of South American origin, weighed 816 $\pm$ 87 g — virtually identical with ours from The Snares.

Despite similarities in the annual cycles and breeding of Sooty and Short-tailed Shearwaters, there is one notable difference between them: the former has only a partial but the latter a total prelaying exodus. Serventy (1967) showed that the exodus of Short-tails includes both breeders and the older prebreeders of both sexes. We do not know what categories of the Sooty Shearwaters leave, i.e., whether the females alone are involved, nor how far they go. If the males alone remain, as with petrels such as *Pachyptilla desolata* (Tickell 1962), it is surprising that Main Island was so quiet during the exodus. One obvious advantage of staying would be to allow the males to defend their nests from usurpation by others, and defending shearwaters usually call vigorously before attacking.

Tickell (1962) postulated that the exodus is needed so that the female can feed while making her large egg, which must be a considerable drain on her resources. In small petrels it may weigh more than 25% of the female's body weight; in *P. tenuirostris* and *P. griseus* it represents 16% and 13% of that weight respectively. Using his yolk-marking technique (Grau 1976, Roundybush *et al.* 1979), C. R. Grau has estimated that yolk formation in Buller's Shearwater *(P. bulleri)* takes about 18 days (pers. comm.). This makes even more understandable the need to feed while building the egg. That the females are indeed under stress is suggested by their prompt departure after laying, leaving the males to perform the first long incubation stint.

Large size being more conducive to energy conservation, *griseus* (819 g) may need to feed less than *tenuirostris* (560 g) to acquire the same proportional reserve of energy. Likewise the female *tenuirostris,* although smaller, produces a proportionately larger egg. She may need longer to acquire the necessary energy stores and/or may have to depend on richer and perhaps more distant food supplies than *griseus.* We do not know how far the average Sooty Shearwater goes for food during the exodus, and we have often seen them feeding close inshore at The Snares (see also Fenwick 1978), but it is known that Short-tails may collect food for their chicks 1600 km from their nests (Serventy 1967). According to Shuntov (1974), these birds penetrate further north into the Bering Sea than do Sooty Shearwaters, and so Short-tails may also favour colder, more distant feeding grounds when nesting.

Another possible reason for the difference in the patterns of exodus in these two birds may be differences in the length of the males' first incubation spans. A Short-tail typically fasts for 12.6 days (Serventy 1967), our Sooty Shearwaters for about 9.5 days. Thus, while the female Sooty Shearwater may need to feed for a full two weeks, and could travel far in that time, a shorter feed in more local waters may suffice for her mate who might also even visit his burrow occasionally and still lay down enough fat to sustain his first incubation stint. The Hornings' observation of a marked increase in night-time activity on 6 November 1972 may have been due to a temporary return of such males. In contrast, the male Short-tailed Shearwaters may have to feed longer to lay down the bigger reserves needed for their longer first fasts on the egg. Naarding (1980) hypothesised that they feed in Antarctic seas on krill concentrations revealed by retreating pack-ice.

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SHORT NOTE

SOUTHERN SKUA IN WELLINGTON HARBOUR

On 26 June at 0830 when off Point Halswell, Wellington Harbour, I saw a Southern Skua *(S. skua lonnbergi)* flying around the ship. The wind was SSW 35-40 knots, and there were heavy passing rain squalls. It is probable that the bad weather had forced the bird into the harbour, where Southern Skuas are rarely seen.

JOHN JENKINS