THE AUK
A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 94 JANUARY 1977 NO. 1

BREEDING OF THE MOTTLED PETREL[1]

JOHN WARHAM, BRUCE R. KEELEY, AND GRAHAM J. WILSON

ABSTRACT—The Mottled Petrel, *Pterodroma inexpectata*, a breeding bird restricted to New Zealand that migrates to subarctic seas, was studied on the Snares Islands at 48°S, 167°E during four summers. This bird avoids inshore waters and on land shuns the light, visiting its burrow only after dark. It rears a single chick in the austral summer. Aspects of vocalizations and displays are described and figured; they resemble those of some other congeners like *P. lessoni*. Adults begin to return to the nesting island in late October and the last chicks depart in early June. Nest sites and partners tend to be retained from year to year. There is probably a pre-laying exodus. The period during which eggs are laid is curtailed and two-thirds of them appear between 15 and 22 December. Incubation is shared fairly equally by both partners in stints of 12 to 14 days and lasts about 50.5 days. The chick is brooded for up to 2 days and thereafter is fed at intervals by both parents. During the first 3 weeks fasts are rather short, between 1 and 3 days long; no data were gained on the later stages of chick rearing but the chicks are believed to fledge when 90 to 105 days old. These petrels have few enemies on land apart from skuas and in small samples of breeding adults the minimum annual survival was from 67% to 76%.—*Zoology Department, University of Canterbury, Christchurch, New Zealand*. Accepted 8 May 1975.

THE Mottled Petrel, *Pterodroma inexpectata* (Frontispiece), also known as the Scaled or Peale's Petrel, is a medium-sized gadfly petrel about 350 mm long with a wingspan of some 825 mm. It breeds only in the New Zealand region during the southern summer, nests in burrows or rock crevices, and comes ashore after dark. Its summer range extends south to the pack ice but the bird is a transequatorial migrant, wintering in the subarctic North Pacific Ocean.

General accounts of the petrel are to be found in Bent (1922), Oliver (1955), Palmer (1962), Falla et al. (1966), and Serventy et al. (1971). Field notes were published by Stead (1932), Richdale (1964), and Warham (1967b), and data on birds seen and collected at sea by Falla (1937). Migration was discussed by Palmer (1962) and King (1967, 1970), while Watson et al. (1971) plotted records from the southern ocean.

The species' breeding places today are rather inaccessible and the bird has been little studied.

Our account results from fieldwork at the Snares Islands (48°S, 167°E) during four University of Canterbury summer expeditions: 17 January to 13 February 1967, 14 November 1968 to 25 February 1969, 20 November 1969 to 19 February 1970, and 18 November 1970 to 11 March 1971. We always had to leave before chick rearing was completed, so that our observations covered only a part of the breeding cycle.

[1]University of Canterbury Snares Islands Expeditions, paper No. 21.

Mottled Petrel in night flight over breeding place; note underwing pattern and gray band on body between wings.

METHODS

Numbered pegs were used to mark 54 study nests. Inspecting them was easy as most access tunnels were only about 1 m long and the sample was probably a random one, although we did ignore nests on dangerous slopes.

In the 1968–69 season one bird of each pair was marked with a stainless steel band supplied by the New Zealand Banding Scheme. If possible the other partner was not handled, but a temporary paint mark was dabbed on its forehead. In the 1969–70 season the unringed partners were banded, the females on the right leg and the males on the left. We have no evidence of band loss, and few instances of nest desertion probably attributable to our activities.

Attentiveness at nests was gauged by direct observation of the marked birds and by the displacements of thin wires set across the burrow entrances. Sexing was by cloacal examination around the time of laying or by palpating shelled eggs in the females. Measurements were made with vernier calipers and weights taken with spring balances; weights above 200 g were accurate to ±10 g, those below 200 g to ±1 g. Measurements are given, where applicable, ±1 SD. The birds' voices were taped on a Grundig TK6 recorder and a Grampian DP4 microphone (without a parabolic reflector) and tapes analyzed on a 6061B Kay Sona-Graph using a narrow band-pass filter. Times given are in New Zealand Standard Time based on the 180° meridian.

BREEDING DISTRIBUTION

This petrel breeds only within the New Zealand region. The main colonies today seem to be on islands around Stewart Island and at the Snares Islands about 110 km to the southwest. The disappearance of the birds believed to have bred in the mountains of both North and South Islands of New Zealand (Stead 1932, Falla 1934) was ascribed by Stead to firing and clearing of the forests and to predation by introduced mammals. The recovery of a Mottled Petrel well inland in 1962 revived the possibility that some may still breed in North Island mountains (Edgar 1972a). We know little about the population that breeds at Stewart Island, but one of us (G.J.W.) saw about 20 burrows on a small unnamed island at Islet Cove, Port Pegasus in 1974. A bird with an egg laid since 2 December was found in a burrow there on 16 December. Petrels were also heard calling on the wing from nearby Ernest Island and elsewhere in Port Pegasus. The only recent reports from the Fiordland coast of South Island refer to nesting at the Shag Islands in Dusky Sound in 1972 and 1973 (Edgar 1972b, 1973). Birds with voices similar to those of Mottled Petrels were heard at night over Big Solander Island in western Foveaux Strait in January and February 1973 (Wilson 1973) suggesting that the species may breed there.

The Mottled Petrel supposedly bred at the Bounty Islands (Oliver 1955), but no recent reports are available and it appears to nest neither on the Auckland Islands (B. D. Bell pers. comm.) nor on Antipodes Island (Warham pers. obs.) as formerly thought. It may also have bred on the Chatham Islands, where bones apparently referable to *P. inexpectata* were found in subfossil deposits (Bourne 1967).

The breeding habitat.—The Snares Group consists of Main Island (280 ha), Broughton Island (48 ha), both with numerous off-lying stacks and islets, and a group of large, almost bare stacks known as the Western Chain (maps in Warham 1967b, Fineran 1969). The plants and animals have largely escaped modification by man and there are no introduced mammals. The islands are classified as a "Reserve for the preservation of flora and fauna," the highest class of protection available within the New Zealand reserves system, and unauthorized landings are illegal.

The Snares experience frequent gales as they lie in the west wind zone. Only in 1972 were a full year's meteorological data collected. The annual rainfall was then about 1100 mm, fairly well distributed throughout the year, and some precipitation occurred

on 301 days. Heavy rain and hail are quite common and mists frequent. Temperatures ranged from −0.8 to 19.8°C in 1972, the yearly mean being 10.8°C. It was seldom warmer than 12°C.

Main and Broughton Islands are composed of granite, mostly overlaid by deep peat, which in turn is covered by grass and forest. Nesting sites for Mottled Petrels are plentiful. Some of the offshore stacks have crowns of tussock grass under which Mottled Petrels probably breed, but they are not known to inhabit the islets of the rocky Western Chain.

Main and Broughton Islands carry a forest of *Olearia lyallii* with some admixture, particularly on Broughton Island, of *Senecio stewartiae*. Both trees produce an almost closed canopy about 6 m above ground level. Surrounding the forest are lush meadows of dense tussock grasses, notable of 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 large stools up to 1 m across and 1 m high and to form fibrous pedestals with bushy tops and dangling skirts. It covers rock ledges and rocky slopes and often occupies a transition zone between the fully vegetated ground and the almost bare supralittoral zone. *Poa astonii* is particularly plentiful along cliff tops and in other very exposed situations. Another important component of the flora is *Hebe elliptica*, a tough-stemmed, salt-resistant bush growing to 3 m high and forming dense thickets in places outside the forest zone. The Snares Island flora has been described by Fineran (1964, 1969) and its geology and soils by Fleming et al. (1953).

The most abundant petrel here is the Sooty Shearwater, *Puffinus griseus*. This is also a summer breeder and frequently nests cheek by jowl with the petrel, particularly along the tops of the cliffs. The shearwaters' activities keep open most of the ground beneath the skirts of the tussock plants, thus facilitating the movements of other ground-frequenting birds like Mottled Petrels and Common Diving-Petrels, *Pelecanoides urinatrix*.

The nest.—Our study burrows were in three groups on the east coast. One, on Station Point, was mostly on the fringe of the *Olearia* forest and among a mixed *Hebe* and *P. astonii* association; the second, on Seal Point, was on rocky terrain with many nests grouped beneath stunted *Hebe elliptica* scrub; and the third and most important area, was among tussock grassland at "*Pterodroma* Slope," opposite the northern end of Rocky Islet.

Nests or evidence of nesting by Mottled Petrels were found in many parts of the *Poa astonii* belt on Main and Broughton Islands. Some burrowed under *Poa tennantiana*, but most of the petrels avoided the central forested zone. Nesting probably occurs on most of the stacks crowned with *Poa astonii*. One of us (G.J.W.) found that the tops of the larger of the two Daption Rocks and of Rocky Islet were extensively undermined by burrows of a similar size to those of *P. inexpectata*. Skeletons of that bird were found, but none of *Puffinus griseus*, nor any sign of their larger and distinctive burrows.

Mottled Petrel nests occurred in a wide variety of situations, in rock crevices and caves, in burrows below tree roots and tussocks, and at elevations of between 10 and about 130 m above sea level, but most nests were in contact with rock, which usually formed the roof or walls of either the tunnel or the nesting chamber.

In some areas nesting densities were quite high, e.g. on the offshore stacks referred to above. A single *Poa astonii* plant that toppled underfoot concealed 3 *inexpectata*

nests with eggs within a space of about 1 m^2. Many nests were in rock crevices and often Fairy Prions, *Pachyptila turtur*, shared such retreats, occupying the smaller crannies. In rather deep vertical clefts between boulders, nests were sometimes visible from above, but we did not find that these were relatively common as Richdale (1964) reported. Most nest chambers were in near darkness, while some poorly concealed entrances were blocked with grass or other local vegetation. This habit has been noted with other members of the genus *Pterodroma*, e.g. *macroptera, lessoni, pycrofti* (Warham 1956, 1967a; Bartle 1968).

The access tunnels were narrower than those of Sooty Shearwaters and often barely admitted one's hand. Most were driven more or less horizontally for about 1 m into a slope and ended in an enlarged nesting chamber, often where the tunnel encountered the rock. The chambers were shallow hollows liberally strewn with grasses and most were rather well drained. Mottled Petrels probably crop the *P. astonii* leaves with their bills, as plants near to the entrances were sometimes heavily grazed, but while we saw Sooty Shearwaters do this, we never saw the more timid Mottled Petrels doing so.

The annual cycle.—Our visits were in midsummer so we missed the start and end of the breeding cycle. The 1971–73 University Expedition spent 13 months at the island and saw no sign of these petrels during the winter until a flying bird called on the night of 24 October. A few days later a burrow known to be of this species had been cleaned out (D. S. Horning pers. comm.). A long pre-egg stage followed, as we found the peak of egg-laying to occur about 19 December. The peak of hatching was about 7 January. In 1972 the Mottled Petrels called overhead until mid-April (Horning and Horning 1974). According to Stead (1932) chicks are ready to fly from the Snares Islands in the first week of May. In 1972 most chicks appeared to have left in May, but one left on 2 June and the last disappeared on 8 June. The birds appear to be away from this breeding station for about 18 weeks, almost exactly the same period as with the Short-tailed Shearwater, *Puffinus tenuirostris*, which undertakes a circulatory migration around the Pacific Ocean (Marshall and Serventy 1956).

MEASUREMENTS

Measurements of sexed museum specimens were given by Loomis (1918) and by Murphy and Pennoyer (1952). Richdale (1964) measured 88–100 live birds of unknown sex or breeding status from Big South Cape Island (near Stewart Island), many with brood patches. The mean weight of 89 was 316.2 ± 32.1 g (247 to 441 g). A similar sample of 42 Snares Island birds on 13 and 14 January 1969 had a mean weight of 329 ± 31.2 g). Mean measurements of 20 unsexed but recently killed birds at the Snares Islands were wing 253.3 ± 9.7 mm, tail 102.7 ± 3.7 mm, bill length 26.8 ± 1.2 mm, tarsus 35.5 ± 1.9 mm, midtoe and claw 45.9 ± 1.8 mm.

ACTIVITY AT SEA

We never saw Mottled Petrels at sea from the island by day, though they would have been easily identifiable had they come within sight range. Nor did we see these birds close to the Snares during our various passages to and from the islands except on a return trip to the mainland on 4 December 1969. Mottled Petrels then appeared about 19 km northwest of the island and became quite plentiful for the next few kilometers with many birds resting on the sea. This being only about a week before egg-laying,

these could have included breeders on a prelaying exodus (see below). We also encountered Mottled Petrels fairly plentifully on 2 January 1967 some 80 km south-southeast of the Snares, but the numbers decreased as we approached the islands, and none were seen nearer than about 50 km from the group (Warham 1967b).

At the height of the breeding season Falla (1937) found birds, probably of this species, in the pack ice off Antarctica as far west as 95°E and recorded a flock of 1000 on 23 January 1931 at 64°S, 113°E. This petrel has been seen in the same waters by others—Van Oordt and Kruijt (1953) from 2 to 29 February 1952 logged single birds just north of the pack ice from east of 113°E around to the entrance to the Ross Sea between 160°E and 180° where the birds were particularly common. Evidently considerable numbers of Mottled Petrels occur close to the antarctic circle 2200 to 4000 km south or southwest of the breeding places while incubation is at its height. Most of these may be nonbreeders; could off-duty breeders also have been involved? With off-duty spells of 12–14 days during incubation (see below) they could easily feed 2200 km from their nesting places; birds flying 640 km daily (at 27 km/h) could reach the Ross Sea in 3½ days and have 6 days of perpetual daylight for feeding before returning in time to relieve their partners, wind and weather permitting. Serventy (1967) provided evidence that Short-tailed Shearwaters, whose chicks are fed on average every 9 days, may travel 1600 km to feed.

Activity over Land

Mottled Petrels arrived over land long after the Sooty Shearwaters had alighted. Despite their white underwings the petrels were difficult to see during their nighttime display flights, but many birds called as they flew, and between 19 December 1968 and 13 February 1969 the times when the first call was heard were noted. These data were used for assessing the effects of different weather conditions on arrival times.

No very clear pattern emerged apart from the birds' increasingly earlier arrival with decreasing day length. The overriding influence appeared to be light intensity, the birds being heard about 53 min after sunset (i.e. about 17 min after civil twilight). Birds tended to arrive earlier on nights with heavy rain and mist and later on clear nights, but seldom by more than 10 min either way. As we had no nights when full moon and clear skies coincided, we cannot assess their combined effects on the petrels' arrival times.

Events on the night of 12–13 January 1969 were typical of the incubation period. The sky was clear with a light breeze and the moon in its last quarter rose about midnight. At 2147 the first distant call was heard followed 3 min later by more calls out to sea; by 2157 the calls sounded closer to land. At 2202 the birds were flying overhead and calling, with increasing numbers audible out at sea. Numbers overhead gradually increased and at 2217 we saw the first landing. From 2230 onwards landings became general.

The buildup of calling before the petrels were heard overland suggests that they may have assembled offshore, perhaps displaying while on the water as briefly seen by Fleming (1948) at Port Pegasus, but we have no direct evidence of their forming rafts offshore, and such behavior seems unusual among gadfly petrels.

Many landings were preceded by repeated aerial circuits during which the birds hovered momentarily where they eventually alighted. Newly landed, the birds often paused with outspread wings, perhaps in order to be ready to take off again if

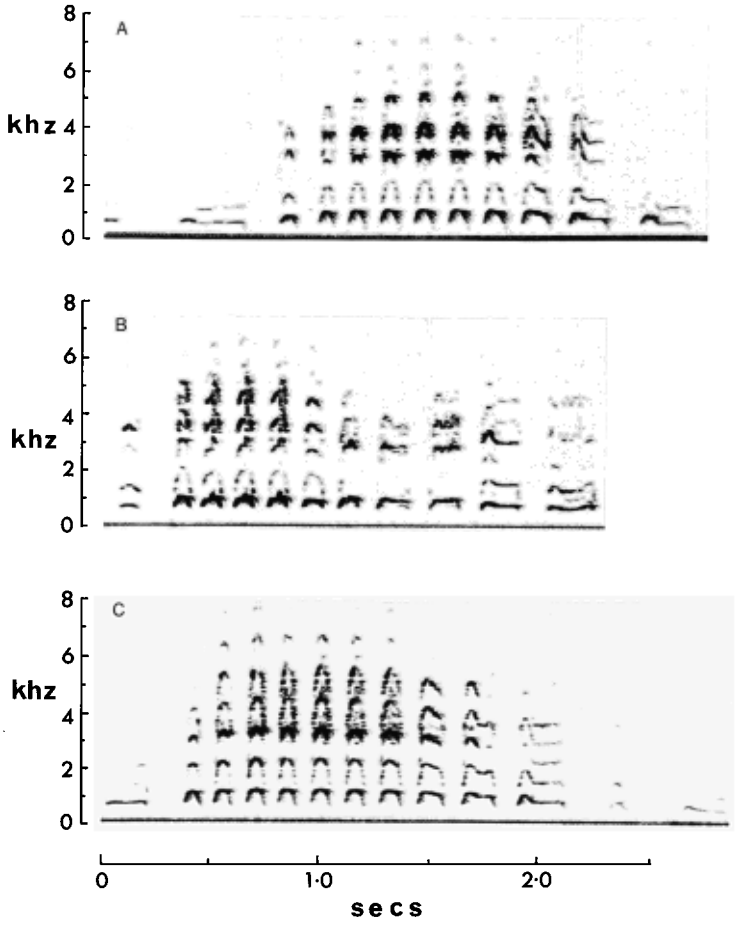

Fig. 1. Spectrograms of "ti-ti-ti" calls of three different Mottled Petrels singing from the ground.

attacked by skuas. Many petrels touched down close to their burrows, calling meanwhile, and their cries often stimulated birds in nearby burrows to reply.

The main aerial activity consisted of pairs, and less often trios, twisting and turning rapidly while uttering loud calls. Because incubation was then in progress most of these display flights were probably by nonbreeders. Often the birds hugged the contours of the slopes at heights of 2 to 3 m as *P. macroptera* does at Eclipse Island, Australia, where this mode of flight may help them avoid being blown out to sea during gales (Warham 1956, 1957). Gill et al. (1970) described similar chases between *P. arminjoniana* at Round Island, Mauritius. Here, in the absence of predators, the flights took place in daylight and these authors noted that the calls always seemed to be given by the pursuer.

Aerial activity at the Snares continued almost unabated for the 5 or 6 h of darkness. The outward movement was hard to follow as the swelling shearwater chorus masked the individual voices, but the petrels disappeared before daylight evidently well before the shearwaters. The petrels were agile and flew directly from some unimpeded place near their nests; we saw none among the queues of shearwaters at the takeoff rocks.

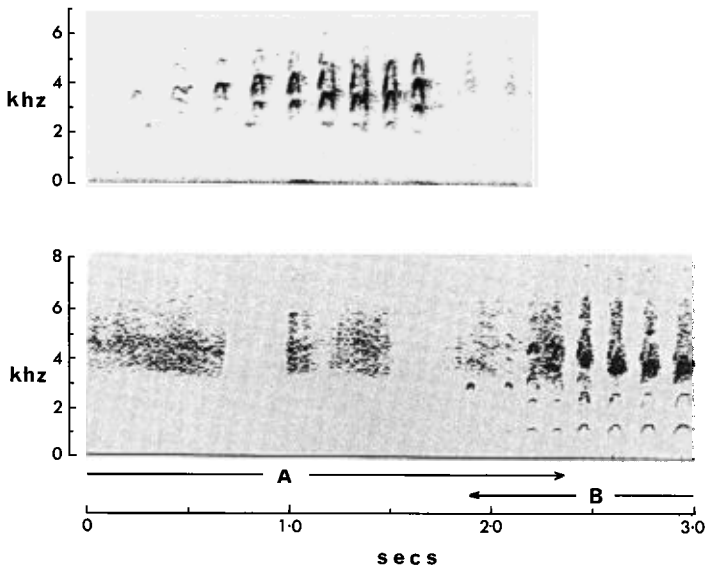

Fig. 2. Spectrograms of "ti-ti-ti" call of Mottled Petrel singing in flight (upper) and of calls of two Mottled Petrels (A and B) from within a burrow (lower).

Vocalizations

The main call used by Mottled Petrels either in the air or from the ground was the far-carrying cry usually rendered as "ti-ti-ti" (Stead 1932). This is a complex cry and we are unable to transcribe it precisely phonetically. The call is a strident, hysterical giggle based on from 8 to about 15 staccato syllables and similar to and probably homologous with the cries of other *Pterodroma* species such as *macroptera, arminjoniana*, and *lessoni* (Warham 1956, 1959, 1967a).

Spectrograms of calls made by six different Mottled Petrels (sexes unknown) are shown in Figs. 1 and 2. The basic patterns of the three solo calls in Fig. 1 are similar, consisting of a quiet, low-pitched introduction, a succession of loud staccato cries (the "ti-ti-tis") and a short, low-pitched ending. Each element or syllable has a marked structure with strong harmonics. The range of frequencies is considerable—from about 700 Hz to about 6.5 kHz. Overall, the calls begin quietly and tend to rise in pitch and in volume, which both decline toward the end.

It will be seen that the "ti" syllables are abrupt and delivered at rather fixed rates with distinct silent intervals of from 50 to 70 msec, but that the rate of delivery tends to decrease towards the end of the call. Each call lasted about 2.0 to 2.5 sec and might be repeated after a brief pause. As is true also of *P. arminjoniana* and *P. macroptera*, once having begun the "ti-ti" sequence a grounded Mottled Petrel seemed unable to stop—like an alarm clock that stops ringing only when the spring has unwound—the bird's body pulsating vigorously in time with its cries.

Each single "ti" syllable seems to be based on a note that rises about 0.5 to 1.0 kHz and then declines to its starting frequency. Such patterns are called "simple cries" by Davis (1964), who points out that such frequency changes often correspond with the expansion and contraction of the buccal cavity. In all three calls the second harmonic is rather faint but otherwise the energy distribution (as revealed by the relative darkness of the patterns) differs. In (A) most of this is carried by the fourth harmonic,

in (B) by the fundamental, and in (C) by the third harmonic. In call (B) the structure of the individual syllables is more complex and the effect was of a harsher vocalization of deeper overall pitch.

These spectrograms illustrate the kind of variation that occur from bird to bird. Sometimes these variations were apparent to the human ear, sometimes not. The calls of a particular bird varied little in structure; except for the number of "ti" syllables used, the resulting spectrogram patterns were similar.

The only comparable published data we know of is a spectrogram of a *P. arminjoniana* call, described as "a rapid series of up to twenty *ki* syllables increasing in intensity followed by an extended series of lower, melodic, oscillating *k-lu* notes" (Gill et al. 1970). Although they used a wide band-pass filter (which enhances time resolution) the general structure of the call they figure is similar to that of the Mottled Petrels shown here, being based on a series of simple cries with strong harmonics.

The call in Fig. 2 (upper), of a flying bird, is basically the same "ti-ti-ti" sequence as given by the grounded birds, but in this case the fundamental is weak and the call had a harsh chattering quality. The bird was flying towards the microphone and the rise in frequencies may have been due to the Doppler effect.

Mottled Petrels have quite a diverse repertoire. We neither succeeded in recording this diversity satisfactorily nor in discovering the circumstances in which the various calls were used. This was partly because of the difficulty of approaching calling birds in the dark and partly because, even when that was done, little overt sexual behavior was seen so that the sexes of the callers were unknown.

Stead (1932) referred to a resonant "bugle" note, which has been sometimes rendered as "goo-oo." We heard this call quite often, describing it as the organ note—it resembles the rich tone of a pipe organ more than the strident bugle. The call was heard only at short distances and either followed or preceded a "ti-ti" call, but it was often used alone when it was generally followed by a short staccato "wik." The whole call could then be written "gor-wik," the emphasis being on the first syllable which was accompanied by a great distension of the throat.

We believe that both these calls were used by either sex, but after listening to many birds we distinguished two basic series: (a) "gor-wik . . . bee-bee-bee-bee . . ." and (b) "tor-wit . . . ti-ti-ti-ti," the latter being the higher pitched. These possibly represent sexual variations of the same call. Gill also distinguished high and low variants of evidently rather similar calls in *Pterodroma baraui* and thought that they might indicate a sexual dimorphism (Jouanin and Gill 1967).

Some instances of the circumstances in which these calls were used follow: On the night of 23 January 1969 a Mottled Petrel was watched closely running erratically over a small piece of ground as if searching for something; at regular intervals it sounded the "gor-wik" organ note. Each time this bird passed the entrance to a particular burrow another petrel appeared at the opening and gave an agitated "ti-ti-ti" cry.

On another occasion one of us simulated the "gor-wik" cry a meter from a female that was due to be relieved by its mate. The bird immediately left its egg and walked toward the source of the sound, at the same time uttering a scolding "ti-ti." Thus there may be some complimentary relationship between the two series of calls that may play a part in sex recognition.

Another glimpse of mutual behavior was seen on 26 January 1967 when a Mottled Petrel giving the organ note through apparently closed bill was seen trailing close

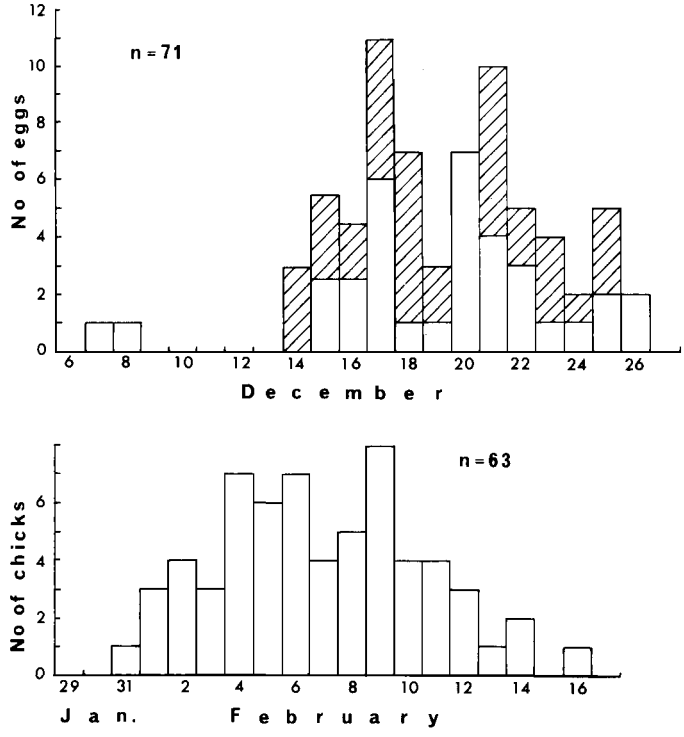

Fig. 3. Upper, progress of laying of 35 Mottled Petrels at the Snares Islands in 1969 and (shaded) of 36 in 1970. Lower, progress of hatching of Mottled Petrel eggs at the Snares Islands in 1969, 1970, and 1971.

behind another petrel. Some mutual billing and mutual allopreening of each others' necks ensued during which the bird that had called attempted to mount the other; evidently the organ note was used on this occasion by a male. His partner also called, not with the "ti-ti" sequence, but with a more sibillant disyllabic cry—probably the call we subsequently syllabilized as "tor-wit."

On 6 February 1967 a bird that had used the organ note was incited to repeat its call by the observer's imitation, whereupon a second bird emerged from a hollow and attacked the calling bird. The attacker used neither of the calls already discussed but a series of harsh rasping cries. On this night there was much ground activity with many petrels sitting outside or at the mouths of burrows or squatting at entrances with their heads inside. Some duets were noted in which one bird used a "ti-ti" sequence and its partner the organ note, and a good deal of fighting accompanied harsh cries. As this was during the hatching period it seems likely that many of the participants were prebreeders attempting to obtain burrows of their own.

Although some birds gave the "ti-ti" call when drawn from their burrows for banding, we never heard the organ note then. Otherwise a bird being handled was either silent, or gave a wild, frenzied scream that immediately alerted any nearby skuas, just as does the similar fear note of *P. lessoni*.

A variety of crooning and growling sounds was heard when both members of a pair were in a burrow. The lower spectrogram of Fig. 2 was made from a recording

of part of such a duet. One bird (A) uttered a series of high-pitched growls that show as noise, spread over a wide band of frequencies. Bird (B) started its song before its partner had finished and used a "ti-ti-ti" call whose energy was mainly concentrated in the third harmonic between 3.5 and 4.1 kHz.

BREEDING

The pre-egg stage.—Owing to the deep tussock beneath which most burrows were dug, the process of scratching out that occurs in November was not obvious, as it was among the Sooty Shearwaters, most of which burrowed in bare ground.

We first saw the Mottled Petrels on land the night of 15 November 1968 and on that day found four freshly killed by Southern Skuas. From then into December the nighttime presence of the petrels was signaled by aerial calling, which decreased slightly in late November and early December and increased about mid-December when egg-laying began.

To establish laying dates we inspected burrows by day for some time before eggs appeared. The absence of birds from the nests was notable, though we made no regular nighttime checks. For instance, in the 1969–70 and 1970–71 seasons, out of 62 burrows where eggs were laid, only on 12 occasions was a bird found in occupation during the week preceding laying. In most of those instances the egg appeared on the day an occupant was first noted. A similar absence of birds before laying was found in *P. lessoni* (Warham 1967a) and in *P. phaeopygia* (Harris 1970) and, in conjunction with the apparent decline in aerial activity, suggests that some *P. inexpectata* leave the island for a period. Assuming that visits were not made during the night, this exodus would have lasted from 9 to at least 16 days.

In the 54 burrows 37 (69%) eggs were subsequently laid. Of the rest, 11 were never known to contain birds by day (although visited by night) whereas the remaining 6 were occupied by day by petrels of unknown status without eggs being laid.

Site and mate tenacity.—From a sample of 45 nests where one occupant had been banded in 1968–69, 31 banded petrels were recovered the following season. None had changed its burrow. One of the other burrows had collapsed and was unusable. In two others only an unbanded bird was seen, but their partners could have been banded. The remaining 11 nests held pairs of unbanded birds and as the 11 petrels originally banded there were not found subsequently, they may have died.

In the 1970–71 season 65 birds banded in earlier years were identified. Of these, 63 were found in the same nests as in the 1969–70 season and 24 petrels banded two seasons before (out of 25 such birds still known to be alive) were in the same burrows as at the time of banding. The two banded birds not using the same nest in 1970–71 were a pair that shifted 0.9 m to a new burrow.

Mate tenacity can only be assessed by comparing recoveries for the 1970–71 and 1969–70 breeding seasons. Of the 30 pairs recovered in 1970–71, 25 (83%) pair bonds remained intact. In the five other instances only one of the previous partners was still present, each with a new, unbanded mate. These five pair bonds were apparently broken by the disappearance and presumed death of one partner, but as no search was made for banded birds outside the study areas, some of the missing birds could have changed mates and moved.

These results show that Mottled Petrels tend to return to the same nest and breed with the same partner in successive years.

Egg-laying and the egg.—In the 1969–70 and 1970–71 seasons the progression of laying was determined by morning inspections of the burrows. Because the hen was nearly always absent the day before laying and the birds did not venture ashore until after dark, any new egg was known to have been laid during the previous 12 h. The mean laying date for both samples (35 eggs in 1969; 36 in 1970) was 19.1 December. The distributions are shown in Fig. 3.

The earliest eggs were seen on 7 December and by far the latest was one laid some time between 2 and 10 January 1970. Nevertheless laying was not protracted, two-thirds of the eggs appearing between 15 and 22 December. In both seasons the number of eggs laid in the study burrows decreased between 18 and 20 December, hence the bimodal distribution in Fig. 3. No biological reason for this bimodality was discovered; the weather for 17 to 21 December was not atypical, there was no full moon to retard landings, and as a few birds laid an early and a late egg in successive seasons the presence of two semi-isolated components in the population seems improbable. It seems more likely that the distribution rose by chance.

Few comparable data are available. Stead (1932) found a fresh broken egg on 2 December and another fresh egg in a burrow on 3 December at Big South Cape Island. Unless these were atypical, they suggest that laying there, some 105 km northeast of our study area, may be at least a week earlier than at the Snares. On the other hand, a specimen from Puysegur Point (210 km north of the Snares) in the California Academy of Sciences collection held a fully formed unshelled egg on 2 January 1922, according to the label of the collector, R. S. Sutherland.

The single white egg is typically short subelliptical in shape, dull white in color and with little gloss. A sample of 62 had the following mean dimensions: 60.53 ± 2.06 (range 55.5 to 64.4 mm) × 43.97 ± 1.30 mm (range 41.8 to 48.9 mm). Ten freshly laid eggs had a mean weight of 61.1 ± 0.52 g (range 54.6 to 68.5 g). The mean weight of 11 eggs in the British Museum (Natural History) collection was likewise calculated at 61 g from measurements of their internal capacities (Warham 1968).

The Snares Island eggs were larger and heavier than 10 eggs from Big South Cape Island Richdale (1964) measured, of which the mean dimensions were 58.6 ± 1.5 mm (range 55.5 to 60.5 mm) × 42.7 ± 0.77 mm (range 41.5 to 44.0 mm) and the mean weight of 8 was 53.2 ± 3.2 g (range 47.5 to 57.5 g). Some of the difference in the mean weight between our sample and that of Richdale's could be due to his eggs being well incubated. On our data the ratio of bird weight to egg weight was 5.4, i.e. the egg was 18.6% of the body weight.

Incubation.—On the morning when the egg was first seen only one of the adults was present. In the 47 instances where the sex of this incubating bird was ascertained, 36 (76%) were females. These tended to stay on the egg only until that night, when the males took over; some males took charge on the night of laying.

In the 1968–69 season the roles of the sexes during incubation were determined by inspecting 30 nests every second day, the handling of the birds being kept to a minimum.

The data for 93 incubation spans are summarized in Table 1. Although some birds sat for only short periods, most spans were long. Of the 76 spans not interrupted by hatching, the 41 spans undertaken by male birds averaged 12.8 days, the 35 by females 13.8 days. It is unlikely that the birds undertaking the long spans had been relieved for 1-day periods on days when no inspections were made because of relatively high frequencies of recorded spans of 12 to 19 days.

TABLE 1
LENGTHS OF 93 INCUBATION SPANS AT 30 NESTS[1]

Length of spans (days)	1	2	3	4	5	6	7	8	9	10	11	12
No. of spans	0	2	4	2	3	0	1	1	3	4	5	7
Length of spans (days)	13	14	15	16	17	18	19	20	21	22	23	
No. of spans	10	11	7	9	9	6	5	2	1	1	0	

[1] As checks were made only every other day, actual spans could be up to 2 days longer.

The division of labor between the sexes was fairly equal; typically each undertook two long stints. The sexes of birds sitting on a particular day tended to be predominantly male or predominantly female. Such in-phase rhythms, if general throughout a population, may help explain instances where birds collected from flocks at sea have been predominantly of one sex. Serventy (1967) gave examples in shearwaters.

We weighed few incubating petrels, but one of 370 g on 12 January scaled only 280 g 13 days later. Incubating birds had well-developed brood patches extending from the rear of the sternum almost to the cloaca. The skin was pink and well vascularized, the patch ovoid in shape with blunt ends, rather matching the shape of the egg. The long axis (parallel to the body) in 5 breeding birds averaged 57 mm with a mean maximum width of 47 mm. The down in this region was not entirely shed; a narrow midline about 10 mm wide was retained except by a few birds whose midline was incomplete. In some of unknown status the midline was wider, so that on first sight the birds appeared to have two brood patches.

Two eggs were weighed every 5 days during incubation. The rate of loss was rather constant, varying between 0.21 and 0.23 g daily, so that an egg weighing 67.0 g when laid decreased to 56.8 g when "starred" 49 days later, having lost about 16.7% of its initial weight.

Half the nests where chicks eventually hatched had them by the night of 5–6 February 1969, and by the afternoon of 6 February in 1970 and 1971. The hatching dates in these seasons were not significantly different and the data are combined in Fig. 3. The mean date of hatching for the 63 eggs was 6.9 February. Hatching was first noted on 31 January and one late-laid egg that might have hatched by 21 February 1970 was still intact when the party sailed on 19 February. Most hatching, like laying, was compressed into a quite short period; two-thirds of the chicks appeared between 4 and 11 February.

The difference between the mean date of laying (19.1 December) and the mean date of hatching (6.9 February) gives a mean incubation period of 49.8 days. During the last two seasons the incubation periods for 21 eggs were determined (data summarized in Table 2). The mean value accurate to ± 1 day was 50.45 ± 1.16 days (range 48.5 to 53.0 days).

We saw no eggs that had been laid on the surface but temporary desertion of eggs did occur. We think that most such instances were entirely natural, the result of the on-duty bird leaving to feed before its mate returned. Two eggs were uncovered for 3 or 4 and 4 or 5 days respectively immediately after laying, and the first of these was again abandoned for 1 day just before hatching. Nevertheless both hatched, after 57 ± 1 and 54 ± 1 days respectively. If the days on which they were unincubated are subtracted, true incubation periods of 52 to 53 and 49 to 50 days are obtained, in line with the data in Table 2.

TABLE 2
INCUBATION PERIODS IN *PTERODROMA INEXPECTATA*[1]

Period (days)	48.0	48.5	49.0	49.5	50.0	50.5	51.0	51.5	52.0	52.5	53.0	53.5
No.	0	1	0	6	3	3	2	5	0	0	1	0

[1] Mean period = 50.45 ± 1.06 days (n = 21).

Such resistance to chilling is known for other *Pterodroma* petrels. An egg of *P. macroptera*, abandoned, cold and wet for 28 h, hatched 3 days later (Warham 1956). Hatching after intermittent incubation is only possible where petrels are free from alien interference, as at the Snares. In contrast, unincubated eggs of *P. phaeopygia* at the Galápagos and Hawaiian Islands are lost to rats, *Rattus rattus* (Harris 1970, Larson 1967).

Hatching.—In 79 burrows where eggs were laid in the first two seasons, 51 (65%) were hatched successfully. The remainder suffered a variety of fates, mostly ending in desertion; 26 eggs (33%) were lost in this way, one when but a day old. Deserted eggs tended to be pushed or raked out of burrows and some such eggs were eaten by Red-billed Gulls, *Larus novaehollandiae*. A few desertions may have been the result of our activities, but the petrels were not very sensitive and abandonment mostly seemed to be a consequence of faulty incubation rhythms. For example, at one nest where the egg was eventually abandoned, the female took her normal incubation spans but the male was very erratic, took frequent days off, and presumably because of the excessive chilling, their egg failed to hatch. Six other eggs that were deserted intermittently did not hatch: two of them became cracked and the other four appeared to be infertile. The remaining 2% of the sample consisted of one nest where Red-billed Gulls are thought to have interfered and another whose egg was still unhatched when checks ended.

The time taken for the chick to free itself after the initial fracturing of the eggshell averaged 4.2 days in the 19 instances followed, range 2–6 days. Whereas eggs were mostly laid overnight, about as many hatched by day as by night. The shells were not removed but were trampled into the nest.

The chick.—The chicks were born bright-eyed, and at 2 days old the dense down was a rather uniform medium gray, slightly lighter ventrally and showing a brownish cast at certain angles of light. A small proportion of chicks had a whitish "bib" on the chin and breast and one had white down on the belly. The longest protoptiles (ca. 16 mm) were on the back and sides of the body; the down was about 10 mm long on the crown and 8 mm on the belly, the shortest down being on the chin and around the base of the bill.

At this stage the chicks' eyelids were blue-gray and the eyes themselves bright blue; they apparently gave poor vision. The bill was black and the egg tooth translucent and inconspicuous, becoming whiter and opaque before its disappearance at 8 days (range 3–16 days) in 18 chicks. The tarsus was pale gray to white with a lilac tinge, darker gray skin covering the joints of the feet and toes, the webs being flesh-colored and the claws blackish. Evidently in this species, as in some other *Pterodroma* spp. with parti-colored feet, the webs darken distally during development (see Warham 1967a, Fig. 2).

Parental attendence and chick growth.—We have little data on growth because only events during the first 3 weeks after hatching could be followed.

Either parent might be with the chick on its 1st day—3 females and 7 males in 10

nests whose parents were identified. At least one chick was alone, dry, fit, and well on its first day, and could only have been brooded for a few hours. More often the hatchling was brooded on its 1st day and in 4 of 10 burrows with chicks, a parent was still present on the 2nd day. Thereafter the chick was usually alone by day, but occasionally, between the chick's 4th and 12th days, a parent remained in the burrow during the daytime. Parents generally arrived at their nests during the first 2 h of darkness. Only once were two parents seen with a chick.

Our sparse data suggest that the alternation of duties started during incubation carried over into the chick-rearing phase. The occurrences of male and female parents tended to alternate in periods of about 10 days, but this pattern was rather obscure owing to missed visits or to our failure to identify the sexes of attendant parents. On several occasions a particular parent was with its chick on 2 or even 3 successive nights, although absent by day. Such birds cannot have foraged very far during the intervening daylight hours.

Chicks being handled were active, kicked strongly, and used their bills in attempts to climb out of sight. Some lunged to eject proventricular oil and food. For small chicks this was a rather ineffective defense as they appeared unable to see properly, directing their lunges at sounds rather than at movements. About half the chicks handled regularly failed to produce any oil but those that did ejected copious amounts. Some chicks gave high-pitched squeaks when disturbed for examination, but a few gave louder strident cries that strongly resembled the scolding "ti-ti-ti's" of disturbed adults.

Weighings showed that during their first fortnight chicks were not fed nightly but fasted 1–3 days between meals. Three chicks reached a mean weight of 221 g at 18 days, 67% of mean adult weight.

We have no data on older chicks and no direct evidence on the nestling period, but judging from the dates of late layings and last sightings of chicks, this period is 90–105 days.

ENEMIES AND MORTALITY

Many chicks soon became hosts for gray-green ticks, *Ixodes uriae* White (det. N. Wilson and R. L. C. Pilgrim). These were generally found attached to the legs and to the webs of the feet, in one bird to a wing. Two chicks less than 24 h old carried one tick while another of that age carried three. A 5-day-old had 12 ticks and a 9-day-old 22 of them. Tick infestations were much greater on chicks from burrows among *Poa* tussocks than on those from rock crevice nests.

Out of 30 chicks under examination in 1968–69, three had numerous orange-red amphipods on their heads. One heavily infested bird had the down grazed off until, when a fortnight old, its crown was bald and partly covered in scabs. These amphipods were unfortunately not identified and such parasitism has not been noted subsequently. Five kinds of terrestrial amphipods occur on these islands, all of the genus *Orchestia* (D. S. Horning pers. comm.). We have no evidence that they contribute to mortality in normal years.

The Mottled Petrel population on Codfish Island, near Stewart Island, seems to have declined after the release there of Wekas, *Gallirallus australis*, which are believed to kill the petrels (Blackburn 1968). Wekas are hardly unnatural predators for they are native to Steward Island and to mainland New Zealand. Otherwise the petrel's only natural enemy today appears to be the Southern Skua, *Stercorarius skua*.

According to Richdale (1964) the Maoris may still harvest some chicks for food as "mutton-birds"; their name for the bird is Korure.

At the Snares many freshly killed adult petrels were found on the skua territories. Most must have been killed after dark; no fit Mottled Petrel remaining on the surface by day and none of the few that fled their burrows by day when accidentally disturbed was seen to be pursued or attacked by skuas. As the skua and petrel nesting places tended to be adjacent, the skuas preferring the rather bare, peripheral rocky areas with scattered *Poa astonii* where most of the crevice-living Mottled Petrels breed, movement after dark could be quite hazardous for the petrels there. As the skuas do not forsake the islands in the winter (Horning and Horning 1974), skuas and perhaps Northern Giant Petrels, *Macronectes halli*, possibly take fledglings in May and June, but we have no information on that.

Mottled Petrels' nests were well drained and we saw no loss of eggs or chicks through flooding of burrows, as happened among the shearwaters.

In the absence of thorough searches for banded birds away from the study areas our data on survival are minimal. None of the 114 birds we banded has been reported dead at the Snares or elsewhere to date. Of 49 adults banded in 1968–69, not less than 33 were still alive the following year (67% survived) and not less than 25 of them the year after (76% survived). Of the 52 adults first banded in 1969–70, at least 39 (75%) were still alive a year later.

Conservation

In view of the decline in the populations of this species elsewhere, it is unfortunate that we were unable to attempt a census of the Snares Mottled Petrels, the more so as they appear to carry quite high levels of P.C.B.'s (Bennington et al. 1975), presumably ingested during their migration. With many pairs nesting on dangerous slopes, nests often hard to distinguish from those of shearwaters, and other problems, even to assess the number of burrows would be a major task, let alone to estimate the size of the breeding population. Mark-recapture techniques are difficult to apply as banded petrels do not "randomize," but tend to be recovered where banded. All that we care to speculate is that the total Snares population probably amounts to tens of thousands of birds, and is unlikely to number in the hundreds of thousands.

These are small figures compared with the millions of other petrels such as the Short-tailed and Sooty Shearwaters that breed on similar islands around New Zealand and Tasmania. Nevertheless the Snares Islands appear to provide the most important and best protected breeding place remaining for Mottled Petrels, thanks to the absence of mustelids, rats, and cats. Adult Mottled Petrels are unaggressive and do not spit stomach oil defensively, and so could be killed with impunity by predatory placentals, as is the White-headed Petrel, *Pterodroma lessoni*, at Macquarie Island (Warham 1967a).

The immediate future of this species still largely depends on the inaccessibility and isolation of the breeding places afforded by their distance from population centers, the absence of any significant locally exploited natural resources, the frequency of severe gales, the lack of good anchorages, and the precautions taken by visiting scientific parties.

How long this isolation will continue is problematical in view of the increased activity in the sub-Antarctic by foreign fishing enterprises, by companies searching for

minerals, and similar developments. Although the legal position of the Snares is clear, the regulations are not effectively policed because government vessels seldom patrol the islands. Illegal landings are known to have occurred in recent years and these involve the risk of inadvertent introductions, particularly of rats. In the long term it seems unlikely that the sensitive faunas of these and similar islands can be preserved without more positive governmental and/or international action. Perhaps it would be better to have small, strictly controlled research stations at such key sites, despite the attendant risks, than to rely on the pious hope that their conservation is assured by adequate regulations inadequately policed.

ACKNOWLEDGMENTS

This work was supported financially by the Nuffield Foundation and the New Zealand University Grants Committee. For assistance with transport we are grateful to Gordon Crowther and to N. Calder, R. Bailey, L. Young, and C. J. West, skippers of fishing boats from Bluff and Stewart Island. The Royal New Zealand Navy also uplifted us on two occasions. M. C. Crawley and Mrs. F. R. Allison kindly read drafts of this paper, and N. A. Doughty provided astronomical data.

LITERATURE CITED

BARTLE, J. A. 1968. Observations on the breeding habits of Pycrofts Petrel. Notornis 15: 70–99.

BENNINGTON, S. L., P. G. CONNORS, C. W. CONNORS, & R. W. RISEBROUGH. 1975. Patterns of chlorinated hydrocarbon contamination in New Zealand sub-antarctic and coastal marine birds. Environ. Pollution, 8: 135–147.

BENT, A. C. 1922. Life histories of North American petrels, pelicans, and their allies, order Tubinares and order Steganopodes. U.S. Natl. Mus. Bull. No. 121.

BLACKBURN, A. 1968. The birdlife of Codfish Island. Notornis 15: 51–65.

BOURNE, W. R. P. 1967. Subfossil petrel bones from the Chatham Islands. Ibis 109: 1–7.

DAVIS, L. I. 1964. Biological acoustics and the use of the sound spectrograph. Southwestern Naturalist 9: 118–145.

EDGAR, A. T. 1972a. Classified summarised notes. Notornis 19: Suppl.

———. 1972b. Classified summarised notes. Notornis 19: 339–364.

———. 1973. Classified summarised notes. Notornis 20: 346–376.

FALLA, R. A. 1934. The distribution and breeding habits of petrels in northern New Zealand. Rec. Auckland Inst. Mus. 1: 247–259.

———. 1937. Birds. British Australian New Zealand Antarct. Res. Exped. Rept., Ser. B, 2.

———, R. B. SIBSON, & E. G. TURBOTT. 1966. A field guide to the birds of New Zealand and outlying islands. London, Collins.

FINERAN, B. A. 1964. An outline of the vegetation of the Snares Islands. Trans. Royal Soc. New Zealand (Bot.) 2: 229–235.

———. 1969. The flora of the Snares Islands, New Zealand. Trans. Royal Soc. New Zealand (Bot.) 3: 237–270.

FLEMING, C. A. 1948. The Snares Islands Expedition, 1947. New Zealand Bird Notes 2: 181–184.

———, J. J. REED, & W. F. HARRIS. 1953. The geology of the Snares Islands. Dept. Sci. Indust. Res. Cape Exp. Ser. Bull. 13: 1–42.

GILL, F. B., C. JOUANIN, & R. W. STORER. 1970. Notes on the seabirds of Round Island, Mauritius. Auk 87: 514–521.

HARRIS, M. P. 1970. The biology of an endangered species, the Dark-rumped Petrel (*Pterodroma phaeopygia*), in the Galapagos Islands. Condor 72: 76–84.

HORNING, D. S., & C. J. HORNING. 1974. Bird records of the 1971–1973 Snares Islands, New Zealand Expedition. Notornis 21: 13–24.

JOUANIN, C., & F. B. GILL. 1967. Recherche du Petrel de Baraui *Pterodroma baraui*. Oiseau 37: 1–19.

KING, W. B. 1967. Seabirds of the tropical Pacific Ocean. Washington, D.C., Preliminary Smithsonian Identification Manual.

———. 1970. The trade wind zone oceanography pilot study. Part 7: observations of sea birds, March 1964 to June 1965. U.S. Dept. Interior, Fish. Wildl. Serv., Spec. Sci. Rept.—Fish No. 586.

LARSON, J. W. 1967. The Dark-rumped Petrel in Haleakala Crater, Maui, Hawaii. U.S. Dept. Interior, Rept. Natl. Park Serv.

LOOMIS, L. M. 1918. A review of the albatrosses, petrels and diving petrels. Proc. California Acad. Sci. 4th Ser., 2, part 2, 12.

MARSHALL, A. J. & D. L. SERVENTY. 1956. The breeding cycle of the Short-tailed Shearwater, *Puffinus tenuirostris* (Temminck) in relation to trans-equatorial migration and its environment. Proc. Zool. Soc. London 127: 489–510.

MURPHY, R. C. & J. M. PENNOYER. 1952. Larger petrels of the genus *Pterodroma*. Amer. Mus. Novitates No. 1580.

OLIVER, W. R. B. 1955. New Zealand birds. Wellington, A. H. & A. W. Reed.

PALMER, R. S. 1962. Handbook of North American birds, vol. 1. New Haven, Connecticut, Yale Univ. Press.

RICHDALE, L. E. 1964. Notes on the Mottled Petrel *Pterodroma inexpectata* and other petrels. Ibis 106: 110–114.

SERVENTY, D. L. 1967. Aspects of the population ecology of the Short-tailed Shearwater *Puffinus tenuirostris*. Proc. 14th Intern. Ornithol. Congr.: 165–190.

———, V. N. SERVENTY, & J. WARHAM. 1971. The handbook of Australian sea-birds. Sydney, A. H. & A. W. Reed.

STEAD, E. G. 1932. Life histories of New Zealand birds. London, Search.

VAN OORDT, G. J., & J. P. KRUIJT. 1953. On the pelagic distribution of some Procellariiformes in the Atlantic and southern Oceans. Ibis 95: 615–637.

WARHAM, J. 1956. The breeding of the Great-winged Petrel, *Pterodroma macroptera*. Ibis 98: 171–185.

———. 1957. Additional notes on the Great-winged Petrel, *Pterodroma macroptera*. Ibis 99: 511–512.

———. 1959. The Trinidad Petrel, *Pterodroma arminjoniana*, a new bird for Australia. Emu 59: 153–158.

———. 1967a. The White-headed Petrel, *Pterodroma lessoni*, at Macquarie Island. Emu 67: 1–22.

———. 1967b. Snares Island Birds. Notornis 14: 122–139.

———. 1968. Biometric studies of birds in the order Procellariiformes. Unpublished M.Sc. thesis, Durham, England, Univ. Durham.

WATSON, G. E., J. P. ANGLE, P. C. HARPER, M. A. BRIDGE, R. P. SCHLATTER, W. L. N. TICKELL, J. C. BOYD, & M. M. BOYD. 1971. Birds of the Antarctic and Subantarctic. Antarctic Map Folio Ser. Folio 14. New York, Amer. Geogr. Soc.

WILSON, G. J. 1973. Birds of the Solander Islands. Notornis 20: 318–323.