THE BREEDING CYCLE OF THE WESTLAND BLACK PETREL (*Procellaria westlandica*)

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ABSTRACT

The breeding cycle of the Westland Black Petrel (*Procellaria westlandica*) is outlined from observations made in the 1970 and 1971 breeding seasons and from the literature. Adults arrive at the colonies in late March to excavate and claim burrows, reform pairs and build nests. Egg laying commences in early May and seems to be preceded by a honeymoon period. Most eggs are laid in a short peak period of about three weeks in May. Hatching begins about the third week in July following an incubation period of about 57-65 days. Chicks are brooded for up to two weeks and then spend the rest of their 120+ day fledging period alone except during feeding visits by the parents. Very heavy egg and chick losses were sustained in the two seasons studied and the disappearance of big chicks in September each season suggests that the colonies may be "birded." The long incubation and fledging periods relative to some other Procellariidae are interpreted as an adaptation to a sparse and variable food supply. Competition for food with summer breeding shearwaters such as *P. parkinsoni* seems the most plausible explanation for the winter breeding season of *P. westlandica.*

INTRODUCTION

Although 30 years have elapsed since Falla (1946) reported the discovery of the Westland Black Petrel (*Procellaria westlandica*) (Fig. 1A), little is known about the general biology of this interesting species. Falla summarized fragmentary information then available on its breeding schedule which Jackson (1958) subsequently enlarged on and also commented briefly on mortality, breeding habitat, population estimates and putative history of breeding sites. It is now established that the *P. westlandica* breeding population is relatively small (Jackson 1958; Bartle 1974), and that its breeding sites are restricted to a precariously small geographic area in the coastal escarpment of the west coast of the South Island (Best & Owen 1976). Despite the aforementioned studies, the breeding cycle is known only in broad outline, and specific data on breeding success are lacking. Because such information is crucial in determining the status of the Westland Black Petrel we undertook a limited study of its breeding biology. We report here observations made on short visits to a study colony during two breeding seasons.

STUDY SITE AND METHODS

Study Site

For study purposes we chose a group of burrows (listed in Fig. 4 *in* Best & Owen (1976) as 100 burrows) in reasonably negotiable terrain with good access from State Highway 6. The colony chosen was situated near the top (ca. 250 m a.s.l.) of a steep north-east facing valley wall on the southern bank of Scotchman's Creek, approximately 2 km south of the Punakaiki rivermouth (see NZMS 1, S37, map ref. 855248). The valley wall is clad in luxuriant coastal vegetation (Fig. 1B) with an obvious altitudinal succession in species composition (see Best & Owen (1976) for a detailed description of the vegetation).

Visits to study site

We made a preliminary visit to reconnoitre the breeding sites of *P. westlandica* on 6-7 May 1968. Subsequent visits, on which this paper is largely based, were made as follows: 1970 — 20-21 June, 11 July, 1-2 August, 25-26 August, 29 September; 1971 — 5 May, 28-29 May, 11 June, 17 July, 7-8 August, 18 September. The second author also visited the colony on 24-25 May 1976.

Fieldwork

In 1970 we marked 50 occupied burrows with sequentially numbered pegs placed near the entrance of each one (Fig. 1C). In 1971 we marked another 31 burrows and emplaced wooden observation portals (150 x 150 x 25 mm) in the wall of nest chambers that were difficult to view through the burrow entrance. The portals were lodged firmly into place and covered with soil and leaf litter for concealment. To avoid disturbance the portals were installed when the birds were absent from their burrows.

During each of our visits to the study site we recorded the contents of all marked burrows. We weighed and measured accessible eggs and chicks, and also weighed, measured and banded adults, especially birds without eggs or chicks. The following measurements were taken with dial calipers accurate to 0.1 mm: bill length (exposed culmen), bill depth, bill width, tarsus length, middle toe length, length of straightened wing, tail length, egg length and egg width. Weight was recorded on spring balances accurate to 1 g for eggs and small chicks, and 20 g for large chicks and adults.

The cloacal condition of each banded adult was noted as a possible guide to sex (Serventy 1956), and a check was made on the development and size of the brood patch. We set up a control group of 25 burrows in 1971 to evaluate the possible effects of our observations on breeding success, and in these burrows we established only the presence or absence of adults, eggs or chicks.

The approximate ages of most chicks were assessed by comparison with growth curves of three chicks of known age, and with growth curves and teleoptile plumage development of chicks of *P. aequinoctialis* in Mougin (1970). The error of estimation is probably small in very young chicks but may be as great as ± 5 days in older ones.

THE PRELAYING PERIOD

Arrival at colonies

Adults arrive at the breeding grounds in late March and early April (Jackson 1958; Bartle 1974). Rafts sometimes containing in excess of 1000 birds are found 1 to 2 km offshore before their nightly arrival at the colonies. At dusk the petrels fly inland to the coastal escarpment along which they often make several passes before turning up valleys in which the burrows are located. They usually circle overhead for several minutes before gliding into the canopy and dropping through to the forest floor. The birds seem able to locate their burrow from above the dense canopy with remarkable accuracy in some cases; one banded bird dropped to with 5 m of its burrow and other birds were seen to enter burrows close to their landing sites.

The population at the colonies

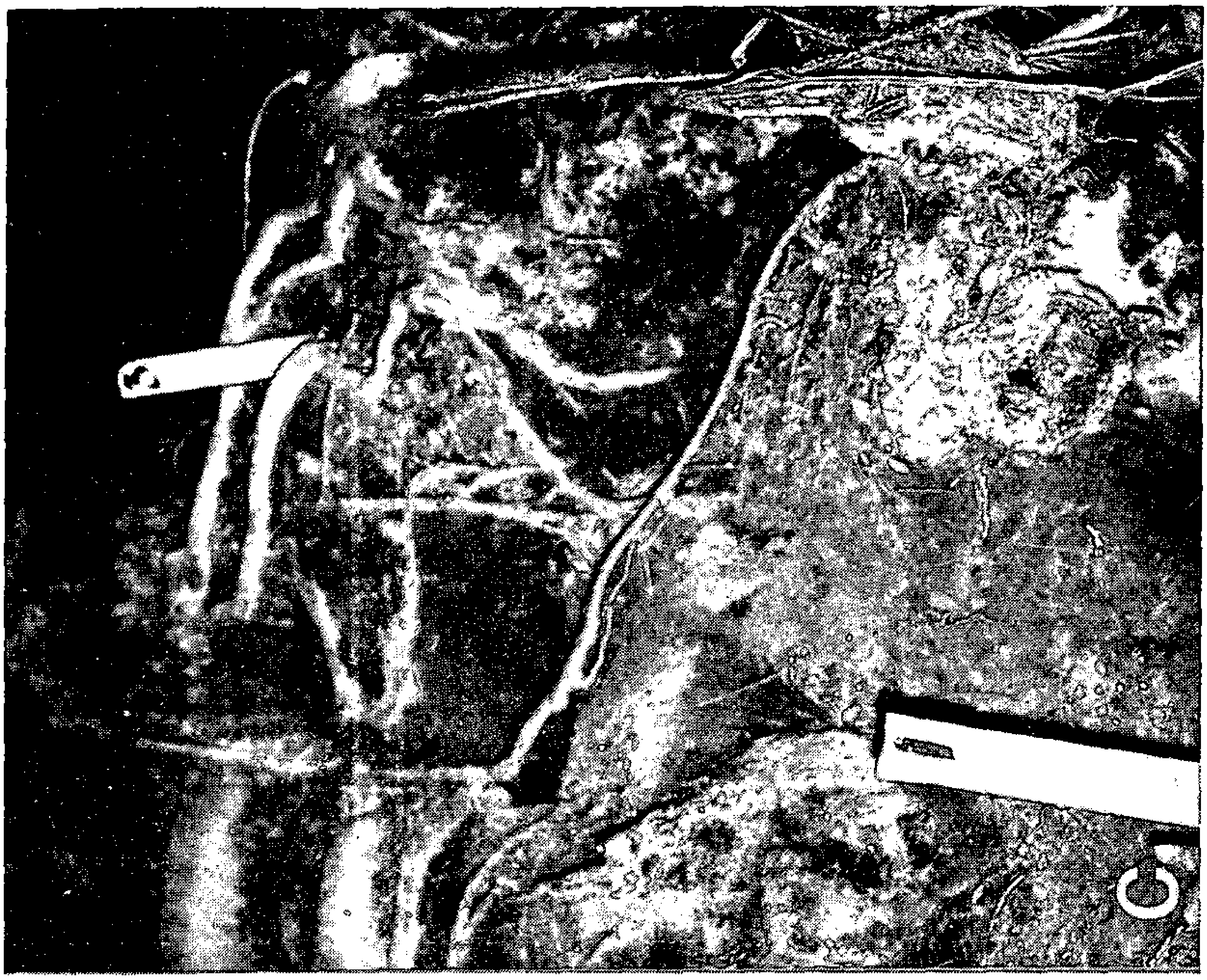
The population of Westland Black Petrels that frequents the breeding colonies has never been estimated accurately. Jackson (1958) judged the population to be between 3,000 and 6,000 birds, and felt that because there were numerous unoccupied burrows in the colonies, the population has undergone a decline. He also noticed a rapid decline over three years in the number of burrows occupied at one colony. More recently Bartle (1974) estimated the population at the colonies in 1972 to be between 6,000 and 10,000 birds and suggested that the apparent increase may in part be attributable to additional food supplies provided by offal from trawlers. Both of the estimates are hard to reconcile with Best & Owen's (1976) estimate of less than 900 occupied burrows in the colonies, unless there is a large number of unemployed birds.

The only index of population size that we obtained was on 25 May 1976, when one of us (JDC) estimated between 1,000 and 2,000 birds were waiting to come ashore at dusk. Without knowing how many of these birds were unemployed or how many were incubating eggs at that time, it is not possible to choose between the above population estimates. Clearly, more precise counts over several years are needed to ascertain whether population numbers are increasing or not.

Prelaying activities

Very few new burrows seem to be constructed near the beginning of the breeding season, but existing burrows are cleaned out and some

FIGURE 1 — A: Adult *Procellaria westlandica;* B: Breeding habitat of *P. westlandica;* C: Marked burrows at the study colony.


C


B

are enlarged by further excavation (Jackson 1958). Excavation reaches a peak in April (H. Best pers. comm.) and extends into early May, though restorative digging of collapsed burrows occurs through much of the breeding season. In April and early May, Westland Black Petrels commonly rest up in freshly cleaned out burrows. Jackson (1958) noted that birds were present during the day in many of the burrows that were occupied on 8 April 1956, and Falla (1946) reported similarly for 27 April 1946. We found 20 petrels in 39 burrows which had nests built in them on 5 May 1971; three burrows contained two birds (presumably pairs) and the remaining 14 had single birds. Birds we banded in early May were subsequently recovered only from burrows at which they were banded (n = 31 recoveries), so it seems likely that most breeding birds had established ownership of burrows by then.

Activity of birds above the ground is most apparent about three weeks before the onset of laying. The petrels are very vocal during this period and may be heard calling on the wing, on the ground or from their burrows. Courtship and copulation have been observed on the ground at this time too (Jackson 1958). Most of the activity at the colonies in May begins with the nightly arrival of birds from the sea, though birds in burrows, especially pairs, occasionally cackle vociferously during the day. The following observations show how vocal behaviour is tied to the daily arrival and departure of birds. On the evening of 24 May 1976, the incoming birds began arriving at 6 p.m., triggering vocalization which lasted through to 9 p.m. The petrels were quiet until 4 a.m. the following morning and then became very vocal again until departure for the sea at about 7.15 a.m. After the morning exodus the remaining birds at the colony lapsed into complete silence.

Westland Black Petrel burrows are not evenly dispersed over the nesting habitat, but are clumped in small groups or colonies (Fig. 1C). Numbers of burrows in the colonies vary considerably, averaging 30 and ranging from isolated groups of 1 or 2 to a maximum of 265 (Best & Owen 1976). Our study site included at least 100 burrows, which is the second largest concentration found in the extensive survey conducted by Best & Owen.

The burrows in the study colony are concentrated near the top of ridges, cliffs and spurs on the valley wall. A small group of 10 burrows is located in the bottom of a shallow gully running down the valley. Burrow location is apparently influenced by altitude; no burrows are located in the study site beneath an altitude of approximately 80 m a.s.l., which corresponds to about two-thirds of the distance down the valley wall.

Each group of burrows in the study colony is situated within easy access of take-off areas such as cliffs, knobs or leaning trees. Trees used for take-off are conspicuous by claw marks on the bark, especially near the base. Birds in the lowest group of burrows use a gap in the canopy caused by windfall as a take-off area, launching themselves into the gap from surrounding trees.

Most of the burrows are excavated in soil denuded of vegetation, though some are located under entangled thickets of Kiekie *(Freycinetia banksii)*, Rata creepers (*Metrosideros* spp), Supplejack *(Rhipogonum scandens)*, Bush Lawyer *(Rubus cissoides)* or Ladder Ferns (*Blechnum* spp). The birds burrow preferentially in the deep soil of the forest floor, but occasionally they also penetrate the underlying sandstone.

Entrance tunnels leading to nest chambers usually face downhill to allow adequate drainage of the burrow. The shape and dimensions of burrows vary with the substrate in which they are excavated. Entrance tunnels in surface soil are often up to 2 m in length and 200 mm in diameter, whereas those in sandstone or among roots of trees are frequently as short as 1 m and have a diameter of 120 mm. Nest chambers are either located at the end of the tunnel or are displaced at right angles to it. Shorter tunnels of about 1 m or less are almost always offset at an angle to nesting chambers unless the topography or substrate is unsuitable.

Nesting chambers are roughly circular in ground plan with a diameter of approximately 500-600 mm and a height of about 200-300 mm. In areas with poor drainage the birds scrape earth into the centre of the chamber to form a nest mound, on top of which they usually place nest materials such as dead twigs, leaves and small pieces of tree fern fronds. We inspected a group of burrows in a gully bottom following a torrential downpour in which the gully became a rivulet; even though the burrows were flooded all nests except one were kept above water by natural drainage around the mound.

Burrow and mate tenacity

Westland Black Petrels show a marked tendency to return to the same burrow from year to year. Of 23 adults banded in 1970 and subsequently recaptured in 1971, 21 were found in the same burrow. The remaining two birds changed sites and were found breeding in adjacent burrows. Burrow tenacity is not confined to birds that had bred in the previous year; eight of the above 23 recaptures were unemployed in 1970. Of the eight unemployed birds, four were possibly pre-breeders because they prospected for burrows in August 1970, well beyond the time at which breeding could have been initiated (see beyond).

Unfortunately, our data on mate tenacity are very limited because we were seldom able to recapture both members of a pair. However, there is some evidence that breeding birds retain mates from year to year. Of four pairs banded in 1970, three were recovered in the same burrow in 1971. One bird of the fourth pair was found breeding in its 1970 burrow, but with a new mate. We were unable to locate its previous mate on the colony, and the short duration of our visits did not allow us to attribute the dissolution of the pair to either death of the mate or divorce.

THE EGG PERIOD

Egg Laying

According to Jackson (1958) the Westland Black Petrel lays eggs over a period of approximately 5 weeks, extending from late May to early June. Falla (1946) reported " fresh eggs late in May," but it is not clear from his account whether these were among the first eggs laid in the colony or not. In 1970 all 14 eggs observed in the study burrows were laid before our first visit on 20 June. In 1971 no eggs were found in burrows on 5 May and all 52 eggs observed were laid by 11 June, with most (45) laid by 28 May. Hence the great majority (87%) of laying in 1971 was compressed into a short period of about 3 weeks in May.

The timing of the laying period seems to be very similar in different breeding seasons. Egg laying in 1976 was scheduled similarly to 1971; on 24 May 1976, most birds were found with eggs. Those without eggs included unemployed birds which would not subsequently lay (see beyond), so the actual number of breeding birds that had not laid by this date was probably quite low.

Egg dimensions

Egg size of *P. westlandica* has been reported to the nearest 0.5 or 1 mm by Falla (1946) for nine eggs, Oliver (1955) for three eggs and Serventy *et al.* (1971) for 14 eggs. We were able to measure a larger sample of 26 eggs with greater accuracy (Table 1).

TABLE 1 Mean dimensions of samples of eggs of the Westland Black Petrel.

Dimension	Sample			
	Falla (1946) (n=9)	Oliver (1955) (n=3)	Serventy et al. (1971) (n=14)	This Study (n=26)
Greatest length (mm)	82 ± 1.0	81 ± 2.0	82	81.1 ± 0.42
Greatest width (mm)	56 ± 0.5	55 ± 1.0	55	55.6 ± 0.24

These four samples are all very similar in mean dimensions, and fall within the range of eggs of *P. aequinoctialis* (see Mougin 1970). Weights of freshly laid eggs were not recorded. However, 11 eggs after approximately 3 weeks of incubation averaged 130 ± 2 g which is similar to the 4½ oz. (128 g) given by Falla for freshly laid eggs. The mean rate of weight loss for five eggs near the middle of the incubation period was 7.6 g per 3 weeks, which extrapolates roughly to a weight loss of 20 g per egg during incubation. Some larger freshly laid eggs could therefore weigh as much as 150 g.

Incubation and hatching

The single egg is incubated in separate spells by both members of a pair. Both sexes therefore have well developed brood patches, the mean length and width being 81 ± 2.6 mm and 62 ± 1.2 mm respectively for 15 birds. The brood patch is heavily vascularized and completely denuded throughout the egg period. As in the closely related White-chinned Petrel, it seems that that female Westland Black Petrel on laying the egg does not immediately leave the burrow so that the male can take the first incubation spell. Three females that laid eggs on 28 May 1971 were found incubating on 29 May. Undamaged eggs were never left unattended during our visits. Of 170 inspections of burrows containing eggs we found single birds in attendance on 169 occasions and a pair in the remaining instance.

Hatching of Westland Black Petrel eggs is known to occur between early August and mid-September (Jackson 1958). In 1970 we first observed chicks on 1 August. The average mean weight of 13 chicks then was 230 ± 36.7 g, but they ranged from 90 g (hatching weight) to 485 g (about 2 weeks old). Thus in 1970 hatching must have commenced in mid-July. In 1971 we did not find any nestlings at the colony on 17 July, though the egg in burrow 0/7 was cracked and may have been pipping. Subsequent weighings of the chick in this burrow are consistent with a hatching date near this time. With one exception, perhaps because of interrupted incubation, all 52 fertile eggs had hatched before 8 August. Thirteen chicks weighed on our visit of 7-8 August averaged 430 ± 35.9 g, which corresponds to a mean age of about 10 days. Weights ranged from 220 to 670 g suggesting an age range of about 4-21 days respectively. These chicks must therefore have hatched between 18 July and 4 August. Eleven of the chicks were hatched from eggs laid before 28 May, so the minimum incubation period is 51 days and the maximum 68+ days.

Individual estimates of the incubation period are available for only three eggs. On the morning of 28 May a female with a red and distended cloaca typical of petrels about to lay (Serventy 1956), a well developed brood patch and an egg in the oviduct was located in burrow 3/5. It seems likely that she laid on this date. On 7 August a 540 g chick (about 14 days old) was found alone in the burrow.

Hence the incubation period for this egg must have been about 57 days. On 28 May another female was found in burrow 10/7 P without an egg and on 7 August a 280 g chick (about 6 days old) was found there, indicating an incubation period of about 65 days. On 29 May a bird (sex not determined) was found without an egg in burrow 10 P, and on 8 August a 370 g chick (about 8 days old) was present, giving an incubation period of about 63 days. These specific estimates of the incubation period are in accord with the general schedule for the colony; most laying in 1971 was completed by 28 May and hatching by 1 August, a period of 65 days.

THE CHICK PERIOD

Adult attentiveness

After hatching the downy chicks are attended by the parents for approximately two weeks (Jackson 1958), but thereafter are left unaccompanied in their burrows except when parents return to feed them at night. The attentive period seems to be quite variable, however, ranging from a few days to more than two weeks. On 7 August 197, 23 of 35 chicks were attended; the remaining 12 were alone in their burrows and ranged in age from 4-21 days. During the day only one parent of a pair was ever found attending the chick so that the relieved bird must depart for sea the morning after changeover.

Prolonged spells of adult attentiveness were noted on three occasions. Two adults were found brooding small chicks that had been dead for some time and one bird was found in its burrow 25 days after we had removed its addled egg.

Chick growth

Growth and development of nestling Westland Black Petrels has never been studied in detail and all that is known about this critical aspect of the life history is that the chick requires at least three months in its burrow before fledging (Jackson 1958). A newly fledged chick was recovered by Falla (1946) in mid-December and Jackson later reported that fledging occurred throughout this month. Because of very heavy chick mortality it was difficult for us to get data on growth beyond about the first three weeks of life. Three newly hatched chicks in 1970 averaged 98.3 ± 8.33 g (Fig. 2A), and 23 days later the two survivors weighed 630 g and 750 g respectively. Thirty-four days later only the smaller chick was alive and weighed 870 g at an age of approximately 2 months. Three further chicks (Figs. 2B-D) were weighed twice during the nesting period in 1970, though their hatching weights were not recorded. Two chicks which weighed 180 g and 420 g on 1 August were reweighed on 25 August at 690 g and 930 g respectively. The third chick progressed from 799 g on 26 August to 1384 g on 29 September, and this was the heaviest chick we weighed during the study.

TABLE 2. Summary growth statistics for five samples of Westland Black Petrel chicks in 1970 and 1971.

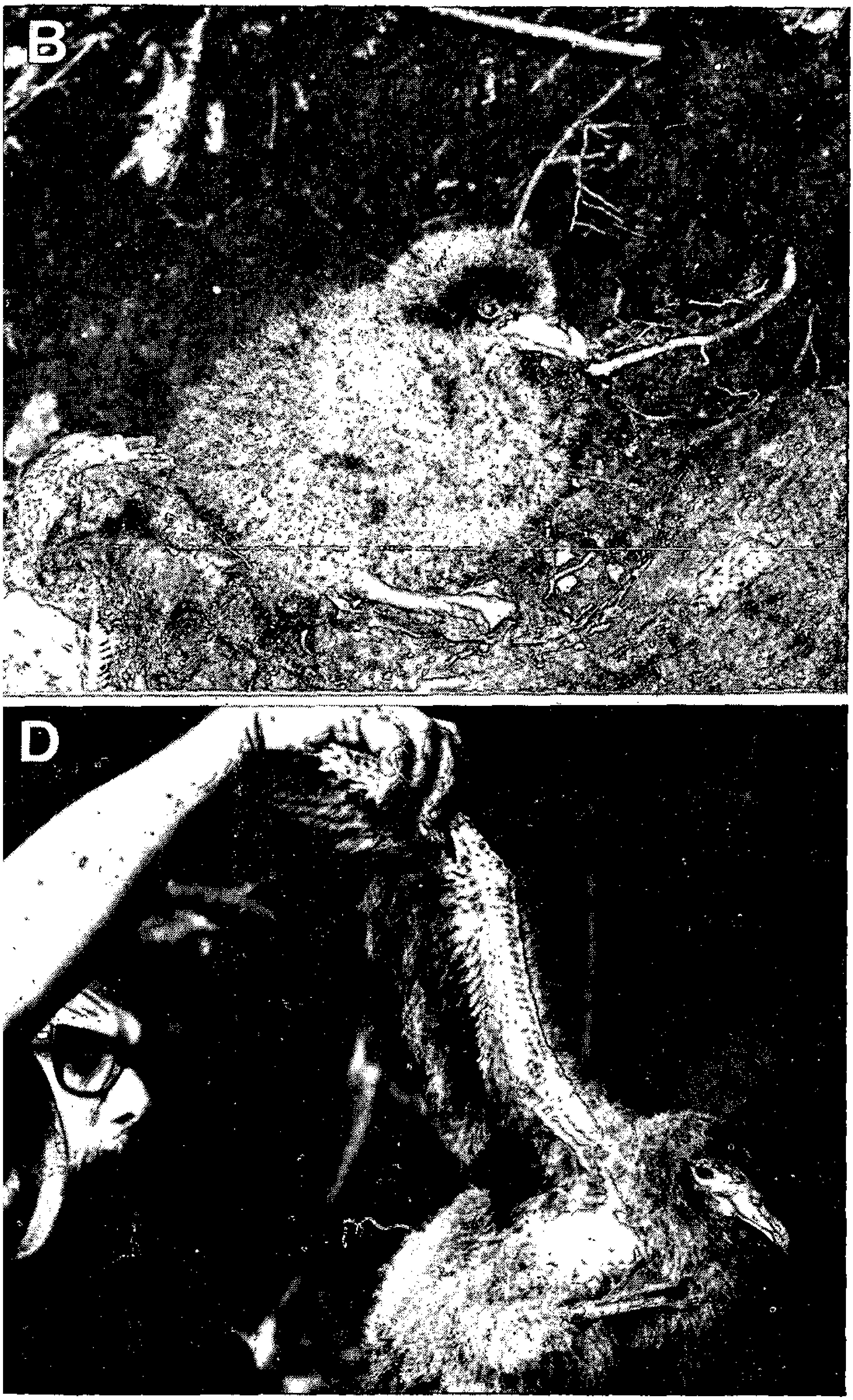
Sample	Date	n	Mean ± S.E.					
			Exposed culmen (mm)	Bill depth (mm)	Bill width (mm)	Tarsus length (mm)	Middle toe length (mm)	Body weight (mm)
1	1. 8.70	13	27.5 ± 0.59	13.9 ± 0.41	10.3 ± 0.44	29.3 ± 1.06	29.1 ± 0.99	230 ± 36.7
2	7 8. 8.71	13	31.1 ± 0.67	14.9 ± 0.28	12.4 ± 0.44	38.7 ± 1.31	37.0 ± 1.14	430 ± 35.9
3	25 -26 8.70	11	36.6 ± 0.78	17.7 ± 0.44	13.4 ± 0.45	49.7 ± 1.24	50.4 ± 1.85	754 ± 27.2
4	18. 9.71	2	44.9 ± 0.70	19.7 ± 0.60	17.1 ± 0.10	61.6 ± 0.80	68.5 ± 1.70	870 ± 14.0
5	29. 9.70	2	47.7 ± 1.60	21.9 ± 1.55	17.1 ± 0.55	63.1 ± 0.95	69.8 ± 3.95	1125 + 260.0

An estimate of the magnitude and progression of the growth rate of the chick population on the colony was obtained from samples of chicks weighed and measured on dates of our visits (Table 2). We have included here data for both 1970 and 1971 because the breeding seasons were very closely synchronised in the two years, as they are in many other Procellariidae (Lack 1968). Within the sampling period there is clearly a sigmoid pattern of growth in all variables except body weight (one chick being extraordinarily heavy at 1384 g, possibly following a large meal the previous night), growth being rapid at first but slowing progressively in older chicks. This trend is best expressed in the long bones. For example, in tarsus length, the increments between successive samples in Table 2 are 9.4 mm for the first 7 days, 11.0 mm for the next 17 days, 11.9 for the following 23 and finally 1.6 mm for 11 days. Corresponding "growth rates" (increment/time) are 1.34, 0.65, 0.52 and 0.15 mm/day. Fledging was not observed as we were unable to visit the colony at an appropriate time. However, large chicks were present on 29 September in 1970 when one banded chick weighed 1384 g (in excess of adult weight — see below). This chick (L-13153) was sighted alive in its burrow on 28 November when it was fully feathered and close to fledging (J. R. Jackson, pers. comm.). As most chicks were hatched by 1 August the chick period appears to be at least 120 days and could be as long as 140 days.

Oil spitting

When handled or disturbed, small chicks characteristically exude copious quantities of dark straw-coloured oil with a strong fishy odour. The exudation of oil does not always seem to be accompanied by lunging movements as described by Armstrong (1951) and Warham (1956, 1967) for Antarctic Fulmars *(Fulmarus glacialoides)*, Great-winged Petrels *(Pterodroma macroptera)* and White-headed Petrels

FIGURE 2 — Growth and development of *P. westlandica* chicks. A: Chick about 2-3 days old with first down; B: Chick about 6-8 days old with second down appearing; C: Chick about 1 month old with feather shafts of teleoptile plumage appearing on body and wings; D: Chick about two months old with emergent primaries, secondaries and contour feathers.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(Pterodroma lessoni) respectively, though spitting chicks always orient themselves towards the source of disturbance. Chicks as young as about 7 days old were observed to spit oil, and they maintained this ability until the end of August when they were about 4-6 weeks old. By mid-September in 1970, the few surviving chicks weighed in excess of 800 g and when handled no longer spat oil. Presumably, they were then sufficiently large and aggressive to repel intruders without recourse to oil spitting.

BREEDING SUCCESS

Breeding success (number of chicks fledged/number of eggs laid) was similar but very low in the two seasons studied (Table 3).

TABLE 3. Breeding success of Westland Black Petrels in 1970 and 1971.

Year	Eggs laid	Eggs hatched	Chicks fledged	Hatching success	Chick success	Breeding success
1970	35	26	2	74.3%	7.7%	5.7%
1971	66	36	2	54.5%	5.6%	3.0%

In 1970 we were unable to determine the exact number of eggs laid because some egg losses had undoubtedly occurred before our first visit to the colony on 20 June. Although only 14 eggs were found before hatching occurred we subsequently expanded our study in August to include a total of 50 burrows in which 26 chicks were present. Five of these chicks hatched from the 14 eggs we found so at least 35 eggs must have been laid in our study burrows. Because the data for 1970 exclude some egg losses during incubation the figures for hatching success (number of eggs hatched/number of eggs laid) and breeding success are overestimates. Conversely, the hatching success (35.7%) of our sample of 14 eggs is underestimated because we were responsible for the failure of three eggs. Excluding these latter three failures the hatching success is then raised to 45.5%, but the reliability of this estimate is suspect given the small sample size on which it is based. Chick success (number of chicks fledged/number of chicks hatched) in 1970 should be relatively unbiased, though it is possible that some very small chicks could have been lost before we first inspected some burrows. Given the dates of our visits this source of error should be minimal, but in any event the estimate of chick success is conservative and can only err on the high side. The data for 1971 are less subject to the above difficulties because we followed 52 of the 66 eggs from laying onwards, but nevertheless any biases that may have been introduced by not observing all eggs through incubation can only have led to overestimates of breeding and hatching success.

Table 4. Egg and chick losses of Westland Black Petrels studied in 1970 and 1971.

Stage of loss	Cause of loss or failure	Years		Totals
		1970	1971	
Eggs	Burrow collapsed	1	4	5
	Infertile	1	1	2
	Embryo died before hatching	0	4	4
	Egg smashed by adult	0	3	3
	Unknown	7	18	25
		9	30	39
Chick	Predation	1	1	2
	Infanticide	2	0	2
	Fell over cliff	0	1	1
	Scratched out of burrow by sub-adults	0	2	2
	Unknown	21	30	51
		24	34	58

Losses of eggs and chicks on the colony are shown in Table 4. Most eggs lost simply disappeared from nests between our visits, always in the last 2-3 weeks before hatching commenced. It is possible that heavy predation of newly hatched chicks occurred (which would account for the apparent disappearance of eggs), but parents are fiercely aggressive at this time and remain in the burrows to brood their young. Furthermore, we did not find any remains of young chicks that had been eaten.

Only two eggs were found to be infertile. Three eggs were smashed by clumsy adults during incubation, possibly during change-over of mates. Of the four eggs that contained dead embryos, two had been pecked and the shell punctured by the incubating birds, and this may have eventually killed the embryos. The only other source of egg loss was from collapsed nest chambers in which case the sitting bird deserted the burrow and did not return.

Most chicks disappeared from their burrows when they were approximately 5-7 weeks old and weigh 800 g or more. Only two instances of chick predation were recorded and in both the skeletal remains bore teeth morks, possibly those of a rat, stoat or feral cat. Similarly, Jackson (1958) found only one instance of mammalian predation in three seasons of study, though he cited Penniket's (1955) report of a high stoat density on the colony. We did not see any obvious signs of stoats or rats on the colony other than the two chicks mentioned above and the remains of an adult that had been eaten. Wekas *(Gallirallus australis)* abound on the colony and may be responsible for some chick losses. One Weka was observed pulling flesh off the neck of a dead chick we placed on the surface and another attacked and killed an emaciated chick which it pulled out of a shallow burrow. It is doubtful whether Wekas are important predators of petrel chicks however, as many burrows have entrance tunnels too small to allow access to Wekas and because they do not venture far into burrows occupied by adults or large chicks. Two apparent instances of infanticide were noted: two adults with blood on their bills were found in burrows with freshly dead chicks that had been severely pecked about the head.

It is curious and perhaps not merely coincidence that in both breeding seasons heavy losses of larger chicks were sustained in September. The size of the chicks taken and the absence of any sign of predation suggest that the colony may be subject to " birding." We found boot marks around burrow entrances and a few portals dug up and removed from nest chambers which on our previous visit contained chicks. Additional information was obtained from concerned residents living near the colony; they were convinced that birding occurred though they were unable to provide corroborating evidence. The Wildlife Service has been alerted to watch for birding in the future, so it is to be hoped that their surveillance will lead to increased breeding success.

It is extremely unlikely that our observations contributed significantly to the heavy losses of eggs and chicks, especially in 1971 when we were careful not to unduly disturb incubating or brooding birds. The 25 control burrows were completely unproductive; no chicks survived in them in September. At the same time we also checked across the valley on the north wall of Scotsman's Creek where the largest concentration of about 265 burrows is situated (Best &

Owen 1976). No chicks were found in 50 used burrows we inspected so it seems that 1971 was a poor breeding season for Westland Black Petrels. Some caution is warranted in extrapolating these mortality rates to future years however, because periodic but short-term failures have been recorded in other Procellariidae (Richdale 1963; Mougin 1969, 1970). Long-term studies are needed to estimate accurately the average breeding success of *P. westlandica.*

UNEMPLOYED BIRDS ON THE COLONY

It is extremely difficult to determine the status of birds at the colony without marked birds of known provenance. However, unemployed birds are common at the colony at certain times, and there is some indirect evidence that they may fall into two categories as outlined by Richdale (1963): non-breeders (presumably adults which may have previously bred but are not breeding in the year of observation) and pre-breeders (birds which are too young to have previously bred).

In May 1971, both breeders and unemployed birds were present on the colony. Of 81 used burrows only 15 apparently did not have eggs later laid in them, and thus the frequency of unemployed non-breeders was maximally 18.5%. However, caution is warranted in interpreting this figure because it is based on two assumptions — that all 15 burrows were occupied by different birds, and that " non-breeders " were actually failed breeders that had lost eggs at laying. Two burrows contained pairs that built nests, though eggs were never seen. Only two of the remaining 13 burrows were known to be occupied with lone birds being found there during the day, but the rest were excavated and appeared to be used. It was not possible to estimate accurately what proportion of the unemployed birds had had previous breeding experience; two banded pairs which bred in 1970 were present on the colony in 1971, but did not breed.

Birds presumed to be pre-breeders were first seen on 11 July, although they could have been present as early as 22 June. On 1 August the colony was subject to a large night-time influx of such birds. Although some may have been failed breeders returning after lengthy feeding forays, the dramatic upsurge in activity at the colony seems likely due to the arrival of pre-breeders. Virtually all burrows that were unused or had been occupied by failed breeders were re-occupied and excavated so that the colony appeared as it did in early May, with widespread occurrence of fresh soil and dung. Further support for the pre-breeding status of these birds was provided by their smaller size in some dimensions (relative to adults — see Table 5), their lack of a brood patch or any obvious dimorphism in cloaca size, and one bird had brown scapulars and belly contour feathers indicative of immaturity.

Of 15 burrows occupied by unemployed birds during the day in August 1970, six contained two birds and nine had lone birds. The pairs were very vocal and often called loudly during the day. Unemployed birds were present at the colony through most of August, and in September they ceased coming ashore so that the colonies were again quiet at night.

TABLE 5. Standard measurements and weights of breeding and pre-breeding Westland Black Petrels captured in 1970 and 1971

Variables	Mean ± S. E. Breeders (n=67)	Mean ± S. E. Pre-breeders (n=30)	F value[1]
Exposed culmen (mm)	50.4 ± 0.25	49.3 ± 0 38	6 014*
Bill depth (mm)	22.9 ± 0.14	22.5 ± 0.22	617 n.s
Bill width (mm)	18.8 ± 0.13	18.6 ± 0.19	0 311 n s
Tarsus length (mm)	64.6 ± 0.21	63.6 ± 0 36	5.883*
Middle toe length (mm)	73.0 ± 0.29	72.0 ± 0.44	4.141*
Wing length (mm)	384 ± 1.2	386 ± 1.9	0.867 n s.
Tail length (mm)	128 ± 0.7	125 ± 0.9	6.138*
Body weight (g)	1199 ± 13.3	1117 ± 14.3	13.877***

[1] Significance levels denoted as follows: *** = $P < 0.001$, * $P < 0.05$
n.s. = not significant, $P > 0.05$

DISCUSSION

The breeding cycle of *P. westlandica* outlined above shows some interesting similarities and differences with the other species of the genus and some well known Procellariidae. Most comparative data are available for the closely related White-chinned Petrel *(P. aequinoctialis)* which has been studied extensively in the islands of the subantarctic and adjacent areas (Hall 1900; Matthews 1929; Murphy 1936; Falla 1937; Gibson-Hill 1949; Rowan *et al.* 1954; Hagen 1952; Paulian 1943; Rand 1954; Westerskov 1960 and Mougin 1970).

Procellariidae which have reached breeding age generally return each year to breed with the same mate in the same burrow. Because of low adult mortality and high mate fidelity in *P. aequinoctialis* on the Crozet Islands, divorce is rare (Mougin 1970), and this seems to hold for *P. westlandica* too. The arrival of adults at the colonies well in advance of laying is a feature of the breeding cycle of petrels. This long re-occupation period is used to prospect for and claim burrows, establish pair-bonds and build nests. In *P. aequinoctialis* the birds return singly and pairs reform in the burrows, and this is consistent with our observations of single birds and pairs in burrows in the Westland colony in early May. Mougin noted a pre-laying exodus in *P. aequinoctialis* about 15 days before the beginning of laying. There is a strong suggestion that *P. westlandica* has a similar honeymoon period as almost half the burrows containing nests in early May were uninhabited. In winter breeding species such as *P. westlandica* the honeymoon period could be even more important than in summer breeding species. For example, the winter breeding Grey-faced Petrel *(Pterodroma macroptera gouldi)* in northern New Zealand has an unusually long pre-laying absence of about 60 days, which is considerably longer than that of its summer breeding congeners (Imber 1976). The pre-laying absence is thought to be necessary to allow both sexes to gather and store further food reserves; females have to form large eggs and males have to fast during the first long incubation spell (Lack 1966). Although the duration of individual incubation spells was not determined in the present study, it is probably similar to that of *P. aequinoctialis* in which the range is 7-15 days (Mougin 1970), and hence considerable food reserves would be required to tide the birds over the lengthy sojourns at the nest.

Although the laying season in *Procellaria* is quite often prolonged (Hall 1900; Murphy 1936; Oliver 1955), the great majority of eggs are laid in a short peak period of about 3 weeks near the beginning of the season (Mougin 1970; this study). The reason for this synchrony in species which do not undertake large migrations is unknown; in the Short-tailed Shearwater *(Puffinus tenuirostris)* (cf Serventy 1963), the Sooty Shearwater *(Puffinus griseus)* (cf Richdale 1963), and the Greater Shearwater *(Puffinus gravis)* (cf Rowan 1952) the average laying date is almost constant from year to year and the laying season is very restricted (3 weeks or less). Lack (1966) interpreted this extreme synchrony as an adaptive response to allow chicks time to fledge and adults to complete breeding duties before migration. It is possible that because of the long incubation and chick periods in *P. westlandica* (and other *Procellaria*), synchrony is needed to allow adults sufficient time to achieve breeding condition in the following season.

The estimated incubation period of 57-65 days for eggs of *P. westlandica* is slightly longer than that of *P. aequinoctialis* of 50-60 days (Murphy 1936; Mougin 1970). The explanation for this long incubation period seems to be that it is the simplest way of retarding the rate of development of the chick, as there is a general correlation in birds between the durations of the incubation and chick periods (Lack 1948, 1966). Although such a strategy exposes the eggs to the risk of nest predation for a longer time, this is compensated for in burrowing petrels by the protection afforded by the burrows. The longer incubation period of *P. westlandica* (relative to *P. aequinoctialis)* may relate to the increased difficulty of gathering food in winter (see beyond).

The chick period is much longer in *P. westlandica* (120+ days) than it is for the winter breeding *P. cinerea* (82 ± 5 days) at Tristan da Cunha (Elliott 1957), or the Crozet Islands (100+ days, Barrat 1974), or the summer breeding *P. aequinoctialis* (91-105 days) at the Crozet Islands (Mougin 1970). As Lack (1968) has pointed out, the chick period is usually longer in petrels breeding at lower latitudes (where the seas are generally less productive), and he therefore advanced the hypothesis that the Procellariiformes have evolved different growth rates in response to the average availability of food for the young. The long fledging period of *P. westlandica* could therefore result from a rather sparse and variable food supply, as might be expected for a winter breeding bird at the latitude of the South Island. The shorter fledging period of *P. cinerea* at Tristan du Cunha is anomalous in this context and suggests that food supplies may be locally abundant there even in winter.

Given the evolution of a slow growth rate to combat sparser and more variable food supplies the question remains as to why *P. westlandica* (and some other Procellariidae) breed in winter. Two competing hypotheses have been considered by Lack (1966): (1) segregation of breeding seasons of congeneric species is due to competition for nesting sites, and thus the same burrows can be used alternately by different species (Lockley 1952), and (2) segregation results from competition for food during the breeding season (Bourne 1955, 1957). The first hypothesis can hardly apply to *P. westlandica.* Although its breeding distribution overlaps that of the summer breeding Black Petrel *(P. parkinsoni)* (see Falla 1946), both species have such long breeding seasons that they could not possibly alternate annually in the same burrows, and additionally, there is no shortage of potential breeding sites in the coastal ranges of Westland. Competition for food with *P. parkinsoni* (and perhaps other shearwaters such as *Puffinus griseus*) seems to be the most plausible explanation for the winter breeding season of the Westland Black Petrel.

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