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ABSTRACT

A STUDY of the southern giant petrel (*Macronectes giganteus*) was carried out at Signy Island, South Orkney Islands. Birds are seen around the breeding colonies throughout the year, numbers being lowest at mid-winter. They return to the island in July and August, when their weight is maximal; between then and the end of October, the pair-bond is re-established and the nest site occupied. Egg-laying, spread over 21 days, is fairly synchronous from year to year (mean date 4 November ± 1·75 days for 13 years' data) and follows a pre-laying exodus, probably involving only the female. No replacement clutch is laid if the single egg is lost or removed. Both sexes take part in incubation, during which period the bird starts body moult. Incubation lasts about 60 days, the chicks hatching in January.

After the guard period which lasts about 21 days, there is a period of 10–15 days during which the parent may return to the chick should the weather deteriorate markedly. The fledging period lasts about 117 days, being similar for both sexes. On leaving the nest, the chicks may remain in the vicinity of the island for a few days before they finally depart. The data suggest that chicks which fledge early are heavier than those which fledge later, probably because the adult birds stop feeding the chicks in early May, regardless of their age.

Sexual dimorphism occurs in both adults and chicks, and a discriminant function can be calculated to sex the adult birds in the field.

Birds return to the island as early as their third year, but more commonly during their fifth and sixth years. The youngest recorded age of first breeding is 5 years, and sight records suggest that birds may breed as early as 3 or 4 years. The males possibly return to the colony and breed at a younger age than the females.

The incidence of white-plumage birds in the population is probably controlled by one or more recessive genes, and there is no selective mating for the maintenance of the white phase in the population. Ringing recoveries, and counts of the proportion of white-phase individuals in populations show that, at least in the juvenile, white-phase individuals are less fit than the brown phase.

Results of twinning experiments are discussed.

The data are compared with the results of studies at other breeding localities.

CONTENTS

I. INTRODUCTION

To travellers in the Southern Ocean giant petrels are well known and easily distinguished from other sea birds by their size and bulky appearance. Seamen call them "nellie", "stinker", "bone-shaker" and the South American "quebranra-huesos"; the latter is probably the oldest name for the bird, being used by the early explorers to the Southern Hemisphere (Cook, 1777).

Giant petrels are both scavengers and birds of prey, feeding at sea and on land. The literature on the genus includes many references to their gluttonous habits, resulting often in over-indulgence and their having to sit around to allow digestion to take place before taking off. If one is disturbed while feeding or immediately afterwards, it will waddle away, disgorging food as if to lighten itself before it can take off.

Two distinct colour phases are identified, white and brown, the latter being represented by various shades (Plate Ia).

1. *Taxonomy*

The nomenclature of the giant petrels has been the subject of much discussion. The first specimens, collected off Staten Island (lat. 54°40'S., long. 64°00'W.) during Cook's second voyage (1772–75), were called "giant petrel" (Latham, 1785). Gmelin (1788) first named the genus *Procellaria* and the species *P. gigantea*. Hombron and Jacquinot (1844) re-named the genus *Ossifraga*, which generic name was used until the beginning of the present century, for example Clarke (1905, 1906, 1907) and Wilson (1907). The present generic name, *Macronectes*, was introduced by Richmond (1905) and throughout the present study the genus referred to is *Macronectes* Richmond.

Unlike most of the Procellariiformes, the genus, which contains only two similar species, shows great variation in plumage colour and body size, the latter related to differences between the sexes (Murphy, 1936; see also p. 11). Formerly these colour and size differences caused much confusion and discussion, and led to the formation of several sub-species (Mathews, 1912, 1916). These have been discussed by Lowe and Kinnear (1930). The white phase was designated as a separate species, *Ossifraga alba* Potts 1874.

These sub-species were based on very small samples, and in some cases on specimens collected far from the breeding grounds, for example from Valparaiso, Sydney and the Ross Sea.

While working through the collection of the *Terra Nova* expedition, Ogilvie-Grant recognized two species: a northern species being "a dark brown form with a lemon-yellow bill met with from about 35°S. to about 55°S. latitude, and a southern form with dimorphic plumage . . . met with from about 45°S. latitude" (Ogilvie-Grant *in* Lowe and Kinnear, 1930). After his death this work was completed by Lowe and Kinnear (1930). They concluded that there was only one species of giant petrel, *Macronectes giganteus* (Gmelin). Murphy (1936), after examining over 100 specimens, from several localities, concluded . . . "Taking into account the variations I have described and keeping in mind the pronounced sexual differences in size, I am unable to recognize among more than 100 adults from all parts of the range the criteria for the several sub-species that have been described . . ."

In the years following the publication of Murphy's book, the idea of a single species, *Macronectes giganteus* (Gmelin), in the genus *Macronectes* Richmond became accepted. Recently, Carrick (personal communication from G. M. Dunnet), while studying the biology of this species on Macquarie Island (lat. 55°00'S., long. 166°00'E.), noted two distinct populations breeding about 6 weeks out of phase. These differences might have been associated with different age classes, but after further study into the Macquarie Island situation (Warham, 1962) and a comparison with photographs and skins collected from other breeding colonies resulted in the confirmation of Ogilvie-Grant's idea of two species of giant petrel (Bourne and Warham, 1966), they concluded there were two sibling species, a southern form which they called *Macronectes giganteus* (Gmelin) and a northern form which they called *Macronectes halli* (Mathews). The forms have been defined by Bourne and Warham (1966) as follows:

> "The name *Macronectes giganteus* (Gmelin) applies to the southern form. This form breeds on the Antarctic Continent, on the islands of the Scotia Arc, north to South Georgia and the Falklands, on Heard Island and Macquarie Island, and possibly on some islands near the Antarctic Convergence. It is polymorphic, with a pale phase that is white with occasional dark feathers throughout life, and a dark phase which is dark brown when immature becoming grey-brown with a pale head or face when adult and at Macquarie Island with an unmarked greenish to yellow bill. It breeds colonially in open situations late in the year and the young are highly migratory.

> "The name *Macronectes halli* (Mathews) applies to the northern form. This form breeds in the sub-Antarctic zone of surface water at the Chatham, Auckland, Antipodes, Campbell, Stewart, Macquarie, Kerguelen, Crozets, Marion and Gough Islands, and possibly elsewhere in this zone at Amsterdam Island. There is no evidence that it is polymorphic. Young birds are also dark brown; old birds resemble the dark phase of the southern form, but are darker and browner with dark heads, and a white face with a well-defined mottled dark border. At Macquarie Island breeding adults have yellow-brown bills with dark markings within the nails. This form tends to nest in August throughout its range, and at Macquarie Island tends to nest alone in sheltered places."

Both species also breed on Iles Crozet (lat. 46°27′S., long. 52°00′E.) (Voisin, 1968) and Marion Island (lat. 46°53′S., long. 37°45′E.) (van Zinderen Bakker, 1971*a*).

Carrick and Ingham (1967, 1970), reviewing Antarctic sea-bird ecology, accepted this separation of the genus but showed that the division is not so marked as suggested by Bourne and Warham. The differences in nest-site selection are not so well defined; although *M. halli* nests in sheltered areas, it may form small colonies and breed within groups of *M. giganteus*. Recoveries of ringed *M. halli* nestlings have shown that the species, like *M. giganteus*, disperses to latitudes far distant from their breeding colonies. Young *M. halli* ringed on Macquarie Island have been recovered at Australia, New Zealand and South America (Carrick and Ingham, 1970; personal communication from D. Purchase), while young birds ringed on Iles Crozet have been recovered at Australia and New Zealand (personal communication from J. Prévost).

Shaughnessy (1970*a*) studied three of the blood proteins of both species on Macquarie Island, but found no differences in the mobilities of those examined.

Johnstone (1971; personal communication) has completed a detailed study of both species at Macquarie Island, and found several differences between them.

The species found on Signy Island is *Macronectes giganteus* (Appendix I); throughout the text this species is referred to as the southern giant petrel and all references to the giant petrel on Signy Island refer to *M. giganteus*.

2. *Breeding distribution*

Macronectes is circum-polar and breeding localities cover a wide latitudinal range, extending from those offshore islands of New Zealand, where the climatic conditions and habitat are suitable for nesting, to the Antarctic mainland (Table I—where known, the sizes of the colonies are given; the classification of Bourne

TABLE I

KNOWN BREEDING LOCATIONS OF THE GENUS *Macronectes*

Location	*Authority*	
Gough Island* (lat. 40°10′S., long. 4°45′W.)	Verril (1895), Swales (1965)	Swales reported 60 nests
Chatham Islands* (lat. 44°00′S., long. 176°40′W.)	Hutton (1872), Fleming (1939), Dawson (1955)	Reported as breeding in large numbers on Forty Fours Island and on the Sisters group
Iles Crozet† (lat. 46°27′S., long. 52°00′E.)	Falla (1937), Voisin (1968)	Both species found (Voisin, 1968)
Marion Island† (lat. 46°53′S., long. 37°45′E.)	Sharpe (1902), Crawford (1952), Rand (1954)	van Zinderen Bakker (1971*a*) reported both species
Stewart Island* (lat. 46°58′S., long. 167°54′E.)	Fleming (1948), personal communication from B. D. Bell and R. H. Taylor	Breed in very small numbers around Port Pegasus
Iles Kerguelen* (lat. 48°30′S., long. 69°40′E.)	Kidder (1875), Hall (1900), Falla (1937), Milon and Jouanin (1953)	
Antipodes Island* (lat. 49°45′S., long. 178°48′E.)	Personal communication from B. D. Bell and R. H. Taylor	100+ pairs
Auckland Islands* (lat. 51°00′S., long. 166°00′E.)	Personal communication from B. D. Bell and R. H. Taylor	About 100 pairs

Falkland Islands (lat. 51°30′S., long. 59°00′W.)	Murphy (1936), Cawkell and Hamilton (1961), personal communication from R. Napier and R. Woods	Probably 6–7 colonies, one of which had over 1,000 birds (Cobb, 1933)
Beauchêne Island (lat. 52°54′S., long. 59°09′W.)	Strange (1965)	Possible breeder
Campbell Island* (lat. 52°30′S., long. 169°00′E.)	Westerskov (1960), Bailey and Sorensen (1962), personal communication from B. D. Bell and R. H. Taylor	About 100 pairs
Heard Island (lat. 53°00′S., long. 54°00′E.)	Downes and others (1959)	At least 8,000 nests
Staten Island (lat. 54°40′S., long. 64°00′W.)	Murphy (1936)	
South Georgia (lat. 54°30′S., long. 37°00′W.)	Matthews (1929)	
Macquarie Island† (lat. 55°00′S., long. 166°00′E.)	Falla (1937), Warham (1962)	Both species found (Bourne and Warham, 1966); 8,600 breeding birds probably both species (Warham, 1962)
South Sandwich Islands (lat. 57°00′S., long. 37°00′W.)	Baker and others (1964)	Breeds on Candlemas Island (personal communication from P. J. Tilbrook); Voous (1965) reported they do not breed there
South Orkney Islands (lat. 60°45′S., long. 45°00′W.)	Clarke (1906), Ardley (1936)	
Elephant and Clarence Islands (lat. 61°00′S., long. 55°00′W.)	Furse and Bruce (1971)	830 pairs
South Shetland Islands (lat. 62°00′S., long. 59°00′W.)	Bennett (1926)	
Antarctic Peninsula		
Anvers Island (lat. 64°30′S., long. 63°40′W.)	Holdgate (1963), Lippert (1967)	
Pourquoi Pas Island (lat. 67°41′S., long. 67°28′W.)	Imray (1957)	About 60 nests
Avian Island (lat. 67°46′S., long. 68°54′W.)	Willey (1969)	About 160 nests

Stonehouse (1950) recorded on Henkes Island (lat. 67°44′S., long. 69°10′W.) but a recent visit to the island showed no breeding birds there, and the terrain looks unsuitable for giant petrel nests (personal communication from I. Willey).

Antarctic continent		
Terre Adélie (lat. 66°39′S., long. 139°15′E.)	Prévost (1953)	Population on decline because of human interference
Frazier group (lat. 66°20′S., long. 110°28′E.)	Law (1958), Korotkevich (1958)	Nests on at least two islands; total 4 colonies, 240 nests
Rookery Island (lat. 67°37′S., long. 62°52′E.)	Dunnet (personal communication)	
Holme Bay (lat. 67°35′S., long. 62°42′E.)	Holdgate (1970)	

* *M. halli* only. † Both *M. giganteus* and *M. halli.* Remainder *M. giganteus.*

and Warham (1966) is used). In addition to these data, breeding has been reported from Snares Island (Waite, 1909; Falla and others, 1966), but Warham (personal communication) reported that the birds do not breed on the islands. The birds once bred on Tristan da Cunha (lat. 37°06'S., long. 12°20'W.) (Moseley, 1892; Elliott, 1957) but became extinct there (Holdgate and Wace, 1961) towards the end of the last century. Hagan (1952) reported birds still bred on the island in 1870. A recent reference to five million giant petrels breeding there (Sparks and Soper, 1967) is obviously unfounded. They referred to a "Victoria Island" as part of the Tristan group, but no such island large enough to hold five million giant petrels exists.

The following islands have been visited and no breeding recorded: Balleny Islands (Dawson and others, 1965), Bouvetøya (Solyanik, 1959), Peter I Øy (Holgersen, 1945), Bounty Islands (Falla, 1965), Ile Amsterdam and Ile St. Paul (Paulian, 1953, 1960). Darby (1970) wrote of the possibility of a colony at Robertson Bay, Cape Adare, quoting B. Reid, who saw 115 birds there, but no proof of nesting was found, although the terrain in the area looked suitable for nesting (personal communication from B. Reid).

Murphy (1936) recorded that Staten Island was the only known breeding colony in South America, although it possibly bred on the islands of Tierra del Fuego. He reported that Paessler (1909) inferred it bred on the west coast of the continent just south of Chiloe. Gould (1841) wrote that it formerly bred along the coast of Patagonia, including the estuary of the Rio Santa Cruz. Reynolds (1935) mentioned a photograph he saw of a giant petrel on a nest on Isla Negra 40 miles [64 km.] west of Brebnock Peninsula, near Cape Horn. Recently, Humphrey and others (1970) reviewed the birds of Tierra del Fuego and recorded the giant petrel as a regular non-breeding resident, but they made no mention of Staten Island, while Johnson (1965) reported that the nearest breeding ground to South America was the Falkland Islands.

3. *Dispersal*

Both adult and immature *Macronectes* range far beyond their breeding stations, and immatures particularly are regular visitors on coasts north to lat. 30°S. In regions influenced by cold water, such as the Humboldt and Benguela Currents, they disperse farther to the north. Records from elsewhere in the Southern Hemisphere's lower latitudes and in the Northern Hemisphere are few. Moreau (1942) reported a giant petrel (identified by its head) at Mafia Island, off Tanganyika; Mougin and others (1969) recorded one at Maturei-Vavao, while Merton (1970) recorded one on the Kermadec Islands. Birds hatched on Signy Island have been recovered on Fiji. Early records from the Northern Hemisphere have been discussed by Bourne (1967) and many of them can be discounted. A bird described as a giant petrel was sighted at Midway Island during December of 1959, 1961 and 1962, and on the last occasion it was identified as *Macronectes* sp. (Fisher, 1965), but no description or photograph of this bird appeared in the text, and the possibility of misidentification cannot be ruled out. The most recent sighting was of a very dark individual in the English Channel on 2 October 1967; the bird was flying with a group of sooty shearwaters (*Puffinus griseus*) from which it was easily distinguished by its robust build (Meeth, 1969).

In the higher Antarctic latitudes, far from their breeding colonies, the birds are also regular visitors. Near Peter I Øy, they were seen by members of the Swedish Antarctic Expedition, 1927–28 (Holgersen, 1951). Along the Antarctic Peninsula regular sightings have been reported from some of the British Antarctic Survey stations. Imray (1957), McGowan (1959) on Horseshoe Island, Lefeurve (1960) on Stonington Island and Willey (personal communication) on Adelaide Island reported that birds were seen regularly throughout the year, with numbers lowest in the winter. Stonehouse (1950) saw a giant petrel as far south as Alexander Island; the nearest known breeding colony to those localities is at Avian Island. From the northern end of the Antarctic Peninsula birds were seen all year round, although no breeding colony was in the immediate vicinity (Araya, 1965). In the Ross Sea sector, the birds have been seen at lat. 70°S. (Ferrar, 1928) and near lat. 78°S. (Holgersen, 1945; Darby, 1970). Sightings in the region of McMurdo Sound are well documented, since this is where many of the early expeditions made their land stations (Sharpe, 1902; Wilson, 1907; Lowe and Kinnear, 1930; Siple and Lindsay, 1937). In the Weddell Sea sightings are less well documented. During the voyage of *Scotia* six giant petrels were recorded off Coats Land on 6 March 1904 (Clarke, 1907; Wilton and others, 1908); on *Quest* they were seen at lat. 68°S. (Wild, 1923). Novatti (1960, 1962) gave details of two cruises in this area, with the most southerly sighting at lat. 77°S., while Cline and others (1969) saw only eight birds on 3 days between January and March 1968.

Winter observations of birds in Antarctic waters are few. During a crossing of the Pacific Ocean, Szijj (1967) saw giant petrels, usually in ones and twos to near the southern limit of the cruise (lat. 62°25′S., long. 159°40′W.) when the ship was in ice.

Routh (1949) is clearly wrong in classifying giant petrels as birds which frequent only the edges of the pack ice.

4. *Previous work in the South Orkney Islands*

Observations on giant petrels in the South Orkney Islands were made by members of the *Scotia* Expedition (1902–04), by biologists of R.R.S. *Discovery* (1931 and 1933), and by the Falkland Islands Dependencies Survey (F.I.D.S.), and the British Antarctic Survey (B.A.S.) (Clarke, 1906; Ardley, 1936; various unpublished F.I.D.S. and B.A.S. base reports).

On Signy Island, studies began soon after the station was established in 1947. During the following summer 22 birds were ringed by Laws (1948) and in July of that year, one of these (a white-phase juvenile) was recovered alive at Fremantle, Western Australia (Serventy, 1948), providing the first definite evidence of the dispersal of the species. Further long-distance recoveries of ringed nestlings led in 1955–56 to the initiation of an annual ringing programme for the island. Initially only nestlings were ringed and adults were first ringed in 1959 (Table IIa and b).

Throughout the period two main types of rings have been used. The early aluminium overlap rings with the double inscription "Inform F.I.D.S. Colonial Office: London" were superseded in 1962 by monel rings (size no. 5: 19 mm.), supplied by the British Trust for Ornithology (B.T.O.). These have been used ever since. They are butt ended and bear the legend "Inform British Museum, London S.W.7". (In 1963 a clip-on monel ring was tried, but proved unsuitable and has subsequently been replaced.) Since their introduction, monel rings have been used to replace the aluminium rings on recaptured birds ("controls"). Consequently, although 2,618 rings have been used on adult birds, 352 have been used on controls, the actual number of adults ringed is 2,266. For the purpose of ringing, the birds are grouped into two categories. Nestlings—birds ringed on the nest, before they can fly. All are ringed on the right tarsus, and when recovered are referred to as birds of known age. Adult birds—include all other birds ringed as breeding birds. Nestlings are ringed on the right tarsus, and replacement rings are placed on the right tarsus. Adult birds are ringed on the left tarsus. In 1958, an attempt was made to distinguish the subsequent age structure of the population by putting a colour ring on the left tarsus of each nestling ringed, each year being designated by a different colour. The rings proved to be very brittle with a short life and the scheme was stopped in 1963.

In addition to bird ringing, routine observations on general aspects of the biology of the giant petrel, particularly its breeding biology, have been collected but remain in unpublished reports.

II. AIMS AND METHODS

SEVERAL authors have already published papers on the genus *Macronectes* and discussed various aspects of the species' biology (Wilson, 1907; Lowe and Kinnear, 1930; Murphy, 1936; Falla, 1937; Downes and others, 1959; Bailey and Sorensen, 1962; Warham, 1962; Bourne and Warham, 1966; Mougin, 1968; Voisin, 1968). With the exception of Mougin, all the breeding data refer to the sub-Antarctic islands; Mougin carried out his work at Terre Adélie and, in addition to his own work, he summarized the relevant observations of Prévost (1953, 1958, 1963, 1964). Since no detailed work has been published from the maritime Antarctic, the purpose of the present study was to describe the biology of *Macronectes giganteus* (Gmelin) in the maritime Antarctic and compare this with work carried out elsewhere.

On account of the data already accumulated on the giant petrel, Signy Island was the most suitable area for a study of *Macronectes giganteus* in the maritime Antarctic. The island is part of the South Orkney Islands, lying on the Scotia arc, its area is approximately 18 km.^{2}, measuring 8 km. by 5 km. at its maximum axes, with a maximum altitude of 280 m. The climate of the island has been described elsewhere (Pepper, 1954; Holdgate, 1967; Holdgate and others, 1967), and has been summarized by Heywood (1967). The mean monthly temperature range is small (+0·8° to −10·5° C) and the island is subjected to high prevailing winds from the north-west (mean annual wind speed 7·6 m./sec.). During the winter the coast is surrounded by sea ice which may persist for up to 8 months (May–December). The permanent ice cover on the island is restricted to the higher central plateau, and the snow on the lower slopes and coastal areas

Table IIa

NUMBER OF CHICKS RINGED ON SIGNY ISLAND AND SUBSEQUENTLY RECOVERED

				Chick recoveries (non-breeding)					*Chick recoveries (breeders)*								
Year of ringing	*Number of rings used*	*Chicks failing to fledge**	*Gaped rings*	*Chicks recovered dead*	*1st year*	*2nd year*	*Subsequent years*	*Non-breeders on Signy Island*	*Re-ringed*	*Not re-ringed*	*Net fledged*	*Net birds recovered away from Signy Island*	*Net birds recovered breeding*	*Total recoveries*	*Per cent of birds recovered away from Signy Island*	*Per cent of birds recovered breeding*	*Per cent of total recoveries*
1948	32				1				1		32	1	1	2	3·13	3·13	6·25
1949	12										12						0·0
1950	46†	2									43†			1		2·33	2·33
1951	63	2			2				1	1	61	2	2	4	3·28	3·28	6·56
1956	597		6		8	1	1		8	5	597	10	13	29	1·68	2·18	4·86
1957	1,000		5	1	33	1			3	5	1,000	34	8	49	3·40	0·80	4·90
1958	1,413	26	5	2	60	1				3‡	1,387	61	3	70	4·40	0·22	5·05
1959	1,185	7	9	1	44	2		1			1,178	46	0	57	3·90	0·0	4·84
1960	1,465	6	5	3	17	2			9	6	1,459	19	15	42	1·50	1·03	2·88
1961	1,211	1	1		18		2		5	3	1,210	20	8	29	1·65	0·66	2·40
1962	1,473	5		10	21	3				10	1,468	24	10	44	1·63	0·66	3·00
1963	1,289	2		6§	35	1	1			4§	1,287	35	4	46	2·72	0·31	3·57
1964	578	1		1	16						577	16		17	2·77		2·95
1965	1,202	6			22	1					1,196	23		23	1·92		1·92
1966	1,041	4		1	25	4	2				1,037	31		32	2·99		3·09
1967	415				7	3		1			415	10		11	2·41		2·46
1968	901	16			24	1					885	25		25	2·82		2·82
1969	1,269	1			41						1,268	41		42	3·23		3·23
	15,192†	79	32	30§	372	20	6	2	27	38‡§	15,113	398	65	523	2·63	0·43	3·45

* Birds found dead on the island within 2 years of being ringed or re-ringed are recorded as having failed to fledge.

† Includes one chick ringed twice which failed to fledge.

‡ Includes one chick recovered in New Zealand and subsequently recovered breeding.

§ Includes one bird recovered breeding and later died.

A more accurate estimate of the proportion of nestlings recovered breeding can be had by taking data to 1963 only. No birds ringed after that date have subsequently been recovered breeding.

Total fledged to 1963: 9,734

TABLE IIb

NUMBER OF ADULT GIANT PETRELS RINGED (AND SUBSEQUENTLY RECOVERED) ON SIGNY ISLAND

Year	*Number of rings used*	*Birds previously ringed*	*Birds previously ringed and re-ringed*	*Nestlings re-ringed*	*Total re-ringed*	*Number of adults ringed for first time*	*Recoveries*				*Net recoveries*	*Per cent recoveries*	*Net live recoveries*	*Per cent live recoveries*
							re-ringed	*recovered*	*dead*	*gaped rings*				
1949	11					11	3	1	2		6	54·6	4	
1956														
1959	818	1	2	1	4	814	204	54	2	33	293	36·0	258	
1960	3					3								
1961	228					228	94	14	1	7	116	50·9	108	
1962	900	262	3	3	268	632	8	274	5	2	289	45·7	284	
1963	52	4	1		5	47	1	4			5	10·6	5	
1964	24	1			1	23		14			14	60·9	14	
1965	12	4		1	5	7		5			5	71·4	5	
1966	3					3								
1967	77	2		8	28	49		40			40	81·6	40	
1968	64	5		8	13	51		35	2	1	38	74·5	35	
1969	426	16		12	28	398			(1)					
Excluding 1969	2,192	297	6	21	324	1,868	310	441	10	43	304	43·0	751	40·2
Including 1969	2,618	313	6	33	352	2,266								

melts during the summer to expose the rocky nature of the island with its moraines and screes (Plate IIa–d). It is on these coastal areas and rocky bluffs that most of the island's birds nest. The giant petrels breed along a 5 km. stretch of the west coast from North Point to Port Jebsen and also on some of the offshore rocks at Port Jebsen and Spindrift Rocks. They formerly bred on the east coast, on the slopes of Borge Bay (Ardley, 1936) and, when the British station was established in 1947, this colony numbered about 200 breeding pairs, but by 1955 it had become extinct (Ewer and Anderson, 1947; Laws, 1948, 1949; Mansfield, 1950; Tickell, 1955). The desertion was probably due to the presence of the station and the disturbance caused by the personnel and dogs. A somewhat similar situation occurred at Pointe Géologie, following the establishment of the French station (Prévost, 1958).

Because of its close proximity to a field hut, which made work possible in conditions when it would have been impracticable to travel from the main station, a main study area was chosen at Foca Point. The size of the study area was approximately 0·3 km.^{2}; the terrain consists of a plateau about 5 m. above sea-level, to the north-west of which rise two rocky outcrops, themselves separated by a plateau. The giant petrels nested along the edges of the plateau and on the rocky bluffs to a height of about 60 m. a.s.l. In 1967–68 there were just over 100 occupied nests in the study colony (Plate Ib).

An important requirement in studying any breeding population is to be able to identify individually an adequate proportion of the population. This was achieved by colour ringing as many of the birds in the study area as possible. Giant petrels are very nervous, and on Signy Island they were invariably captured on their nests using a modified puffin hook (Lockley and Russell, 1953). It was easier for two people to handle and deal with a captured bird, one to hold it, the other to work on it. The bill can inflict a nasty gash on exposed skin, and it was essential to wear heavy leather gloves. The bird was caught by hooking it around the leg, the head was then grasped and the wing gathered around the body. When only one person was available, the best method was to kneel around the bird, holding it by its legs and trapping the head in the crook of the knee, leaving the hands free. Once caught, the bird was ringed with a B.T.O. monel ring on one leg, and a triple combination of colour rings on both legs. (These rings were easily identified on birds at the nest (Plate IIIa) or in groups of birds some distance away, using × 9 binoculars or a × 15 telescope; it was also occasionally possible to identify birds in flight.) During the first two summers, plastic spiral rings were used, but because of their brittle nature and tendency to twist over one another they proved unsatisfactory. In the final summer, plastic overlap rings were used; these were much better and could be sealed with acetone, so reducing the dangers of their slipping. Initially seven colours were used: black, blue, yellow, green, red, white and orange. Orange was later removed because in the succeeding summer it could not be satisfactorily distinguished from "faded red" at a distance. Only birds from the main study area were colour ringed.

On release, the majority of the birds flew off, some returning within a few minutes to resume incubation; few returned directly to the nest and some were still absent after an hour. Whenever an egg or young chick was deserted it was covered by nest material to camouflage it from predatory skuas (*Catharacta skua lönnbergi*). Although not 100 per cent successful, this did markedly reduce egg and chick loss to skuas. (In 1966, the eggs, if deserted, were not covered and 30 eggs out of a total of 41 were taken by skuas. In 1967 and 1968, the eggs were covered and the corresponding loss was 81 out of 183.)

Two methods of sexing birds in the field have been described. Accordingly, whenever a bird was handled certain measurements were taken:

i. Bill length—from the feathers at the base of the culmen to the distal part of the hook (Plate IIIb).
ii. Bill depth—maximum depth from the dorsal surface of the hook, in front of the nostril, to the base of the gonys.
iii. Wing length—measured from the carpal joint to the tip of the longest primary (not recorded in birds showing primary moult).
iv. Tarsus length—from the mid-tarsus joint to the distal end of the tarso-metatarsus.
v. Mid toe and claw (M.T.C.)—from the distal end of the metatarsus to the tip of the mid claw when the foot is held flat.
vi. Tail—from the base of the preen gland to the end of the longest tail feathers (not recorded in birds showing tail moult).
vii. Weight—the birds were weighed in a string bag using a 6 kg. "Pesola" balance graduated to 0·1 kg. The bill was measured using vernier calipers, accurate to 0·1 mm., the wing, tail and M.T.C. were measured on a ruler and the tarsus was measured using dividers.

Nest sites were marked by painting a number on a nearby rock. A photograph of the nest site, in relation to other sites and the local topography, was also taken. This method of recording nest sites is not as useful as in temperate regions, because the amount of snow cover can change the appearance of the terrain from season to season.

In an attempt to study the components of the population present in the study area throughout the year, the number of birds in the air above the study area and on the ground was counted on every visit. During the winter months the appearance of colour-ringed birds would establish whether the birds present during these months were local birds or not.

To obtain information on the pre-breeding season, a certain area of the colony, approximately 30 nests, was studied from a tent hide. Once the birds had started to lay, the colony was visited daily during the period of egg-laying and at least every second day during the incubation period. Once the eggs had started to hatch, daily visits were resumed during the guard period (p. 28), followed by visits at least every second day until the chicks fledged.

During their nestling period, the chicks were weighed and measured, at first daily then, after the guard period, every second day. The details of measuring and weighing were similar to those described for adult birds.

The data previously recorded on the island were used to compare the start of the breeding seasons in previous years to see if there were any marked differences in the breeding season from one year to another. Because it proved almost impossible to catch birds except on the nest, a series of suspected pre-breeders was shot, during February 1969, in an attempt to find out the age at which young birds return to the colony. These were birds previously ringed as nestlings, and of known age. They were measured and sexed by dissection, then frozen and the skins are now deposited in the museum of the Department of Zoology, University of Aberdeen. The gonads were also collected but are not discussed here. As in previous years, all the chicks on the island were ringed in March, the number of chicks ringed then being a good indication of the number which finally leave the island. (Less than 3 per cent of the chicks ringed in March were subsequently found dead on the island.)

Food samples were collected by regurgitation and examination of stomachs. The regurgitated samples were collected by putting the bird's head into a polythene bag and collecting whatever came up.

To see how far a young bird moved between the natal colony and subsequent nest site, the breeding colonies of the island were divided into seven areas, each approximately 700 m. long. This does not take into account the position of the nest within an area. Thus a chick ringed at the south end of area 1 and found breeding at the north end of area 2, will be recorded as having moved "one area", the same distance as a chick ringed at the north end of area 1 and recovered breeding at the south end of area 2, although in the first case the distance could be less than 100 m., while in the second case greater than 1,300 m. Since the positions of the nests are not recorded, this method probably gives the best feasible index of movement between natal area and breeding area.

Record keeping

Once a chick had been ringed it was given a bird register number; this number referred to the bird even after the ring had been replaced. An individual record of all birds in the study colony was maintained. Every nest site in the study area was numbered and a separate record was kept for each nest.

III. SEXING ADULT GIANT PETRELS

One of the major problems in the study of the breeding biology of birds is to identify the sex of individuals in the field.

Birds can be sexed by the following methods:

Cloacal inspection—Serventy (1956*a*) described how the cloaca of the female short-tailed shearwater (*Puffinus tenuirostris*) was swollen and bloody in the period immediately before and after egg-laying.

Egg-laying—a bird seen laying an egg can be positively identified as a female; the egg can be felt in the abdomen of females, if caught immediately prior to egg-laying.

Copulation—a pair can usually be identified if both are seen copulating, but the possibility of inverse copulation, as described in the moorhen (*Gallinula chlorophus*), Adélie (*Pygoscelis adeliae*), gentoo

(*P. papua*) and erect-crested (*Eudyptes sclateri*) penguins (personal communication from A. Anderson; Roberts, 1940*b*; Richdale, 1941; Taylor, 1962), cannot be ruled out.

The above methods of sexing have two major drawbacks: the period during which the sex can be established is very short and with the exception of the last is applicable to only one sex, and in surface-nesting species which desert their nest after being handled, there is a danger that the egg will be taken by predators.

Measurements—Dunnet and Anderson (1961) used the differences in bill measurements between known male and female North Atlantic fulmars (*Fulmarus glacialis*) to establish a discriminant function, from which the sex of any measured bird can be estimated with varying degrees of confidence. The value of this method of sexing is that, providing they can be caught, birds can be sexed at any time of the year. If the sex of one bird is known, that of its mate, if ringed, is also known.

In the giant petrel, Condon (1939) suggested that the limey encrustation at the base of the bill was found only in females, but my own observations have shown this not to be the case.

Within any giant petrel population there is a great variation in size. Murphy (1936) has shown that these differences can be related to sex, the males being larger than the females in all measurements. Although this has been accepted by later authors (Warham, 1962; Bourne and Warham, 1966, Mougin, 1968; Voisin, 1968), no statistical comparisons have been made on these differences to confirm that they are significant or useful in the field. In the present study it was routine to weigh and measure all birds handled. 299 birds were measured, the sex of 126 being confirmed later by dissection, copulation, egg-laying or from the sitting bird during early incubation (Appendix II) (Table III).

TABLE III

NUMBER OF ADULT BIRDS SEXED BY MEANS OTHER THAN THEIR MEASUREMENTS

Method of sexing	*Number* *Male birds*	 *Female birds*
Dissection	17	22
Egg-laying	3	5
Copulation	16	13
Incubation	20	30
TOTAL	56	70

Initially, measurements taken included weight, bill length and depth, wing, tail, tarsus and mid toe with claw lengths. Because of the difficulty in holding living birds still for an appreciable time, only bill length and depth were measured from living birds (Fig. 1; Table IV). With the exception of weight, there is very little overlap in the measurements between the sexes, and the differences between them are very significant ($p < 0{\cdot}001$). These relative differences are similar to those found in some other Procellariiformes, North Atlantic fulmar and wandering albatross (*Diomedea exulans*), royal albatross (*Diomedea epomophora*) (Dunnet and Anderson, 1961; Tickell, 1968; Sorensen, 1950*a*; Westerskov, 1960), but not in the cape pigeon (*Daption capensis*) (personal observation).

Following Moroney (1951), discriminant functions were calculated for the southern giant petrel on Signy Island using:

i. Bill length, depth and bird weight.

Function $A = 2{\cdot}86l - d + 3{\cdot}12w$ (where l is bill length, d is bill depth and w is bird's weight)

$(2{\cdot}86l - d + 3{\cdot}12w = 234{\cdot}5)$

This gave a discriminant value of 234·5 (males more; females less) with a possibility of misclassification of about 1 per cent.

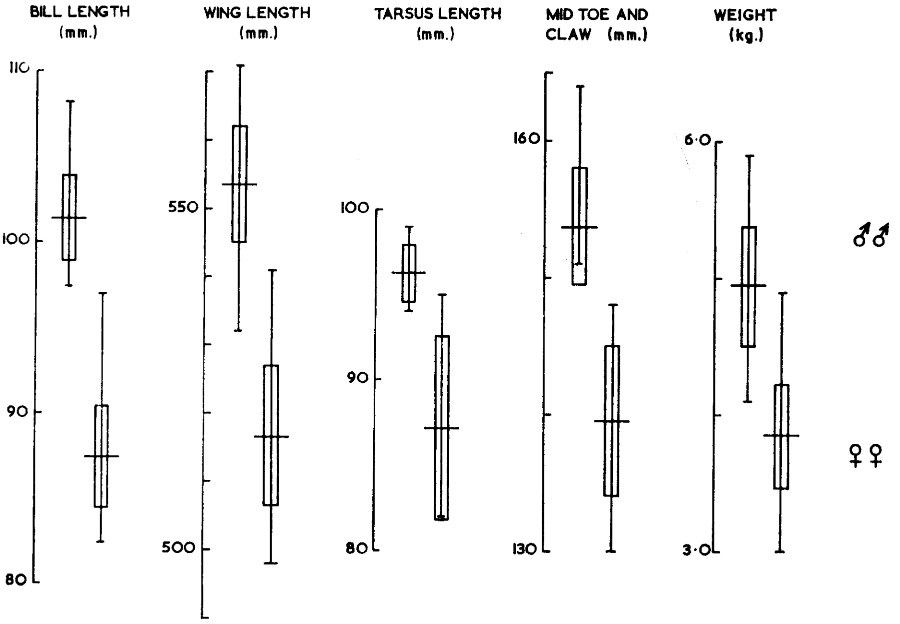

FIGURE 1

Summary of measurements used in sexing *M. giganteus* on Signy Island, indicating mean, range and ± one standard deviation.

TABLE IV
COMPARISON BETWEEN MEASUREMENTS OF SEXED GIANT PETRELS ON SIGNY ISLAND

	Bill (mm.) *l*	*Bill* (mm.) *d*	*Weight* (kg.) *w*	*Wing* (mm.)	*Tarsus* (mm.)	*Tail* (mm.)	*M.T.C.* (mm.)
Male							
Mean	101·40	34·40	4·94	553·50	96·30	196·30	153·10
S.D.	2·45	3·20	0·41	10·86	1·69	1·93	4·17
Range	97·4–108·2	29·7–37·1	4·1–5·8	534–571	94–99	189–205	151–164
Number	66	66	37	13	13	10	13
Female							
Mean	87·4	30·17	3·85	5·80	87·10	182·40	139·80
S.D.	3·0	3·80	0·37	15·21	5·45	5·27	5·55
Range	82·4–97	26·7–35·5	3·0–4·8	498–541	82–95	172–190	130–148
Number	73	73	37	13	13	8	13
t	9·468		0·834	6·85	5·8	7·303	6·965
p	<0·001		<0·001	<0·001	<0·001	<0·001	<0·001

ii. Bill length and depth only.

$$\text{Function } B = l - 0{\cdot}122d$$

$$(l - 0{\cdot}122d = 90)$$

This gave a discriminant value of 90 (males more; females less) with a possibility of misclassification of about 1 per cent.

A scatter diagram of bill measurements is given in Fig. 2.

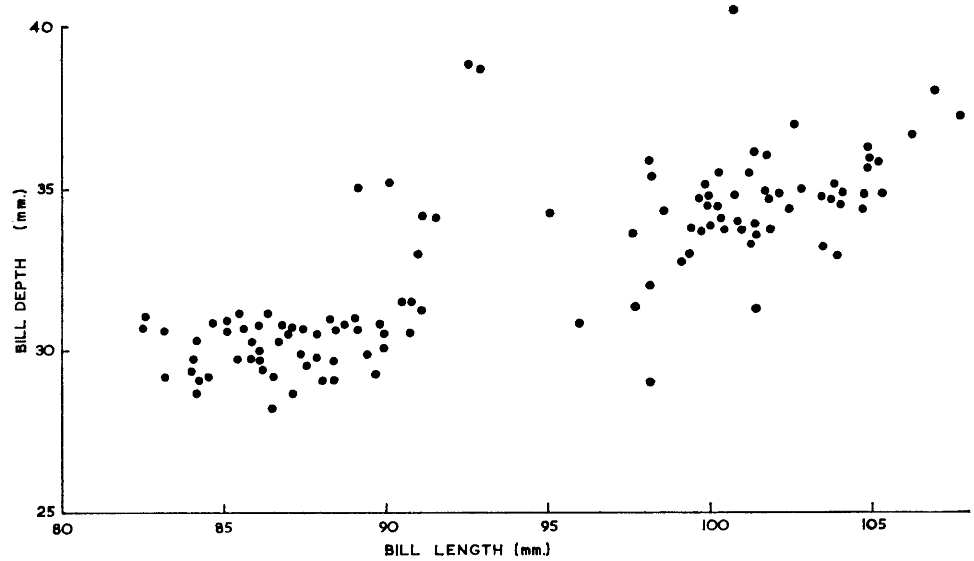

FIGURE 2

Scatter diagram of the distribution of *M. giganteus* culmen measurements (length and depth) used in sexing adult birds.

IV. THE ANNUAL CYCLE ON SIGNY ISLAND

UNLIKE the other petrels on Signy Island, with the possible exception of the snow petrel (*Pagodroma nivea*) (paper in preparation by J. W. H. Conroy and J. R. Beck), southern giant petrels are seen around the colonies throughout the year. In an attempt to study the components of the population present throughout the year, the number of birds on the ground and in the air immediately above the colony was counted on each visit between April 1968 and March 1969 during the late morning or early afternoon. A weekly mean was calculated by adding the total number of birds seen per week, and dividing this by the number of visits (Fig. 3). Similar counts were also carried out away from the nesting colonies, at Borge Bay, in the area immediately in front of the station. These counts were usually carried out between 09.00 and 10.00 hr. The colony was also counted at weekly intervals between 21.00 and 22.00 hr. throughout the period of re-occupation to egg-laying (June–October). Between June and March a varying number of captured or shot birds was weighed, measured and sexed (by dissection or bill measurements).

The following discussion on the population structure is based on a single year's observations, in an area where just over 60 per cent of the breeding population had been individually colour ringed. Consequently, the conclusions expressed are tentative and another winter's observations would have been useful for comparison. During most of the winter months (June–September) the birds are very nervous and will take to the wing at the slightest disturbance. They are also very mobile, birds from the study area being seen at North Point and Port Jebsen. It is not until September, when the birds have become established at a nest site, that they can easily be identified.

April until mid-June. During early April, in addition to the breeding birds attending the colony to feed their chicks, there are still a few known failed breeders (identified by their colour rings) and suspected pre-breeders (identified by rings on their right tarsi) around the colony. As April proceeds, these birds leave the island, and by the end of the month only breeding adults remain. In early May, these birds also appear to leave the island and the birds seen in the air during the remainder of May and early June consist

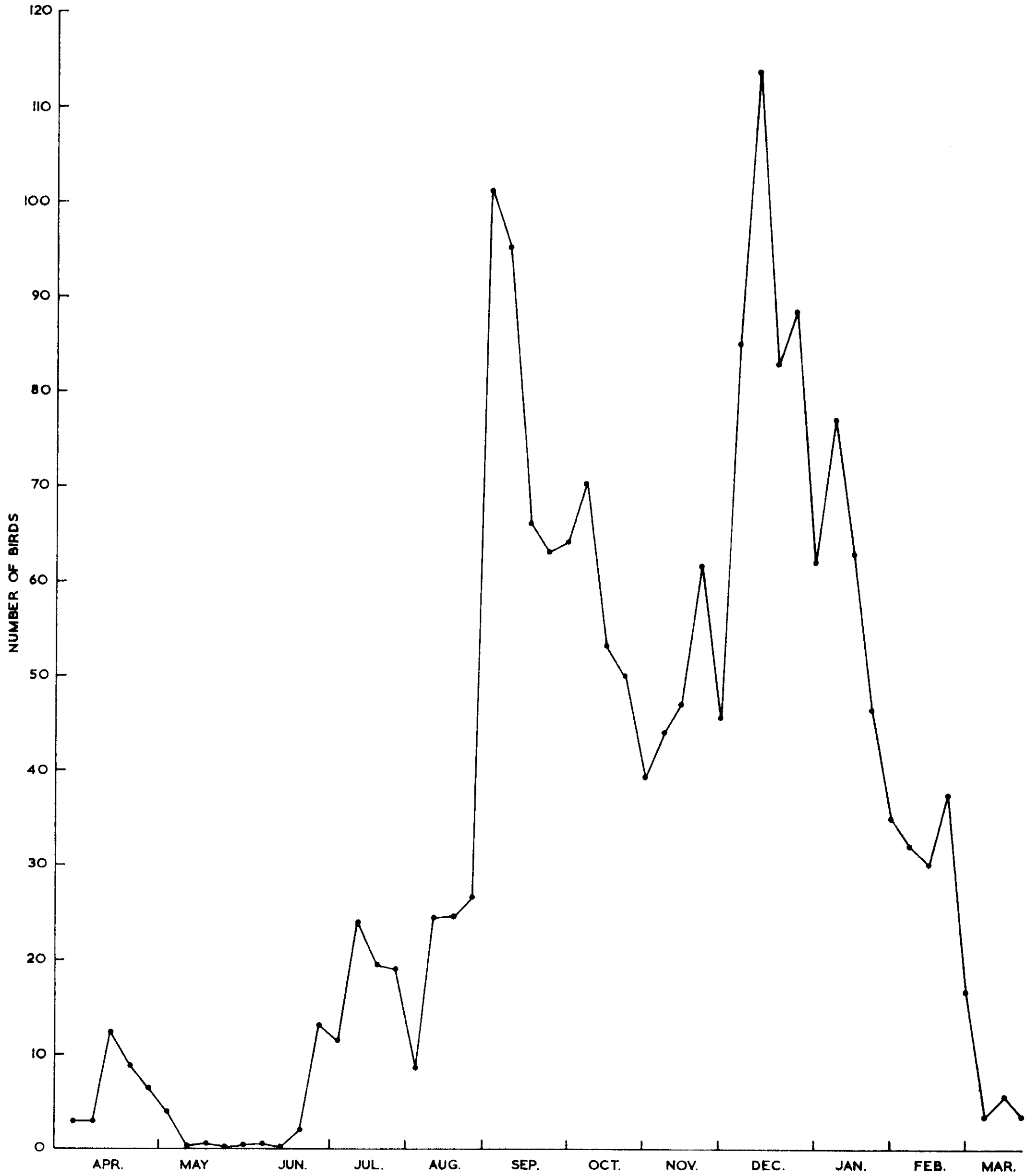

FIGURE 3

The weekly mean counts of *M. giganteus* at the Foca Point colony, April 1968–March 1969.

of the fledglings, which may remain around the island for a few days after fledging, and the occasional unidentified adult bird. Numbers are at their lowest at this time.

June–August. During the latter part of June and early July, few birds are seen around the colonies and none was individually identified. The adults leave the island, some dispersing to the coasts of South America and New Zealand (Appendix IV). As July progresses there is a build-up, involving largely the previous summer's failed breeders (67·5 per cent of the 92 birds identified at this time were known to be failed breeders, the remainder were successful breeders). There seems to be a general return of the birds in August and by the end of that month many potential breeders are returning to the colony.

September–November—the pre-egg period. During the first few weeks of September the number of birds in the colony is still high, and they are still very mobile, but by the end of the month there is a marked drop in numbers which continues until the end of October. This drop is probably caused by two factors:

in late September, the birds are established on their territories, and the amount of visiting is greatly reduced; at most sites, only a pair of birds is in residence.

During the period July–November the giant petrels showed a marked diurnal fluctuation, with numbers at night far lower than during the day. The weekly night counts showed there was an increase in night attendance as egg-laying approached. The average number of birds counted per night visit in June was two (daytime average, four), July five (17), August 12 (23), September 24 (77) and October 37 (49). Once egg-laying started these counts ceased. A dawn to dusk watch showed that the colony population increased sharply in the 2 hr. following sunrise, fluctuated slightly during the day and dropped off towards sunset as the birds flew out to sea.

By the end of October, there was a departure of females for a short pre-laying exodus (p. 20).

November–January—the incubation period. Many of the birds are incubating. There is an increase in the number of birds around the colony, reaching a peak in mid-December. This increase is attributed to the breeders on their nests accounting for a fairly regular 50–60 birds; failed breeders returning to the colony for a period after losing their eggs; although the majority of the mates of the incubating birds are probably at sea, a few are in the colony (five were observed in flight) or at the nest, alongside their mates, and by mid-December the first of the suspected pre-breeders appear in the colony.

January–March—the fledging period. From January there is a steady decline in the number of birds seen at the colony. This is because, towards the end of January, the parents have stopped brooding their chicks and both parents spend more time at sea. Although during January, and into February, suspected pre-breeders are still returning to the island, these along with the failed breeders start to leave the island by mid-March, and by April few are left. Older chicks are probably fed less frequently so that parents are much less likely to be seen in the colony.

The numbers of giant petrels counted at Borge Bay varied throughout the year, reaching a maximum between August and October, the period of re-occupation of the nesting areas. In November there is a sharp drop, which slowly builds up again until March, followed by another drop in April and remaining low until the end of July.

The higher numbers in August, September and early October are probably a reflection of the wanderings of the birds during this period, possibly in search of food. Throughout October there is a decline as the birds begin to spend much more time at their nest sites. The increase in numbers later in the breeding season could be the result of the failed breeders flying around the island in search of food. The drop in April is caused by the departure of the birds from the island.

Weight changes during the annual cycle

Bird's weights are maximal on their return to the island in August when males average 5·16±0·32 kg., but from then until November their weight declines slowly so that by the beginning of egg-laying their weight is minimal, averaging 4·79±0·35 kg. (Table V). The lowest weight of any male (4·1 kg.) was recorded in late October.

By contrast, the females maintain a fairly constant weight throughout this period, their mean weights being 4·06±0·33, 3·92±0·24 and 4·0±0·28 kg., respectively, in August, September and October. In November, after the egg has been laid the mean weight drops to 3·76 kg.

During the incubation period both sexes again put on weight, and by the time of hatching, weights are again high, the means being 5·03±0·26 kg. for males and 3·84±0·28 kg. for females.

The weights of both sexes drop appreciably in February, and breeding birds and suspected failed breeders showed no significant difference. (Breeders' mean weight 4·71±0·62 kg., non-breeders mean weight 4·34±0·78 kg. ($t = 0{\cdot}2339, p > 0{\cdot}1$); the respective weights for male and female breeders and non-breeders were males 4·41±0·48 kg.; 4·85±0·42 kg. ($t = 0{\cdot}3045$, $p > 0{\cdot}1$); females 3·74±0·25 kg.; 3·57±0·28 kg. ($t = 0{\cdot}9295, p > 0{\cdot}1$).) By March, the weights of the non-breeders (failed and suspected pre-breeders) increase but there are no data available for breeding birds during this month.

While away from the colony, the birds put on weight. They evidently find a good food source which they may exploit for some time. Data based on ringing recoveries by the New South Wales Albatross Study Group show that giant petrels (including birds from Signy Island) may remain in the same area, around Malabar, for up to a month (personal communication from J. D. Gibson).

On their return to the island the birds examined had very heavy abdominal fat deposits, but their

TABLE V

MEAN WEIGHT OF ADULT GIANT PETRELS ON SIGNY ISLAND FROM JUNE UNTIL MARCH

Month	*Male mean weight* (kg.)	*S.D.*	*N*	*Female mean weight* (kg.)	*S.D.*	*N*	*All birds mean weight* (kg.)	*S.D.*	*N*
June	4·75	0·32	4	4·05	0·22	2	4·52	0·45	6
July	4·97	0·35	4	3·50	0·44	3	4·34	0·52	7
August	5·16	0·32	5	4·06	0·33	5	4·61	0·65	10
September	4·87	0·31	3	3·92	0·24	5	4·28	0·54	8
October	4·89	0·42	7	4·00	0·28	12	4·33	0·54	19
November	4·79	0·35	17	3·76	0·31	12	4·36	0·61	29
December	4·97	0·35	9	3·85	0·45	21	4·18	0·67	30
January	5·03	0·26	11	3·84	0·28	9	4·50	0·66	20
February	4·76	0·47	17*	3·67	0·46	9*	4·38	0·68	26
March	5·10	0·48	6†	4·00	0·25	4†	4·67	0·62	10†

* Includes suspected pre-breeders.
† Suspected and failed breeders only.

stomachs were empty. This fat is utilized during the pre-breeding period and, by the start of incubation, the amount of abdominal fat is already reduced (based on subjective observations of nine birds, five killed during the winter (August–October) and four during November–January).

Between September and November, the male's weight drops while that of the female remains fairly constant. Males were more regularly seen at the nest than females. During August–October at one site, the male bird was seen at the nest 17 times, the female three times, although she was seen in the vicinity of the nest an additional five times. Males would sit on the nest for much of the day, whereas females would come in, remain for a few hours or minutes, then fly off; this could be repeated several times a day. The male's extended sojourn at the nest site should result in the utilization of some of his fat reserves and reflect a mean weight drop during the pre-egg period. By comparison, the female spends more time away from the nest, possibly feeding.

The reason the male remains on the nest is not because there is a danger of its being taken by another bird (pp. 19-20). If, as has been suggested for the short-tailed shearwater and Gould petrel (*Pterodroma leucoptera*) (Hindwood and Serventy, 1949; Marshall and Serventy, 1956), the ovaries are mature only for a short period, it is essential that both sexes have a common centre at which to meet when the female is ready for mating. This centre is the nest. The male may be ready to mate earlier and for a longer period than the female.

The female's weight loss, averaging 300 g., between October and November is probably caused by the energy drain associated with egg production. From November until January there is a weight increase, suggesting a plentiful supply of food, and very little stress, if any, on the incubating birds. The weight drop in February is associated with the feeding of the chick.

V. THE NEST

THE nesting habitat of *Macronectes giganteus* varies throughout its range, depending very much on the terrain available. The birds are essentially colonial nesters, choice of site being governed by the need for a runway to assist take off on calm days. Colonies are usually found on raised beaches or rocky outcrops from 5 to 120 m. a.s.l. The nests are never densely arranged, the minimum distance between nests being about 1·5 m. and averaging about 3·5 m. The colonies tend to be exposed to the prevailing winds, as at

Signy Island (personal observation), Pointe Géologie (Mougin, 1968), Heard Island (Downes and others, 1959) and Iles Crozet (Voisin, 1968).

On sub-Antarctic islands, nests are found in tussock grass (*Poa flabellata*) (personal observation; South Georgia), while on Sea Lion Island, Falkland Islands, a photograph by R. H. Beck shows the birds nesting on sandy beaches (Murphy, 1936). Falla (1937) reported that, on Macquarie Island, they nest near the shore as well as on high terraces. In the Antarctic, the colonies tend to be on open flats or rocky outcrops and, with the exception of Elephant Island (personal communication from G. Bruce),* no nests are found on beaches. The latter may be ice-covered at the beginning of the breeding season, and even if ice-free then, pack ice may encroach on the shore and ice rubble may build up over the beach later in the summer.

On Signy Island, the majority of the nests are built of small stones but moss, if available, may be used while some nests are mere depressions in the rock, with no apparent cover. The incubating bird on one such nest appeared "uncomfortable", and after 3 days deserted the egg. The nests are usually substantial structures; one measured in external diameter 56 cm., internal diameter 45 cm., maximum height 23 cm. and depth from rim to base of the cup 13 cm. (Plate IVa and b).

Despite their exposed situation, the nests offer some protection from the elements. At Terre Adélie, in April, when a wind speed of 23 m./sec. was being recorded on the anemometer tower, inside the nest cup it was only 3·8 m./sec. (Mougin, 1968). At Robert Island (South Shetland Islands), the air temperature inside an abandoned nest was about 2° C higher than the ambient air temperature (Saiz and Hajek, 1968). Nests built of small stones protect the egg from flooding during periods of melt because melt water runs through them, without entering the cup and cooling the eggs.

1. *Nest building*

Nest material is not usually carried to the nest, only that in the immediate vicinity of the nest being used in its construction and either sex takes part in nest building. The bird sits in the cup, picking up whatever material is within reach of its bill and drops it over its shoulder, eventually building the cup up around it.

In the period immediately before and after her pre-laying exodus the female is very active in nest building and repair. While incubating and brooding, she will pick up stones from around the nest and re-build any of the wall which might have been broken down during change-over. The chicks, once they are of sufficient size, also contribute to nest maintenance. In mossy areas, nesting birds are seen to pull up moss and place it around the cup.

At South Georgia, chicks, about 80 days old, were seen pulling tussock grass and placing it around the nest cup about a month before they fledged (personal observation). Similar behaviour has been reported in other petrels, cape pigeon, and North Atlantic fulmar (personal observation), while Campbell (1970) saw North Atlantic fulmar chicks repairing the nest by dropping stones over their shoulders. Rowan (1951) reported similar behaviour in juvenile yellow-nosed albatrosses (*Diomedea chlororhynchos*) on Tristan da Cunha.

In addition to nest building and repair by the breeding birds, there was during March nest activity among the unemployed birds. Failed breeders were seen at their nests moving stones, and pairs which were going to take up new sites in the following breeding season were seen at their prospective sites during this month. In 1966–67, the pair at nest 22 lost their egg in December, and in the following February and March the pair, but in particular the male, was regularly seen at a new nesting area about 100 m. from nest 22, where they nested the following season. Similarly, in 1966–67 nest 69 was not used, but during March the pair, which successfully bred there in the following season, were seen at nest 69 on at least six occasions "tidying up".

During March, when all the southern giant petrel colonies were visited, several groups of birds were found tidying up empty nests and in two of these areas eggs were found in the following season, although no chicks were there in March. Autumn nest building has also been recorded in giant petrels at Macquarie Island (Warham, 1962), although he reported such activity only at the edges of the colony, and from the birds' plumage colour concluded that they might be pre-breeders. This is not the case on Signy Island, where autumn nest building takes place through the colony, and it is known that some of the birds involved are failed breeders.

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* The nests on Elephant Island were on sheltered beaches where it was unlikely that pack ice would encroach (personal communication from G. Bruce).

2. *Colony size*

On Signy Island, the nests tend to be in small groups rarely exceeding 50, averaging about 27 per colony (Table VI), comparable with an average of 41 per colony at Macquarie Island (Warham, 1962).

TABLE VI

NUMBER OF NESTS IN THE COLONIES OF SOUTHERN GIANT PETRELS (*M. giganteus*) ON SIGNY ISLAND

Colony size (nests)	*Number of colonies*	*Colony size* (nests)	*Number of colonies*
0–10	19	51–60	3
11–20	28	61–70	3
21–30	14	71–80	3
31–40	13	81–90	3
41–50	5	91–100	1

3. *Interspecific competition for nest sites*

Being the only exposed surface-nesting petrel on Signy Island, there is no competition with other Procellariiformes over the choice of nest site. Of the remaining species on the island perhaps only the penguins offer competition for nesting areas. On the west coast, two penguin rookeries are found in the areas where the giant petrels breed. Part of the rookery at North Point is on terrain which is suitable for giant petrel nests; they nest on the ground immediately above but not immediately adjacent to the penguins. At Spindrift Rocks, where the penguin colony extends onto one of three offshore flat rocks, no giant petrels breed, but on the other two rocks, where no penguins breed, large numbers of giant petrels nest.

VI. THE BREEDING CYCLE

1. *The pre-egg period*

a. *Re-establishment of the pair-bond.* Although the adult birds start scraping their nest sites clean of snow shortly after they return to the island in July, they spend little time at the nests during this month. Nest activity increases towards the end of August and during September there is much coming and going at the colony and four or five birds are regularly seen at most occupied nests. Male birds are at their nests more often than females, and observations on a small group of nests within the main study area showed that the male tended to be the first bird to visit the nest (17 from 20 nests—85 per cent). By the end of September, most of the birds have become paired, usually with their previous mate and at their former nest site. Once the pair have become established, they sit side by side at the nest billing occasionally.

In the absence of the mate, birds will display with others. While on the nest, the male was often surrounded by several birds not necessarily including his mate. He would display with other females which approached him and often such a female would sit alongside the male as if she was the mate. When the mate appeared she quickly chased off the other female. However, if another male was to approach the nest, he was greeted with a threat display, often ending with the male on the nest making a lunge at the intruder, which was sufficient to send him away. Likewise, the female will display with other males, showing no signs of aggression even when her mate is on the nest. On at least three occasions in September, the female from site 45 was seen displaying with the male from site 75, although her own mate was on site 45 only 2 m. away. At no time did the two males dispute the female. After a few minutes at site 75 she returned to her own mate. During one of the female's sessions at site 75, her mate started to display with another female, and she immediately left site 75 and chased off the intruding female.

There is no evidence of established males being displaced by intruding males. If a male, other than the established male, is sitting on a nest site, he will display to other birds as if the rightful owner, but on the return of the owner, he quickly leaves the nest, often without any apparent aggression on the part of the owner. If the male can evict intruders from its nest, there is no need for him to remain at the nest site to defend it.

The pair usually return to their old site each year, and of 127 pairs under observation during the three summers, only nine were known to have changed their nest sites (mean distance moved, 0·59±0·54 km., range 2 m.–1·5 km.). Although there are examples of new pairs taking over previously occupied nests, while the original pair were still in the colony, the latter had always established a new site.

b. *Copulation*. There were 13 records of copulation during 1968, occurring from 8 October until 11 November (mean date, 27 October±0·54 days), and on only three occasions was a bird other than the normal mate involved. At site 12, on two occasions, the female copulated with other males. In both cases the male landed beside the female and immediately mounted her, without any preliminary behaviour. On completion he jumped off and departed within 5 min.

Copulation, described by Warham (1962) from Macquarie Island, followed the same general pattern on Signy Island, the pair taking part in pre-mounting billing, usually initiated by the male, followed by the male mounting the female, and after a more rapid billing session, copulation ensued. The male then jumped off and the pair again sat side by side.

It would appear that copulation usually occurs before the female's pre-laying exodus; although there is one record of copulation occurring within 12 hr. of the egg being laid, a previous copulation before the exodus is more than likely to have occurred.

c. *Pre-laying exodus*. By the end of the 1968–69 season, 129 birds had been individually colour ringed and sexed; of these 69 (53·3 per cent) were females. Throughout the winter, whenever conditions would allow, birds were counted and identified, and assuming that the likelihood of identifying males and females is the same, then it should be possible to test (χ^2 test) the observed proportion of males and females in the identified population with the expected proportion assuming a 46·7/53·3 ratio of males to females (Table VII). The counts do not include birds seen immediately before or after the egg was laid. The values for the last 3 weeks are the most interesting. For the fortnight 22 October–5 November the values of p approach 0·05, but the differences are not significant; for the week starting 5 November, $p < 0\cdot 001$, and the difference between the proportion of males and females in the colony is significant. It is probable that, in common with other Procellariiformes which spend several weeks or even months at the breeding grounds before egg-laying, a pre-laying exodus occurs. In the case of the southern giant petrel, either the female alone is involved or she has a longer absence than the male.

The actual length of the absence is difficult to calculate but it is likely that it lasts less than 14 days, possibly about 12 days (Appendix III).

Only the data for the last 2 weeks show a significant difference, probably because, if the pre-laying exodus is only 12 days, and the peak of egg-laying does not occur until after 10 November (23 per cent of the eggs were laid in the 7 days before this date compared with 50 per cent in the succeeding 7 days), more than 50 per cent of the females which will lay eggs will still be on the colony before 1 November.

2. *The egg*

a. *Egg measurements*. Weights and linear measurements of eggs were collected in both 1963–64 and 1968–69. In 1968–69, measurements were made with vernier calipers, accurate to 0·1 mm., and the weights were recorded on a "Pesola" balance measuring up to 300 g. The 1963–64 measurements were recorded to the nearest millimetre and the weight, recorded in ounces, was measured on post office scales, the readings being later converted to grams. The internal volume was calculated from the formula, $v = 0\cdot 5\, ld^2$, where v is the internal volume, l and d the maximum length and diameter, respectively.* When the measurements for the 2 years are compared, there are no significant differences between their respective means (Table VIII), nor are there any significant differences in the measurements of eggs from other localities (Etchecopar and Prévost, 1954). Voisin (1968) has also shown that on Iles Crozet there are no differences in the measure-

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* The internal volume was calculated from the formula $v = 0\cdot 5235\, ld^2k$, where k is a correction factor (Coulson, 1963). By measuring the internal volumes of 28 giant petrel eggs (16 from Signy Island, 12 from the British Museum (Nat. Hist.)), k for giant petrel was found to average 0·953±0·028 (range 0·921–1·009). This gave a formula $v = 0\cdot 5000\, ld^2$. The mean error between measured and calculated volumes was 1·73±0·99 per cent with 75 per cent within the range 0·17–2·5 per cent. These errors are similar to those calculated for kittiwake (*Rissa tridactyla*) eggs (Coulson, 1963), tropical sea birds and black swans (*Cygnus atratus*) (Stonehouse, 1963, 1966).

TABLE VII

χ^2 TEST—COMPARING THE PROPORTION OF SEXED GIANT PETRELS SEEN IN THE COLONY, AND THE KNOWN PROPORTION OF SEXED BIRDS IN THE RINGED POPULATION

Date	*1–7 October*		*8–14 October*		*15–21 October*		*22–28 October*		*29 October–4 November*		*5–11 November*		*12–18 November*	
	O	E	O	E	O	E	O	E	O	E	O	E	O	E
Male	11	11·63	10	13·02	8	5·59	18	11·16	16	10·7	24	13·49	7	4
Female	14	13·38	18	14·98	4	6·41	6	12·84	7	12·3	5	15·52	2	5
χ^2	0·2877		0·6088		0·9061		3·64		2·28		7·13		4·05	
p	>0·9		>0·3		>0·3		$0{\cdot}1>p>0{\cdot}05$		$0{\cdot}1>p>0{\cdot}05$		<0·001		<0·05	

TABLE VIII

COMPARISON OF THE EGG DIMENSIONS OF THE GIANT PETREL FROM TWO SEPARATE BREEDING SEASONS, 1963–64 AND 1968–69, ON SIGNY ISLAND AND THEIR OVERALL MEANS

Year	*Length* (cm.)				*Width* (cm.)			
	Mean (S.E.)	S.D.	*t*	*p*	Mean (S.E.)	S.D.	*t*	*p*
1963–64	10·42 (0·052)	0·383			6·61 (0·023)	0·173		
			0·4141	>0·6			1·76	>0·05
1968–69	10·57 (0·054)	0·398			6·53 (0·034)	0·25		
All eggs	10·49 (0·038)	0·398			6·57 (0·021)	0·219		

Year	*Weight* (g.)				*Volume* (cm.^{3})			
	Mean (S.E.)	S.D.	*t*	*p*	Mean (S.E.)	S.D.	*t*	*p*
1963–64	252·7 (1·99)	14·8			227·96 (1·5)	11·13		
			1·27	>0·1			0·57	>0·6
1968–69	248·4 (2·66)	19·8			226·14 (2·76)	20·47		
All eggs	250·56 (1·76)	17·75			227·05 (1·58)	16·6		

ments of *Macronectes giganteus* and *M. halli*, but on Macquarie Island, Johnstone (personal communication) found the differences in weight between the two species were significant. On Signy Island, the egg is 6·8±1·2 per cent, range 6·15–7·5 per cent, of the female body weight.

In 1967, 11 eggs collected immediately after being laid, were weighed, hard boiled to facilitate separation of parts, weighed again, and the shell, albumen and yolk weighed separately (Table IX).

b. *Egg-laying*. Egg-laying usually starts during the first week in November and records of laying dates of the first eggs since 1947 are given in Table X. On Signy Island, egg-laying is fairly synchronous. Data on the spread of 243 clutches were collected in two seasons on Signy Island: 1963–64 (64 clutches) and 1968–69 (169 clutches). In 1963–64 the colony was visited every third day, whereas in 1968–69 it was visited every day throughout the laying period. The mean laying date for each year was 13 November (13·00±4·00 in 1963 and 13·32±4·00 in 1968). In both years laying was spread over 22 days, with 90 per cent of the eggs being laid within 8 days of the mean.

In the daily data for 1968 (Fig. 4) there appear to be two distinct drops on days nine and ten and day 12. These could be due to the extremely heavy snowfalls and high winds which occurred on these days, either stopping the birds from coming into the colonies or else inhibiting their laying.

Although at any one breeding colony the annual laying dates* are fairly well synchronized, there is a wide latitudinal variation in the mean laying dates of *Macronectes giganteus* (Table XI).

Macronectes halli breeds much earlier than *M. giganteus* and shows little latitudinal variation, laying taking place at all locations in August (Bailey and Sorensen, 1962; Bourne and Warham, 1966). On Marion Island, Crawford (1952) reported nest building in June and first eggs on 10 August; on Chatham Island, Fleming (1939) reported eggs appearing between 5 and 19 August; on Gough Island, Verril (1895) reported laying on 11 September (1888), with a possibility that it occurred earlier, while on Antipodes Island laying is in early September (Bollons *in* Ogilvie-Grant, 1905). Where both species breed on the same island, there is a gap of about 5 to 6 weeks between the onset of laying of each species, as at Iles Crozet and Macquarie Island (Bourne and Warham, 1966; Voisin, 1968).

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* The data supplied by Holdgate (1963) concerning hatching dates would suggest that the laying dates recorded were somewhat late, and that laying probably began in early November.

TABLE IX

MEAN WEIGHTS (g.) AND THEIR PERCENTAGE OF THE FRESH WEIGHT OF THE CONSTITUENTS OF SOUTHERN GIANT PETREL EGGS

	Fresh weight	*Boiled weight*	*Water weight*	*Per cent water weight*	*Shell weight*	*Per cent shell weight*	*Yolk weight*	*Per cent yolk weight*	*Albumen weight*	*Per cent albumen weight*
	260·4	249·96	10·44	4·01	28·67	11·01	85·62	32·88	135·67	52·10
	265·6	252·55	12·05	4·54	35·65	13·42	88·29	33·24	128·61	48·42
	263·0	251·77	11·23	4·27	35·15	13·37	80·23	30·51	136·39	51·86
	253·7	241·06	12·64	4·98	29·08	11·46	77·93	30·72	134·05	52·84
	261·5	250·02	11·48	4·39	36·90	14·11	76·56	29·27	136·56	52·22
	224·5	216·37	8·13	3·62	36·95	12·00	73·11	32·57	116·31	51·81
	252·7	244·22	8·48	3·36	28·64	11·33	72·87	28·84	142·71	56·47
	249·5	234·49	15·01	6·02	29·92	11·99	80·33	32·20	124·24	49·80
	248·6	235·52	13·08	5·26	28·73	11·56	92·17	37·08	113·62	45·70
	241·0	230·68	10·32	4·28	28·25	11·72	77·19	32·03	125·23	51·96
	264·2	251·72	12·48	4·72	29·72	11·25	93·41	35·35	128·59	48·67
MEAN	253·15	241·66	11·39	4·49	30·69	12·11	81·61	32·25	129·27	51·07
S.E.	3·5	3·3	0·216	0·216	0·995	0·298	2·08	0·708	2·58	0·814
S.D.	11·7	11·4	1·92	0·71	3·3	0·98	6·89	2·34	8·55	2·7
Min.	224·5	216·37	8·13	3·36	28·64	11·01	72·87	28·84	113·62	45·7
Max.	265·6	252·55	15·01	6·02	36·95	14·11	93·41	37·08	142·71	56·47

The weight difference between the fresh and boiled eggs is accounted for by the loss of some free water boiled from the egg.

TABLE X

RECORDED LAYING DATES OF FIRST EGGS ON SIGNY ISLAND SINCE 1947

Breeding season	*Date*	*Breeding season*	*Date*
1947–48	5 November	1962–63	5 November
1948–49	5 November	1963–64	4 November
1951–52	6 November	1965–66	3 November
1952–53	6 November	1967–68	3 November
1958–59	31 October	1968–69	4 November
1960–61	7 November	1969–70	5 November
1961–62	4 November	1970–71	7 November

Mean laying date of first egg: 4 November (4·58±1·77 days), range 30 October to 8 November.

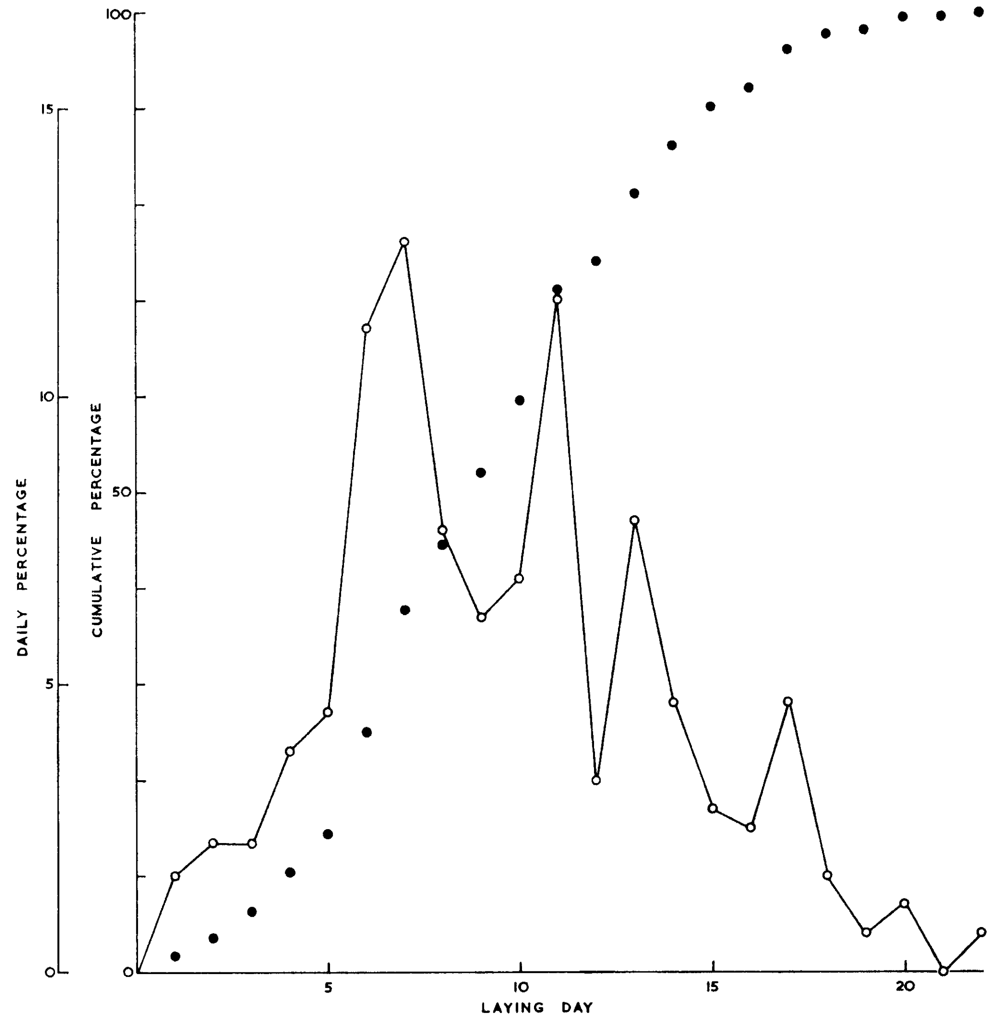

FIGURE 4

Daily percentage of eggs laid by *M. giganteus* at the Foca Point colony, November 1968.

TABLE XI
LAYING DATES OF THE FIRST EGG OF *Macronectes giganteus* FROM OTHER BREEDING COLONIES

Location	*Date*	*Reference*
Iles Crozet	26 September	Voisin (1968)
Iles Kerguelen	25 September	Milon and Jouanin (1953)
Falkland Islands	4 November Last week in October	Murphy (1936) Woods (personal communication)
Macquarie Island	1 October	Warham (1962)
Heard Island	20 October	Downes and others (1959)
South Georgia	18 September– 11 November	Tickell (personal communication)
Anvers Island	22 November	Holdgate (1963)
Pointe Géologie	23 October	Mougin (1968)
Signy Island	4 November	

c. *Incubation period.* Unlike some of the burrowing petrels, for example the Manx shearwater (*Puffinus puffinus*) and Wilson's storm petrel (*Oceanites oceanicus*) (Roberts, 1940*a*; Mathews, 1954; Harris, 1966*a*; Beck and Brown, 1972), there are no records of giant petrel eggs being deserted for any appreciable time, surviving skua predation and hatching. Consequently, the incubation periods described for the southern giant petrel on Signy Island are equivalent to the incubation periods for undisturbed birds and are accurate to within 12 hr.

The mean incubation period for 37 eggs was 60·13±1·27 days, range 56–63 days.

As in all petrels, both sexes incubate the egg, the male taking over the incubation shortly after the egg is laid. (In 22 of 37 nests, the male was incubating the egg within 24 hr. of its being laid; Appendix I.) The longest recorded initial incubation span by a female was 8 days. On average there were 11 incubation spans (11·4±2·5, range 7–14) between laying and hatching, but the length of each span varied greatly. The initial incubation span of the female immediately following laying of the egg (2·05±2·20 days, range 1–8 days) is significantly shorter than the other spans; the second span, the first by the male, is on average the longest (8·25±1·9 days, range 6–11 days); there then follow four spans of similar duration (about 7·3 days) after which there is a decline as hatching approaches. The difference between spans 8 and 9 is significant (Table XII). The males on average incubate significantly longer spans than the females, 6·4 : 5·35 days, respectively.

A comparison of the number of incubation spans and the total length of the incubation period showed a correlation (Fig. 5), the incubation period being shorter in those pairs with the least number of change-overs ($r = 0{\cdot}76$, $t = 4{\cdot}466$, $p < 0{\cdot}001$). When the data for the cape pigeon on Signy Island (Pinder, 1966) were examined, a similar correlation was found, but when the data from Pointe Géologie were examined no correlation was found (data supplied by J. L. Mougin).

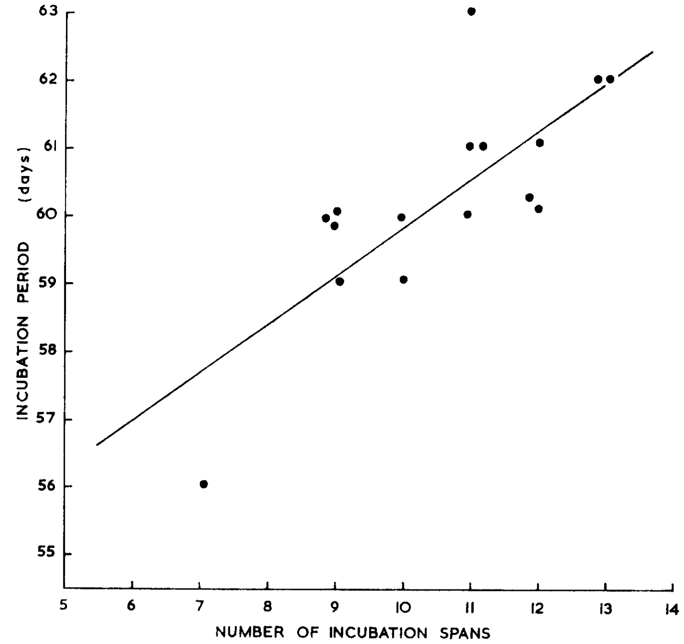

FIGURE 5

Comparison between the number of incubation spans and total incubation period of *M. giganteus* eggs.

Data on incubation periods from other breeding localities have been collected, but unfortunately most are imprecise. At Iles Crozet, Voisin (1968) recorded a mean of 63±4 days (range "62–65±6 days"); at Pointe Géologie the mean was 59 days (range 55–61) (Mougin, 1968), while a mean of 59·4 days was calculated from Warham's (1962) data for Macquarie Island. The value of 70 days from Heard Island (Downes and others, 1959) must be treated with caution.

Mougin (personal communication) recorded incubation periods of 59 (2), 60 (1) and 61 (1) days for *Macronectes halli* at Iles Crozet, which would suggest that within the genus *Macronectes* there is little variation in the incubation period between latitudes, and little difference between species.

TABLE XII

NUMBER AND THE LENGTH OF INCUBATION SPANS UNDERTAKEN BY THE GIANT PETREL IN 16 NESTS

	Number of incubation spans													
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th	14th
Length of spans (days)	3	6	6	6	4	4	5	3	7	3	5	4	6	4
	1	6	6	13	15	5	6	8	4					
	1	9	6	11	6	7	5	8	4	2	2	3		
	1	8	9	5	4	4	4	4	4	11	4	5		
	8	11	12	8	6	8	5							
	1	6	7	8	11	9	9	7	3					
	4	7	5	4	7	6	7	8	6	4	3	3		
	1	8	8	7	9	6	3	9	7	9				
	3	9	5	7	6	7	6	3	3	3	7	2		
	1	8	7	6	9	8	3	4	6	4	3	3	2	
	3	8	15	12	7	9	5	2	2					
	3	10	6	6	6	6	6	9	5	4				
	1	9	9	8	9	9	10	5	2					
	1	8	5	7	6	15	8	5	2	4	3			
	1	8	13	6	4	6	8	9	2	4	2			
	1	11	7	7	5	7	7	9	5	1	4			
MEAN	2·1	8·3	7·3	7·6	7·1	7·1	6·0	6·2	4·1	4·4	3·7	3·7	3·3	4·0
MODE	1	8	6	7	6	6	5	9	2	4	3	3		
S.D.	1·9	1·9	2·9	2·5	2·8	2·6	1·9	2·5	2·4	1·9	1·5	0·6		

Mean number of incubation spans 11·4 (±2·5).
Odd numbers, incubation spans undertaken by female.
Even numbers, incubation spans undertaken by male.

d. *The hatch.* Hatching occurs in January. A chick is said to have hatched when it is completely free of the egg shell, while the duration of hatching is calculated from the time the first scarring of the egg shell is seen until the chick is completely free of its egg shell. Table XIII shows the dates the first chicks were found on Signy Island in most years since 1948. The mean date for 14 years' data is 5 January (5·08±2·33), range 1–9 January.

TABLE XIII

DATE THE FIRST CHICKS WERE RECORDED ON SIGNY ISLAND BETWEEN 1948 AND 1970

Breeding season	*Date first chick hatched*	*Breeding season*	*Date first chick hatched*
1948–49	10 January*	1964–65	1 January
1952–53	6 January	1965–66	7 January
1953–54	8 January	1966–67	7 January
1957–58	9 January	1967–68	3 January
1958–59	6 January	1968–69	5 January
1960–61	9 January	1969–70	3 January
1962–63	9 January†	1970–71	3 January

* Mean date for 20 chicks. † Most nests had chicks.

Hatching continued throughout January, and the data for the three seasons in the study are shown in Fig. 6.

The mean hatching dates for 1967–68 and 1968–69 are not significantly different; 1967–68, mean date 12 January (13·07±4·45 days, range 3–27 January—223 eggs). 1968–69 mean date, 12 January (11·74±3·79 days, range 5–25 January—53 eggs).

The total hatching period lasted 25 days in 1967–68 and 21 days in 1968–69. 12 pairs which successfully

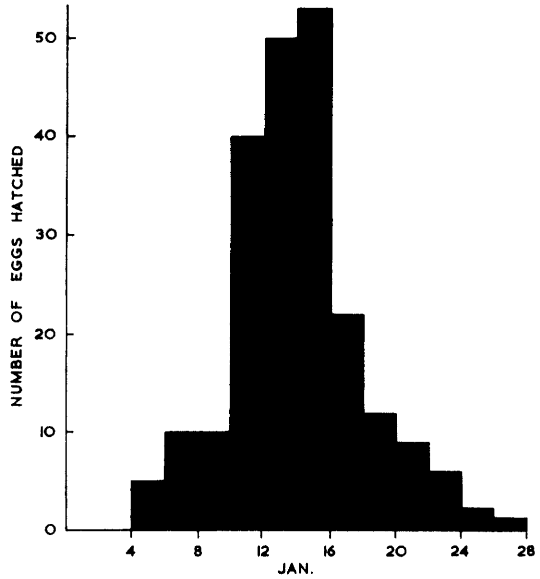

FIGURE 6

Histogram showing date of hatching of *M. giganteus* chicks on Signy Island, January 1968; class interval is 2 days.

hatched chicks in 1968 did so again in 1969. It appears that birds which hatch their chick early one season do so the following year. Only three pairs hatched later by an average 2·33 days (range 1–4) in 1969.

Either sex can be on the egg when it hatches and the male was present on 21 occasions, the female on 23. While some eggs appeared to hatch between visits, i.e. within 24 hr., others took longer; the average time appeared to be between 24 and 48 hr., although one egg took nearly 4 days.

The dates at which hatching starts at other breeding localities are shown in Table XIV.

TABLE XIV

DATES OF FIRST HATCHING OF *Macronectes giganteus* AT VARIOUS COLONIES THROUGHOUT ITS RANGE

Location	*Date of first chick*	*References*
Heard Island	30 December*	Downes and others (1959)
Macquarie Island	5 December	Warham (1962)
Laurie Island	1 January	Robin (1947)
South Georgia	24 November†	Szielasko (1907)
	19 November†	Tickell (personal communication)
Anvers Island	8 January	Holdgate (1963)
Falkland Islands	16 December	Beck *in* Murphy (1936)
Pointe Géologie	26 December	Mougin (1968)

* Most eggs in varying stages of hatching.

† These dates might refer to *M. halli.*

3. *The nestling*

a. *Parental attention.* The newly hatched chick is incapable of withstanding changes in temperature and needs to be brooded by its parents until it is able to regulate, at least in part, its own body temperature (Fig. 7). In *Macronectes giganteus,* this stage is not usually reached until the chick is 24–26 days old. For its first 18 days of life the chick requires a continuous thermic contribution from its parents (Saiz and Hajek, 1968), after which it is capable of withstanding small temperature changes although its body temperature drops in cold conditions. As the chick gets older, it becomes better able to withstand fluctuations in the weather. The behaviour of the parents towards the chick during the early part of the nestling period can probably be related to the chick's inability to withstand the local climatic conditions on its own.

After the egg has hatched, the chick is brooded alternately by both parents for about 21 days. This period, from the time the egg hatches until the first day that the chick is left alone, is known as the guard period, and generally has two components: the brooding stage, during which the chick is actually covered

FIGURE 7

The observed percentage attendance of parents at aged chicks during the fledging period.

by the parent, and the non-brooding stage, which usually follows, and during which the parent sits beside the chick. This definition of guard period is similar to that used by Richdale (1952) and Rice and Kenyon (1962), but it differs from that of Tickell (1968), who used the term brood stage to cover both components.

After the guard period there is a gradual waning in the attention of the parent towards the chick, and once the latter achieves homeothermy the parents return to the nest only to feed the chick.

Daily observations on 37 nests gave a mean guard period of 21·9 days (range 17–26 days) of which, on average, 18·9 days constituted the brood stage. The average brooding span (2·4 days; range 1–6 days) is shorter than the average incubation span (Table XV).

Of 590 daily observations during the guard period, the males were present on 290 (49·15 per cent) days, the females on 300 (50·85 per cent) days. This includes 14 observations when both birds were seen at the nest together, four of which did not result in change-overs. The average number of spans during the guard period, including the span during which the chick hatched, was 9 (range 6–13), the male and female equally sharing the spans.

Until the sixteenth day the chicks always have at least one parent in attendance, and during the next 5 days about 3 per cent of the chicks are left unattended for at least part of the day. From then until the twenty-fifth day the percentage of adults seen either brooding or feeding their chicks drops to 78 per cent, by which age the guard period for most chicks is over. Between the twenty-fifth and thirtieth days this percentage drops to 40. From then until the sixty-fifth day there is a fairly slow decline to about 17 per cent, after which attendance drops markedly, and from about the seventy-fifth day onwards few parents are seen at the nest.

During February 1968 there were days of very heavy snowfall and drifting. The study area was visited during two of these days, and there were large numbers of adult birds at the nests. At this time, the chicks were between 3 and 5 weeks old.

On 14 February, after 4 days of snow, 22 nests were observed without disturbing the birds. Table XVI shows the age of the chicks and which of them were accompanied by a parent. The survival value of parental return at times of adverse weather towards the end of the guard period is reflected in the number of chicks which actually died as a result of drifting (Plate Va and b). (49 per cent of all chicks which died in the study area did so during this period of bad weather.)

The brood stage, lasting on average 18·9 days, compares favourably with the average time (18 days) that the chick needs a constant heat supply (Saiz and Hajek, 1968). During the remainder of the guard period the chick is able to live outside the brood pouch of the parent, but it is quickly covered by the parent if there is any marked change in the weather.

As the chick gets older, its ability to withstand temperature fluctuations increases. The parent can leave the chick for varying lengths of time, returning only when there is a marked worsening of the weather, which suggests that immediately following the end of the guard period one parent at least is still feeding near enough to the island to allow it to return quickly to the chick. The need for the parent declines when the chick can effectively regulate its own body temperature, and after this the parents need only return to the chick to feed it.

From about the fortieth to sixtieth days, the chicks are usually visited by their parents every 3–4 days, until they reach their maximum weight. After this there follows a starvation period. The sightings of parents at the nest during this period are very few indeed.

b. *Chick behaviour in varying climatic conditions.* Even after the chick has attained homeothermy it behaves in different weather conditions either to conserve or dissipate heat. On windy days, the chicks are very still with their heads tucked under their wings. In drifting snow, the bird faces into the wind and allows the snow to build up around it and almost cover it. From the absence of snow and water in the nest cup, it would appear that during these periods the bird is very still, the layers of snow around the body perhaps serving as an additional insulation against the wind.

Although the chick's down is very good insulation against the cold, chicks appear to be less able to dissipate heat when there is a high temperature and no wind. On such days they sit and pant in the heat. The chicks were never seen to lift their feet as if to lose heat through them as described in young Pacific albatrosses (Howell and Bartholomew, 1961).

c. *Chick activity on the nest, first flight and departure.* For the first 6 weeks of life, the chicks are fairly inactive, sitting still on the nests, occasionally nibbling at stones on the nest cup, but sleeping for much of

TABLE XV
BROODING SPANS OF THE PARENTS DURING THE GUARD PERIOD

	Span number 1	2	3	4	5	6	7	8	9	10	11	12	13
Length of span (days)	2	4	1	4	3	3	2	2					
	2	1	1	3	2	1	5	4	4				
	2	1	1·5	4·5	1·5	2·5	2	1·5	2·5	1	3		
	1	2	3	2	4	2	1	3	1				
	2	3	4	4	5	4	1						
	3	3	2	3	2	2	1	2	2	2			
	2	1	4	1	2	3	1	3	5				
	1	1	3	2	4	2	3	3	2	1			
	2	2	2	3	2	2	1	2	1	2	3	3	
	1	1	3	2	4	3	3	5	2	4			
	4	1	1	4	4	2	2	2	1				
	3	2	1	2	2	4	2	3	3	1			
	2	2	1·5	3·5	2	1	1	2	1	1	3	4	
	2	3	4	2	3	4	2						
	1·5	2·5	1	2	3	2	2	1	3	2	1	1	1
	3	3	4	2	2	2	2	1	1				
	3	4	1	3	2	2	2	2					
	2	2	3	2	5	2	2	2·5	1·5				
	3	3	2	3	3	3	2	1					
	2	2	3	4	2·5	2·5	2	2	2				
	2	2	5	6	3	4	1						
	0·5	3·5	2	2	3	2	3	2	2	2	2		
	3	2	3	2	3	3	3	2	2	2	1		
	3	4	3	3	3	1							
	3	5	2	4	4	3	3	2					
	1	3	1	1	2	2	1	3	3				
	2	1	1	2	1	4	2	3	2				
MEAN	2·15	2·37	2·33	2·62	2·85	2·52	2·33	2·35	2·16	1·80			

Table XVI

AGES OF CHICKS OBSERVED AT THEIR NEST SITES DURING THE HEAVY SNOWFALLS OF MID-FEBRUARY 1968

		Age of chicks (days)		
	Number	*Mean*	*S.D.*	*Range*
Chicks with parent	11	30·6	3·2	26–36
Chicks alone	6	27·2	4·9	33–45
Chicks dead	5	28·6	3·8	25–34

the time. As they grow older, they take an interest in their surroundings and are often found wandering away from the nest. Their wanderings extend as they grow older, and some chicks have been recovered up to 12 m. from their nests.

For several days before fledging, the chicks spend a lot of time exercising their wings on the edge of the nest cup and periodically jumping in the air. Such flapping and jumping may result in the birds being caught in the wind and carried some distance in a glide, these early glide flights invariably result in crash landings.

After the chicks fledge, some, at least, do not leave the island immediately but fly around the vicinity. Thus in early May a chick was recovered 3 km. away from its nest. Several of the birds undertook trial flights before finally leaving the island, returning to their nests during this period. There is one record of a nestling being back at its nest 5 and 8 days after it had fledged; on both occasions it flew off without any apparent difficulty.

While on the nest, the chick's usual method of defence against intruders is to eject a stream of oil and regurgitated food in their direction. The earliest record of oil ejection is from a 6 day old chick, and the young chick's aim is fairly accurate over about 2 m. The initial colour of the oil is usually pink, occasionally green, and it contains few or no food particles, but as the chick becomes older, food particles become a more common feature and the oil is darker, probably being influenced by the colour of the foodstuffs. On one occasion, a 6 week old chick, when disturbed by the author, took up a posture very similar to the adult defensive posture (Warham, 1962) with its tail held high, neck extended and head held low over the nest. It uttered a deep "grhrhrhrh" bray, which was followed by oil spitting, but no head waving was recorded.

d. *Chick feeding*. Chicks are fed by regurgitation from the parents. The chick strokes the parent's bill for about a minute before the latter opens its beak. The chick then inserts its head between the mandibles and feeds for about 10 sec. This occurs three or four times, then the chick takes a short rest, and the whole procedure is repeated. As the chick's head gets bigger, it feeds by placing its own open mandibles between and at right-angles to those of the parent. Chicks appear to recognize their parents; at no time during the study were chicks seen soliciting food from any of the many other birds which sat around the nest sites.

When a chick is being fed, it is to the nest and not the chick that the parent returns. If the chick is not in the immediate area of the nest when the parent returns, it makes no attempt to look for it, in contrast to the Pacific albatrosses (Rice and Kenyon, 1962).

e. *Plumage of the chick* (Plate VIa–d). The chicks are wet at hatching, but the light grey down dries within 5 hr. (white-phase chicks hatch with a white down). After about 2 weeks, this natal down starts to be replaced by a much coarser down which may not be completely lost until the chick has fledged. The first feather sheaths appear after 30 days, initially on the belly and breast, and in some cases the ventral surface is completely feathered by the fifty-fifth day, the feathers on the back start to appear about a week after the belly feathers, and the primary feathers appear about the forty-fifth day and grow very quickly. One of the last areas to lose its down completely is the face, but by the hundredth day most of the birds have only a few wisps of down, and by the time they fledge most are in their near-black juvenile plumage.

f. *Development of the chick*. During the summer of 1967–68, the chicks which hatched in the study area were weighed and measured regularly throughout the fledging period. The following measurements were recorded in the field: wing, tarsus, mid toe and claw and the length and depth of the bill (p. 10).

g. *Measurements.* Fig. 8 shows the growth rate of the chicks from hatching until they either died or fledged. Histograms of bill lengths (Fig. 9) showed a marked bimodal distribution after the sixtieth day, and examination of the other measurements showed a similar pattern. The distribution was thought to be due to different growth rates of the male and female chicks, and in late April 12 chicks aged between 85 and 100 days were selected to test this. These birds were measured and sexed by dissection (Table XVII).

The 20 chicks which fledged in the study area were sexed on these criteria, giving nine males and 11 females. Their growth curves for bill length are given separately (Fig. 10). Such is the difference in growth of the males and females that the means are significantly different after 36 days ($t = 3{\cdot}89, p < 0{\cdot}005$).

Male chicks show a more rapid weight increase than the female chicks, the difference in weight reaching

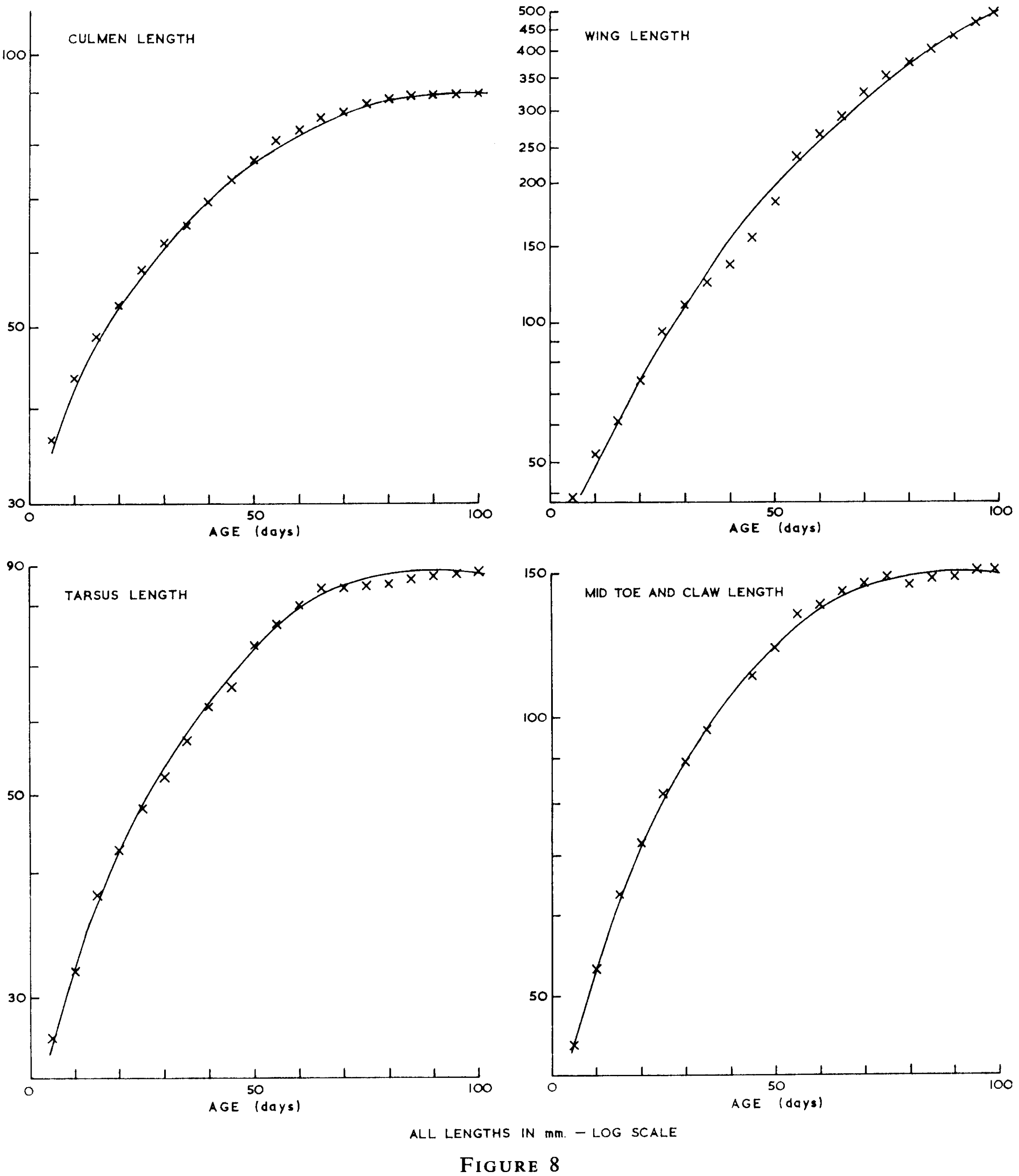

FIGURE 8

Growth curves of culmen, wing, tarsus, and mid toe and claw of aged *M. giganteus* chicks on Signy Island (log scale). (Curves fitted to mean values by eye.)

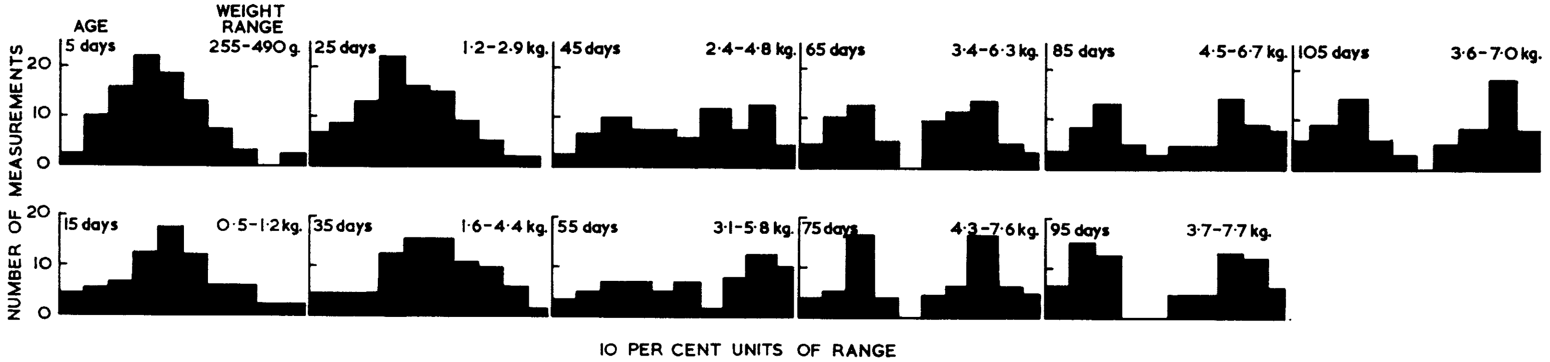

FIGURE 9

Frequency distribution of bill measurements of known aged chicks. The histograms are built as 10 per cent units of the range of weights for any specific age.

TABLE XVII

WEIGHTS AND MEASUREMENTS OF 12 SEXED CHICKS AGED BETWEEN 85 AND 100 days

	Weight (kg.)	*Bill* (mm.)	*Wing* (mm.)	*Tarsus* (mm.)	*Mid toe and claw* (mm.)
Male					
Mean	5·8	97·9	517	93	148
S.D.	1·3	2·7	21	3·9	1·7
Female					
Mean	4·45	85·8	481	81	134
S.D.	0·67	5·7	14	4·3	1·7
t	2·055	2·28	4·37	7·46	6·07
p	0·05<*p*<0·1	0·02<*p*<0·05	0·001>*p*>0·002	>0·001	>0·001

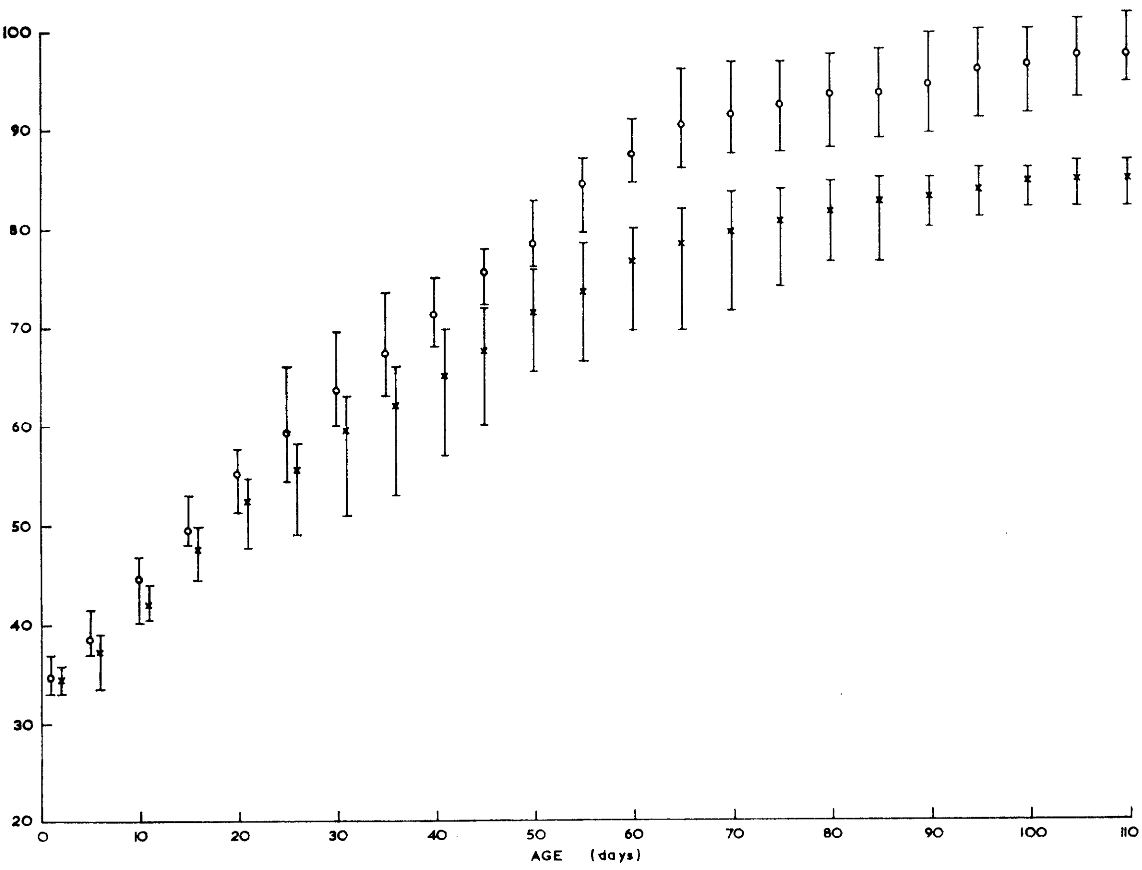

FIGURE 10

Means and ranges of culmen lengths of known aged and sexed chicks on Signy Island.

a maximum of 2·41 kg. at 56 days, and falling off as fledging approaches. Although there is no significant difference in the number of feeds each sex receives, males tend to receive heavier meals (60 per cent of the feeds received by the males were heavier than the females), and this could account for the weight difference between the sexes.

The reason the males received more food than the females could be related to the male chick begging more strongly than the female and the males could well be better assimilators of food than the females, but no data are available on food assimilation.

h. *Weights and meal sizes.* A chick is said to have had a meal if, between successive weighings (daily or every 2 days), an increase in body weight is recorded. The increase in weight is taken as an index of the meal size. Because the birds were not weighed immediately before and after a meal, this index is an underestimate of the actual amount of food received. Nor does the definition allow for the number of times the chicks were fed between weighings. A drop in weight between weighings will mean that the chick has either received no meal, or a very small meal, not sufficient to allow the chick to continue normal growth without utilizing some of its fat reserves. This method of calculating meal sizes does not take into account the energetics of the chick's development. As a chick grows older, so its energy demands in respiration and growth will change, and the chick's growth efficiency will drop. While the chick is putting on weight much of the food taken in is laid down as fat reserves, reflected by a sharp increase in the chick's weight, but as the chick grows older, the proportion of food needed for development increases and less food is laid down as food reserves. Therefore, particularly after the chick has reached its peak weight, the underestimation of the meal sizes is greater. Bearing this in mind, the records of weight changes of the chicks may still serve as an index of the amount of food the chick is receiving.

During the brood period, the chicks were fed several times a day, but because they were weighed only once a day, these feeds are looked upon as a single meal.

The mean weight of seven chicks weighed while still wet, probably within 5 hr. of hatching, was 161·4±11·8 g., range 150–170 g. (Fig. 11). This compares with a mean of 155 g. from Pointe Géologie (Mougin, 1968) and 173±2·55 g., range 155–190 g., for nine still wet chicks from Macquarie Island (personal communication from G. W. Johnstone). 30 chicks weighed within 12 hr. of hatching (Fig. 11) weighed 169·6±16·3 g., range 140–210 g., while on Macquarie Island two just dry chicks (probably less than 12 hr. old) weighed 220 g. (Warham, 1962). This is a far heavier mean weight than recorded on Signy Island; (a mean weight of 220 g. was not reached on Signy Island until the birds were 36 hr. old). These data suggest the possibility of a latitudinal difference in the weight of newly hatched chicks, but more data are necessary before reliable comparisons can be made. (It is unlikely that the chicks weighed by Warham were *M. halli*, because Johnstone (personal communication) found that, on hatching, these chicks were significantly lighter than *M. giganteus*.)

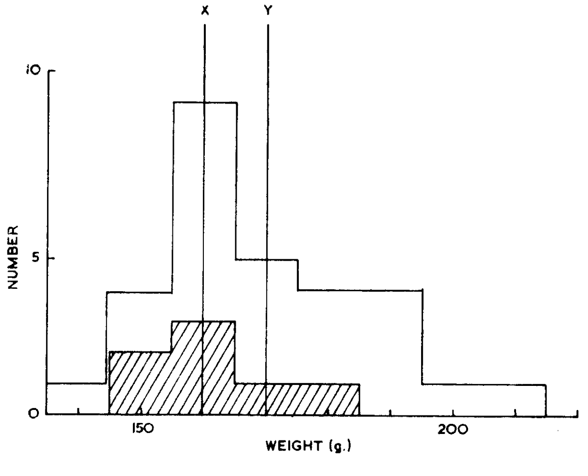

FIGURE 11

Weight–frequency distributions of *M. giganteus* chicks weighed within 5 (shaded area, mean X) and 12 (mean Y) hr. of hatching on Signy Island; class interval is 10 g.

During the first 15 days, chicks received food nearly every day (Table XVIII), and after a fortnight the weight passed 1 kg. With the cessation of brooding the feeding frequency drops, although the meal size increases. From the fifteenth until the twentieth day, the proportion of days on which the chick was fed dropped from 72 to 53 per cent and thereafter remained fairly constant until the sixtieth day when there was a marked drop to 30 per cent; from then until fledging, the chick was fed every 3 or 4 days.

The individual meal sizes varied greatly, based on the above definition of a "meal" (albeit an under-estimate of the "real meal" weight). During the first 5 days, meals averaged 4·2±3 g. per day and between 60 and 70 days reached a maximum of 153 g. per day. This was followed by an apparent drop in meal size until the chick left the nest. During the starvation period the chick continued to be fed and, although generally there is a drop in the chick's weight, feeds are reflected by a temporary increase in an individual chick's weight. During this period there is an apparent drop in meal size but this may be a misinterpretation; the meal sizes may remain the same but more food may be used in respiration than in growth giving an apparent decrease in meal size.

There was no difference in the amount of food chicks received in the first 2 days of a brood span, but the difference between days 2 and 3 is significant. The average brood span was 2·4 days with 61·6 per cent of all brood spans lasting 2 days or less, suggesting that the brood span most beneficial to a chick would be approximately 2 days.

Of 200 spans studied, there were 14 cases including one case of two consecutive spans each of 2 days during which the chick received no meals. The meals received before and after these spans were normal for chicks of comparable ages. It is unlikely that these non-feeding spans are the result of the parent, while at sea, being unable to collect enough food to feed the chick during its brood span, because the spans immediately before and after the non-feeding span are similar to the "normal" mean brood span (2·3, 2·3 and 2·4 days, respectively). Because there is no relationship between the number of change-overs during the guard period and the weight of the chick at the end of this period (Table XIX), parents can visit a nest without a change-over occurring, and the adult weights in January are heavier than in December, despite having the chick to feed (pp. 16-17); it would appear that the frequency of change-over is not related to the availability of food, there being no pressure on the brooding bird to be relieved.

Therefore, during the early part of the fledging period, food is neither sparse, irregular, nor distant from the colonies (probably within 24 hr. flying time) and it is probable that the brooding urge is under a control other than the urge of the parent (or the chick) to receive food.

i. *The fledging period.* A chick is said to have fledged when it disappeared, for the first time, from its nest and could not be seen near it.

In 1968, the mean fledging date in the study area was 10 May (10·35±5·20 days), range 29 April to 28 May. An additional 387 fledging dates were collected by visiting adjacent colonies every second day. In these colonies the mean fledging date was 12 May (11·86±5·28 days), range 27–28 April to 29–30 May, 90 per cent of the chicks fledging within 8 days of the mean (Fig. 12).

The average fledging period for 21 chicks was 118·5±5·1 days, range 107–128 days, no significant difference occurring between the fledging periods of male and female chicks (117·3±3·1 days, range 106–125 days, and 119·1±5·5 days, range 112–128 days, respectively).

The difference between the maximum chick weight (mean 6·67 kg.), recorded between 60 and 100 days, and the weight at fledging (mean 4·43 kg.) is significant ($p<0{\cdot}001$) as is the sex difference between the maximum ($p<0{\cdot}001$) and fledging ($p<0{\cdot}02$) weights of the chick (maximum weight—male 6·97 kg., female 5·89 kg., fledging weight—male 4·84 kg., female 4·02 kg.). No data are available on the weights of parents at the time the chicks fledge, but taking the data on adult weight for the summer months as a whole, the mean adult weight is 4·32 kg. (males 4·9 kg., females 3·9 kg.) and there is no significant difference between the weight of the adult birds and the weight at which the chicks fledge.

In the present study, a relationship was found between the weight at which a chick fledged and the date it hatched (Fig. 13). A regression line $y = 0{\cdot}0796x+54{\cdot}3$, ($r = 0{\cdot}497$, $0{\cdot}02<p<0{\cdot}05$) has been calculated for all the data.

The weight at which a chick fledges is affected by the desertion period. Those which fledge before 10 May have an average desertion period of 6·85±4·10 days compared with 14·40±5·25 days for chicks which fledge after this date. This occurs because the parents appear to stop feeding their chicks in early May, regardless of the age, sex or weight of the latter. In 1968, no chicks appeared to be fed after 6 May,

TABLE XVIII

NUMBER OF DAYS ON WHICH A CHICK RECEIVED A MEAL AND THE PERCENTAGE OF THE TOTAL

	Time intervals (days) 0–5	6–10	11–15	16–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120
Number of meals received	5	4	4	5	4	2								
	5	5	3	4	3	2								
	5	3	3	4	2	1	3	3	2	2	1	1	1	
	5	3	4	2	4	2	2	2	2	2	1	1	1	
	5	5	3	2	4	3	1	2	3	0	1	2	2	
	5	3	3	4										
	5	3	5	2	3	1	2	2	2	2	1	2	2	1
	5	4	3	2	3	2	1	2	1	2	0	1	1	1
	5	4	2	4	3									
	5	3	4	3										
	5	4	4	2	1	4	3	2	1	2	0	2	0	
	5	4	4	2										
	5	5	4	2	2	3	3	1	2	0	2	1	0	1
	5	5	4	3	2	3	2	2	2	2	1	1	1	1
	4	5	4	2	1	3	2	2	0	1	1	2	1	1
	5	5	4	4	1	3	2	2	0	1	1	3	2	
	5	5	3	2	4	2	1	1	2	2	1	0	2	1
	5	4	4	3	1	4	2	2	2	1	2	1	0	1
	5	4	4	3	3	3	1	2	3	1	1	2	1	
	5	5												
	5	5	2	2	2									
	5	4	3	2	3	1	3	2						
	5	4	5	2	3	2	1	3	1	1	2	0	2	1
	5	4	4	2										
	5	5	3	3										
	5	4	3	3	1	2	4	4	0	1	1	1	0	
	5	5	3	4	1	2	2	2	1	2	1	1	1	2
	5	4	4	3	1	2	2	2	1	2	1	2	1	1
	5	3	4	3	0	1	2							
	5	4	3	3	4	3								
	5	5	3	3	2	2	2	1	2	1	1	1		
	4	5	3											
	98·7	84·0	72·0	53·0	46·0	46·0	41·0	43·0	30·0	27·0	21·0	27·0	22·0	22·0

Percentage of days on which birds received a meal

After 20 days, the time intervals are in 2 days, and percentages are worked out on a time of 5 double days, and not a 10 day period, i.e. the figures are still taken as a unit of five.

Table XIX

HATCHING WEIGHTS, WEIGHT AT 20 days OLD, DIFFERENCE IN WEIGHTS OF 24 CHICKS AND THE NUMBER OF CHANGE-OVERS RECORDED DURING THE GUARD PERIOD

Hatching weight (g.)	*Weight at 20 days* (kg.)	*Weight increase* (kg.)	*Number of change-overs*
200	1·60	1·40	8
160	1·85	1·69	7
150	1·55	1·40	9
175	1·35	1·175	11
160	1·50	1·34	8
150	1·40	1·25	12
160	1·55	1·39	9
150	1·45	1·30	6
150	1·35	1·20	9
210	2·10	1·89	8
190	1·75	1·56	11
160	2·05	1·89	9
180	1·50	1·32	8
150	1·30	1·15	9
155	1·50	1·345	10
160	1·45	1·29	6
170	1·90	1·73	9
190	1·40	1·21	8
160	1·40	1·24	9
185	1·25	1·065	9
150	1·50	1·35	9
170	1·20	1·03	6
175	1·40	1·225	9
160	1·55	1·39	9

although some of the chicks did not fledge until the end of the month. Chicks which fledged by 10 May* lost on average 12·9 per cent of their body weight during their desertion period, while chicks which fledged after this date, lost 21·5 per cent. The difference between these values is significant ($t = 2{\cdot}209$, $p < 0{\cdot}05$).

In the Manx shearwater, evidence based on ringed nestlings and their subsequent recovery at the breeding

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* At the end of the fledging period, the chicks are fed on average every fourth day. If feeding stopped on 6 May, it would be 10 May before the next meal would be received, and it is not until after this date that the effects of desertion would differ from the normal interfeed period.

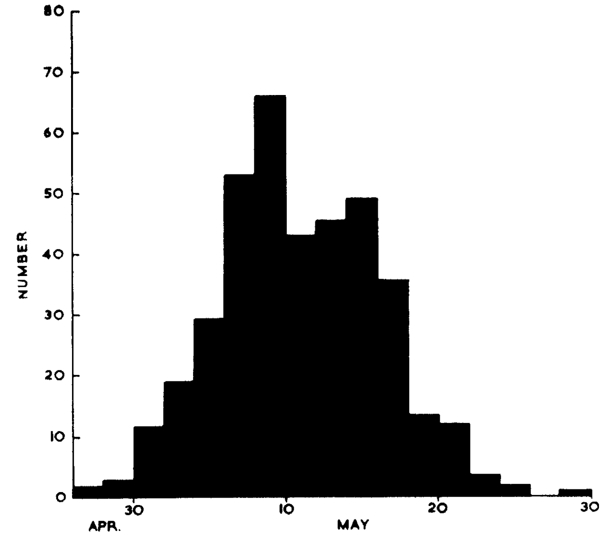

FIGURE 12
Frequency distribution of dates of fledging of *M. giganteus* chicks from Signy Island; class interval is 2 days.

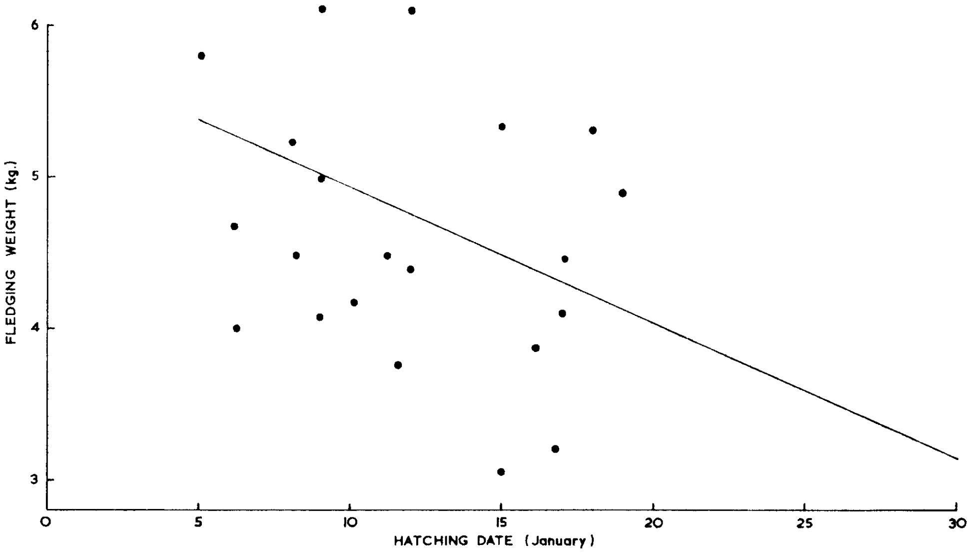

FIGURE 13
Comparison between chick weights at fledging and their hatching date.

colony shows that the chicks which fledge earlier have a better chance of survival (Perrins, 1966), although no differences have been recorded in the weights of chicks which fledge early and those which fledge later (Harris, 1966*b*). Perrins (1963) showed that in the great tit (*Parus major*) the subsequent survival of the fledgling was related to its weight at fledging, a similar conclusion being drawn by Elliott (1970) from his study on the great shearwater (*Puffinus gravis*).

Data on fledging from other breeding colonies are few. At Macquarie Island, the chicks fledged by 15 April, after which "only occasional stragglers were seen near the rookeries", the period of fledging lasting from 25 March until 15 April (Warham, 1962). At Pointe Géologie, the fledging period is more in line with but still somewhat earlier than Signy Island, ranging between 12 April and 10 May based on 4 years' data (Mougin, 1968). The single year's data from Anvers Island suggest that the chicks depart about 3 May (Holdgate, 1963).

The fledging period of 117·5 days for Signy Island compares with a maximum mean value* of 111·57 days (range 98–119) for Macquarie Island (Warham, 1962) and 111 days (range 104–118) and 119 days (range 112–128) for Pointe Géologie in 2 years (Mougin, 1968). All are based on small samples, Macquarie Island 7, Pointe Géologie 8 and 15. The data from Pointe Géologie suggest that the fledging period in different years may vary appreciably; it would therefore be worth comparing the two seasons at Pointe Géologie to see if there is anything, such as the nearness of open water, and the availability of food, which was markedly different in the 2 years. Although the difference between Macquarie Island and Signy Island is significant, it may be the result of an annual variation (cf. Pointe Géologie) rather than a zonal variation.

By May, most of the birds and seals upon which the southern giant petrel subsists during the summer months have left the island, and the plankton standing crop is declining in the sea (Foxton, 1956), so that when the chick fledges food would appear to be far less abundant than during the summer months.

For chicks to survive after the parents have stopped feeding them, they must live through a desertion period while still on the nest, learn to fly, find and secure food. Therefore, it would be advantageous for chicks to build up large fat reserves before fledging, and have a short desertion period. The data above suggest that this is best attained by chicks hatching and fledging as early as possible. Such chicks will have more energy and possibly more time available before harsh weather sets in, during which they can gain experience in flying, and withstand a period of partial starvation during which they learn to catch food, which itself may be made easier if the chicks are more adept at flying.

The giant petrel chick on Signy Island fledges at the beginning of the winter, during late April and May. Farther to the south, at Pointe Géologie, they fledge earlier (Mougin, 1968) as they do on South Georgia farther to the north (personal communication from W. L. N. Tickell).

The evidence suggests that the breeding cycle of the southern giant petrel is sufficiently short to allow the species to breed in the Antarctic proper but that the time taken is near the maximum permitting success. If the breeding cycle was much longer, the chicks would not fledge until later in the winter, with a possibility that the chick would be less likely to fledge successfully because of the climate. Late breeders stand a smaller chance of successfully rearing a chick. On Signy Island it appears that the adult birds leave the chick at approximately the same date, the beginning of May. About 50 per cent of the chicks have fledged by the end of the first week of May. The time the parents desert their chicks is not affected by the age, sex or weight of the chicks (Table XX). The parents may also leave the island before the chicks.

4. *Failed breeders*

During the incubation period, if an egg was lost, both birds were often seen at the nest for a few days immediately following its disappearance. During this period their behaviour reverts to that of a pair at the pre-breeding period, sitting side by side and billing. This period usually lasted about 5 days (range 1–9 days for seven nests). Thereafter their attendance at the nest drops off and, although they are still occasionally seen at their nest, they are more often seen with groups of birds standing in the colony. They also appear to form large roosting flocks in areas separate from the breeding colonies, but possibly just as traditional as the nest sites.

Between November and March, a group of birds was regularly seen sitting on a snow bank to the south of the study area. This group existed in all 3 years of the study, and in 1967–68 it was counted on every

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* Warham's (1962) data are all given with a plus and minus value, e.g. 106±2, 108±4 days, etc. These figures are taken as 108, 112, etc., their maximum value, making the mean difference between Signy and Macquarie Islands minimal.

TABLE XX

DATE, AGE, WEIGHT AND SEX OF *Macronectes giganteus* CHICKS AT THE TIME OF DESERTION

Date chick deserted 1968	*Age of chick at desertion* (days)	*Weight of chick at desertion* (kg.)	*Sex of chick*
19 April	103	5·8	Female
22 April	98	6·0	Male
22 April	100	5·3	Female
24 April	105	5·1	Female
24 April	96	7·7	Male
27 April	105	7·25	Male
27 April	109	6·25	Female
29 April	114	5·8	Male
29 April	100	5·3	Female
1 May	110	5·4	Female
1 May	112	5·5	Male
1 May	111	4·2	Female
3 May	112	5·5	Male
3 May	117	4·5	Female
3 May	100	4·2	Female
4 May	116	4·6	Female
4 May	108	4·2	Male
4 May	109	4·9	Female
6 May	111	4·2	Male
6 May	109	6·6	Male

visit to the colony (Fig. 14). The numbers increased throughout November into January, and decreased later in that month, until, by the end of March, the group had disappeared. It was difficult to identify these birds, because they were very nervous, but several colour-ringed birds were known to roost in the group. Seven identified were failed breeders. From the end of December, the birds in this group were also seen to be in moult, and often during January–February when the group was disturbed, the ground was covered with feathers. By the middle of April, the failed breeders had left the island.

5. *The moult*

a. *Moult in the southern giant petrel.* On their return to the breeding colony in August, all the birds seen and handled appeared to have completed their moult. Body moult commences in late November, shortly after the end of egg-laying, and by the end of that month, about one-third of the incubating adults are shedding their contour feathers. Incubating birds are often seen preening themselves, and have their bills covered with small feathers. Body moult may not be completed until March. Suspected pre-breeders handled in February and March showed little difference from the breeding birds in the amount of new

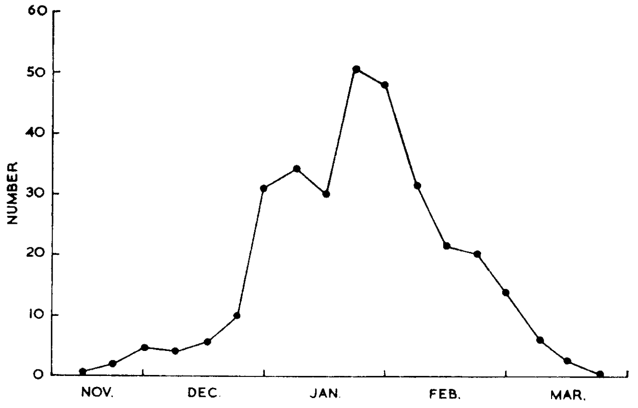

FIGURE 14

The weekly mean counts of non-breeding birds during 1967–69.

feathers still growing, suggesting that the pre-breeders might commence their body moult at the same time as the breeding birds, although at this time the pre-breeders are still at sea. Alternatively, if moult does not start until their return to the island, they may moult their body feathers faster than breeding birds.

The first area to develop new feathers is the abdomen, followed by the breast, head and neck, back, wings and tail.

Primary wing moult begins with the inner primaries, extending outwards, and rarely are there more than three feathers missing or being replaced at any one time. Primary wing moult was not positively observed in breeding birds until the second half of February, when several had very worn primaries, but birds flying around the colony had gaps in their wing feathers during January. These are mainly failed, and possibly pre-breeding birds. No breeding birds seen flying over the colony showed wing moult.

The first record of wing moult in the flying birds was 15 December; by 16 January, 40 per cent of a group of 400 flying birds were in primary moult and this had risen to 71 per cent by 13 February. On 22 January, three birds, which had lost their eggs 3–4 weeks previously, had their innermost primaries moulting.

Primary moult was first recorded in a breeding bird on 18 February when an unringed bird, caught while feeding a month-old chick, had a moult score of 14; and on 22 February a ringed bird, seen feeding a 7 week old chick, had a moult score of about 18. By mid-March most of the breeders still attending chicks were in primary moult, some with the middle primaries missing.

The following data on primary wing moult were collected from 69 birds seen or handled during the study period. Of these, 43 were breeding birds, nine were failed breeders and 17 assumed to be pre-breeders. The method described by Ashmole (1962) was used to measure moult. An old feather receives no score, a missing feather one, and a fully grown new feather five. New feathers score two, three or four depending upon their development. The scores are shown in Fig. 15. Although the data are inadequate for statistical comparison, the difference between breeding birds and those which have failed is noticeable, the former being later in moulting their primaries. A calculated regression line $y = 1\cdot082x - 10\cdot45$, ($r = 0\cdot751$, $p < 0\cdot001$) indicates a mean primary moult period in the failed and pre-breeders of about 93 days. More data, particularly from breeding birds, are really needed.

Tail moult has not been noticed until after primary moult is well advanced, and specimens examined in the British Museum (Nat. Hist.) also show this. There does not appear to be any "post-moult" exodus comparable with the cape pigeon and snow petrel (Beck, 1969).

Moult in the giant petrel appears to follow the same pattern in both the adult birds and the nestlings, in the appearance of their juvenile plumage (i.e. the first feathers to appear are those on the abdomen, followed by the neck, head, wing and finally the tail).

The deferment of primary moult in the breeding birds can be accounted for by their need to remain as airworthy as possible to obtain sufficient food for themselves and the chick. This is particularly important at least during the early feeding, if not the total feeding period of the chick's growth, when it is putting on weight. By doing this, the parents can save energy on two counts. There is the energy required to replace feathers and, since birds in wing moult are less efficient fliers, they will need to expend more energy in

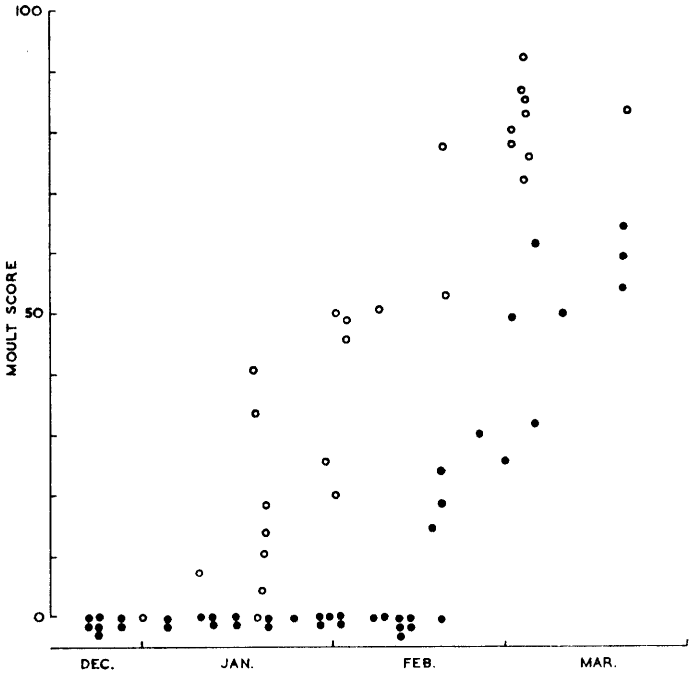

FIGURE 15

Moult scores of breeding (●) and failed/pre-breeding (○) *M. giganteus* during 1968–69.

remaining airborne and to fly as far as birds not in wing moult. Therefore, it would be advantageous to defer wing moult until as late as possible, at least until the chick has laid down some fat reserves. Wing moult reaches a score of 50 plus in mid-March at about the time the chicks are at the same weight as the adults. Williamson (1957) also pointed out that in the wheatear (*Oneanthe oneanthe*) it was improbable that adults in wing moult could obtain enough food for both themselves and their chicks and moult is deferred until breeding is finished.)

The non-breeders have no responsibility, except to themselves, and can afford to start their wing moult early in the season. If, on the completion of their moult, these failed and pre-breeders leave the island, the feeding grounds around the colonies will be left to the breeding birds. By April, this reduction of the feeding population could be important, because not only has the plankton standing crop started to decline (Foxton, 1956) but also there are few animals and carcasses around the island, upon which the birds can scavenge and these might be snow-covered. The failed breeding group (pp. 39-40) appears to break up and leave the island during mid-March. If it is disadvantageous for the breeding birds to wait until after they have reared their chicks to commence their moult, because winter would arrive before they could complete it, the alternative would be to moult while away from the colony during the winter months.

The physiological mechanisms of moult depend on two factors: an ultimate factor—the need for a bird to replace all its feathers, and a proximate factor which triggers off the mechanism. There must also be built into the mechanism some stages at which it can be arrested if needs demand it. Moult starts probably during the pre-breeding period with the development of the brood pouch, which is completed sometime before egg-laying. Once the egg has been laid the breeding birds start their body moult which, if the data from other species are comparable, for example the bullfinch (*Pyrrhula pyrrhula*) (Newton, 1966), may account for upwards of 75 per cent of the total plumage. For a breeding giant petrel, the energy demands of body moult can be spread over 5 months (November–March).

Since failed breeders begin primary moult before the breeding birds, there must be some stimulus to the breeding bird which prevents the onset of wing moult. This may be the presence of the chick or egg in the brood pouch inducing a feedback to the endocrine system controlling the moult process. Roberts (1940*b*) suggested that the presence of the egg might stimulate broodiness in the gentoo penguin, quoting the work of Taibell (1928) on turkeys which showed this. If this is the case, it could possibly arrest moult.

After the egg has been lost, the brood pouch in the failed breeders becomes down-covered more quickly than in the breeding birds. Similar development of the brood pouch has been recorded in the black-bellied storm petrel (*Fregetta tropica*) (Beck and Brown, 1971), in Wilson's storm petrel (Beck and Brown, 1972) and in the North Atlantic fulmar (personal observation). Therefore, the presence of an egg appears to inhibit the re-lining of the brood pouch, and this inhibition can possibly restrict moult to the body feathers. Wagner (1962) *in* Ashmole (1968) stressed the importance of sex hormones in arresting the moult process; Ashmole (1968), reviewing moult, suggested that it may be a continuous process inhibited by specific hormones.

The deferment of wing moult in breeding birds does not last throughout the nestling period. However, it may be that, by the time breeding birds start replacing their primaries, the chicks have large enough food reserves to withstand the reduction in feeding frequency which might result from the parents moulting.

b. *Moult in Procellariiformes.* Body moult during the incubation period is a common feature of several species of petrel: snow petrel, cape pigeon, white-headed petrel (*Pterodroma lessoni*) (where it might even start before egg-laying) and short-tailed shearwater (Marshall and Serventy, 1956; Maher, 1962; Warham, 1967*a*; Beck, 1969, 1970). Beck (1969) suggested that primary moult in the cape pigeon lasted about 85 days, and ended with a post-moult exodus.

The data collected suggest that the time taken for the completion of primary moult in the southern giant petrel is about 93 days (p. 41), about 10 days longer than in the cape pigeon. The fledging period of the giant petrel is 117 days, more than twice that of the cape pigeon (about 50 days) (Pinder, 1966). Both enter wing moult during the fledging period, but with the shorter fledging period, the chicks of the cape pigeon have fledged before the breeding birds have finished their moult. The parent birds are then free to leave the colonies to complete their moult. In the southern giant petrel, with the longer fledging period but a similar moult period (93 days), the adult birds can probably complete most, if not all, of their moult before the chicks fledge and do not need such an exodus.

Primary moult during the breeding season is a common feature of other polar species: dunlin (*Calidris alpina*), glaucous gull (*Larus hyperboreus*) and Steller's jay (*Cyanocitta stelleri*) in the Arctic (Pitelka, 1958; Johnston, 1961; Holmes, 1966); the snow petrel, cape pigeon and possibly the other fulmarine petrels in the Antarctic (Biermann and Voous, 1950; Maher, 1962; Brown, 1966; Beck, 1970).

The Wilson's petrels in the Antarctic do not appear to have such a moult/breeding cycle, primary moult occurring in their winter quarters (Roberts, 1940*a*). The young of the Wilson's petrel are still in their burrows in April and early May, by which time there is a danger that they will become snowed in (Beck and Brown, 1972). It would therefore appear necessary for the young birds to fledge as early as possible, and for the parents to keep feeding them. There does not appear to be a desertion period as fledging approaches (personal communication from J. R. Beck). With a reduction in the availability of food, the breeding birds probably need to remain as efficient as possible to collect sufficient food for the chicks and consequently cannot afford to reduce this efficiency by starting to moult their primaries before the chicks have fledged. By contrast, southern giant petrel chicks with relatively larger food reserves are much larger than the Wilson's petrel chicks, and are more likely to survive short periods of food shortage during April and May.

The need for a bird to complete both moult and breeding in as short a space of time as possible has probably resulted in the evolution of a combined moult/breeding cycle, but this has not evolved in species where the success of the chick would be impaired by their parents starting primary moult before fledging had been completed.

6. *Breeding success*

Human disturbance caused a very high chick mortality (1967, 90 per cent; 1968, 62 per cent; 1969, 67 per cent) and so the data collected from the intensive study area were not used in the analysis of survival. During 1968–69, four separate colonies, in relatively undisturbed areas, were selected and data collected on their breeding success. The colonies were chosen in different predator situations. Colony A was in a single skua territory, B was surrounded by at least four skua territories, while C and D had two or three skua territories around them.

Each colony, checked every 5 days, was observed from a distance and never disturbed. The position of each egg was plotted on a sketch map, and Table XXI shows the results.

TABLE XXI

BREEDING SUCCESS OF FOUR DIFFERENT COLONIES OF GIANT PETRELS (*Macronectes giganteus*) ON SIGNY ISLAND FROM EGG-LAYING UNTIL THE CHICKS ARE AGED 90 DAYS OR MORE*

Colony	*Eggs laid*	*Eggs lost*	*Per cent survived*	*Chicks hatched*	*Chicks died*	*Per cent survived*	*Overall survival* (per cent)
A	72	21	70·8	51	14	72·5	51·4
B	46	26	43·4	20	8	60·0	26·1
C	19	8	57·9	11	3	72·7	57·9
D	37	14	54·0	23	8	65·2	40·5
TOTAL	174	69	60·3	105	33	68·6	41·4

* If chick survives to 90 days, it has a 97 per cent chance of fledging.

a. *Infertile and addled eggs.* A collection of eggs for embryological examination provided an accurate figure for the proportion of infertile eggs, and in the intensive study area counts were made of the number of eggs which failed to hatch. From these two estimates and the data in Table XXI, it is possible to calculate egg loss due to infertility, faulty incubation and direct predation (Table XXII).

TABLE XXII

ANALYSIS OF EGG LOSS

Conditions of eggs	*Year*	*Sample*	*Number*	*Per cent*
Addled and infertile	1968	45	5	11·1
	1969	48	6	12·5
Infertile (from a collection)	1969	57	5	8·8

Assuming both the above samples are representative, about 3 per cent of the eggs are poorly incubated.

Analysis of egg loss	
Proportion of eggs hatching	59·3 per cent
Proportion infertile	8·8 per cent
Proportion poorly incubated	3·0 per cent
Proportion of eggs lost to predators or by breakage	29·1 per cent

There are two main periods of egg loss; 45 per cent of all egg losses occurred within 15 days of laying and there is an increased loss at the end of the incubation period when parents desert their addled eggs.

Of the 105 chicks which hatched, 35 failed to fledge, giving a survival of 69 per cent. Most chicks were lost during the first half of the fledging period. The overall breeding success was 41·4 per cent, range 26·1–57·9 per cent. A comparable figure for fledging success on Macquarie Island is 57·1 per cent, range 39–76 per cent (Warham, 1962), but no data are given for the overall breeding success there.

b. *Egg mortality.* The major predator of the eggs is the skua (Plate VIIa and b). At the Foca Point colony they were responsible for about 80 per cent of egg loss; an examination of Table XXII will show that where skua pressure is highest (colony B) egg loss is greatest. The skuas were very quick to spot and rob any deserted egg, even when it was only a few metres from a human or when a giant petrel was returning to the nest.

The sheathbill (*Chionis alba*) is the only other predator but it is of minor importance; only five eggs were recorded broken by the sheathbills, and three of these were immediately taken by skuas. Both the skua and the sheathbill are effective only against unprotected eggs. The egg is also lost at change-overs, when the incubating bird might knock it out of the cup while being relieved. The parent bird appears to be unconcerned, and will watch skuas eat it without moving from the nest.

c. *Chick mortality*. 21 chicks died in the Foca Point colony, the main cause of death being the weather, heavy drifting snow in February resulting directly or indirectly in the deaths of 10 chicks. The nests, if sheltered, became drifted over, or the chicks became encumbered by snow and were attacked by skuas. This mortality could well have been greater if some parents had not returned to the nests and cleared them of snow.

Four chicks were killed by skuas, all in the first fortnight of life. Skuas can kill and remove a chick weighing up to 1 kg.; they kill the chick either by tearing it to pieces or dropping it from a height. Other causes of mortality were: two chicks were squashed under their parents; two chicks starved; one died as a result of a broken wing; one was possibly cannibalized—at one site, a chick showed a marked increase in weight following the disappearance of an adjacent chick, and a fresh giant petrel tarsus bone was found in the nest with the chick; and one chick died for "no apparent reason". Other causes of death recorded from elsewhere on the island were as follows:

Infection (?)—a very light chick (weight 1·25 kg.) was found in April in poor condition. The flesh of the wing appeared to have been "eaten away" exposing the feather sheaths. The chick was killed and frozen for examination, but no infective agent could be isolated (personal communication from J. W. MacDonald). A second chick with the same symptoms died before it fledged, while a third which successfully fledged was later recovered in South Africa.

Flying accident—chicks found at the bottom of high bluffs, still with some of their natal down, had fallen from the nests above, suggesting that they were attempting to fly too early.

Drowning—one chick took to the water, still with some natal down and was in difficulties. An ebb tide was running so it could not return ashore and, despite a good breeze, could not take off. While being watched, it settled lower in the water, as if becoming waterlogged.

VII. DISPERSAL, AGE OF RETURN TO THE COLONY AND AGE OF FIRST BREEDING

1. *Dispersal of juvenile birds*

The dispersal of juvenile giant petrels from their colonies to the subtropical and temperate latitudes is well documented: F.I.D.S./B.A.S.* recoveries have been analysed by Roberts and Sladen (1952), Sladen and Tickell (1958), Stonehouse (1958), and Tickell and Scotland (1961). A.N.A.R.E.* data (including recoveries from colonies on the Antarctic continent) have been published by Chittleborough and Ealey (1950), Downes and others (1954), Howard (1956), Ingham (1959) and Orton (1963). E.P.F.* data have been published by Prévost (1965), Mougin and others (1969), and Lacan and others (1969), and U.S.A.R.P.* data have been summarized by Sladen and others (1968). An overall analysis of the dispersal of juveniles from various ringing centres is at present in progress. Juvenile birds on leaving Signy Island appear to disperse in an easterly direction (Table XXIII). When the recovery dates within 12 months are compared (particularly the birds which are recovered alive), the route appears to be South Africa, Australia, from west to east, New Zealand and the west coast of South America. Recoveries along the east coast of South America occur earlier than in South Africa, indicating that in some years, perhaps in the presence of an easterly air stream, some of the birds travel directly to South America.

At sea, birds may remain in an area for some time (Kinsky, 1958; Ingham, 1959). Gibson (personal communication) has given details of seven giant petrels which were each recovered twice at Malabar (New South Wales) after intervals of 7, 9, 18, 18, 20, 35 and 49 days, respectively.

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* F.I.D.S./B.A.S.	Falkland Islands Dependencies Survey/British Antarctic Survey.
A.N.A.R.E.	Australian National Antarctic Research Expeditions.
E.P.F.	Expéditions Polaires Françaises.
U.S.A.R.P.	United States Antarctic Research Program.

TABLE XXIII

TIME INTERVAL BETWEEN A BIRD FLEDGING* ON SIGNY ISLAND AND ITS SUBSEQUENT RECOVERY, WITHIN THE FIRST YEAR OF LIFE, IN THE LOW LATITUDES

Area of recovery	*Recoveries*					
	Alive			*Total*		
	Mean interval between fledging and recovery* (months)	*Range* (months)	*Number recovered*	*Mean interval between fledging* and recovery* (months)	*Range* (months)	*Number recovered*
East coast of South America	1·25	0·75–1·50	4	1·25	0·75–1·50	4
South Africa	1·93	0·50–6·00	37	2·40	0·50–8·50	61
Western Australia	2·38	0·75–7·00	61	2·83	0·75–9·75	117
South Australia	2·80	1·50–5·00	23	3·69	1·25–11·00	48
New South Wales, Australia	3·40	2·00–8·00	29	3·76	0·75–8·00	36
Victoria, Australia	3·41	1·75–6·50	10	4·33	1·25–6·50	20
Queensland, Australia	2·25	1·75–2·75	4	2·42	1·75–3·00	6
North Island, New Zealand	4·31	2·00–8·50	12	5·36	2·00–9·50	39
South Island, New Zealand	5·47	4·00–11·25	8	5·24	1·75–11·25	20
West coast of South America	9·60	4·00–9·00	10	10·49	4·00–9·00	18

* Fledging—the birds fledge over a period of weeks from the end of April until the end of May. For the purposes of this table, the date of fledging is taken as 1 May.

94 per cent of the recoveries are of birds in their first year, although, in common with most other Procellariiformes, the juvenile birds spend several years at sea before returning to breed (see below).

2. *Age of return to the colony*

There is an increase in the number of birds at the colony from December through until March. Many of these are suspected to be pre-breeders (identified by a ring on their right tarsus) returning to the colony. They are a common sight, spending much of their time visiting different nests but do not appear to become associated with a specific one. If this increase from December onwards is a true reflection of the time these birds return, then they would not have bred in the current season. Serventy (1957) and Fisher and Fisher (1969) have shown in the short-tailed shearwater and Laysan albatross (*Diomedea immutabilis*) that immature birds return to the colonies after breeding has started. Giant petrels are very nervous, and difficult to catch unless actually nesting. As a result, to obtain data on the age at which these birds return to the colony, it was necessary to shoot a sample. Between late January and March 1969, 17 birds of known age were shot, sexed by dissection and their gonads removed.

Six females were aged between 6 and 8 years and 11 males ranged from 5 to 8 years. Although the difference is not significant, of the seven birds recovered at 6 years, six were male. Another two unsexed birds, both ringed as nestlings, were recovered on Signy Island aged about 27 months. No. 56798, ringed February 1959, was recovered in April 1961, and No. 5018465, ringed March 1966, was recovered dead in March 1968. The carcass was fresh when found, and the plumage was not so dark as that of a newly fledged nestling. It would therefore appear from the small sample on Signy Island that some southern giant petrels return to the colony as early as the beginning of their third year, but the vast majority not until later, probably between their fifth and sixth years. There is a slight indication that males may return at a younger age than females.

3. *Age at first breeding*

Although birds ringed as nestlings have been recovered breeding on Signy Island, it was not until 1967 that an effort was made to recover as many of these birds as possible. Consequently, birds recovered breeding for the first time in 1967 and 1968 may well have bred for some years previously but had gone undetected (only 32 per cent of the total number of birds recovered breeding were found before 1967).

Of 65 birds, ringed as nestlings on Signy Island, and subsequently recorded as breeding there, 31 have been sexed (Table XXIV).

TABLE XXIV

AGE OF FIRST RECORDED BREEDING OF *M. giganteus* ON SIGNY ISLAND

	Years 5	6	7	8	9	10	11	12	13
Total number	2	12	12	11	12	3	4	6	3
Males		2	10	3	2		1	1	
Females				1	4		1	4	2

The ages at recovery range from 5 to 13 years, males from 6 to 12 years, females from 8 to 13 years. Records of males and females breeding at ages as early as 5 and 7 years, respectively, have been made, and the possibility of even earlier breeding cannot be ruled out. During 1961–62 a bird ringed as a nestling in 1959 (a bird in its third year) was seen feeding a chick. In the same season, birds with red plastic rings (therefore in their fourth year) were seen nesting, but unfortunately, none was caught and positively identified (Pinder, 1961; Jones and Pinder, 1962).

a. *Position of breeding in relation to the natal colony.* Data have been collected on where 44 birds, ringed as nestlings, subsequently bred. By comparing the age of first recorded breeding with the distances between the colonies where the chicks hatch and later breed it is possible to draw a regression line, $y = 0 \cdot 599x - 2 \cdot 3367$, significant at the 98 per cent level, through the points (Fig. 16).

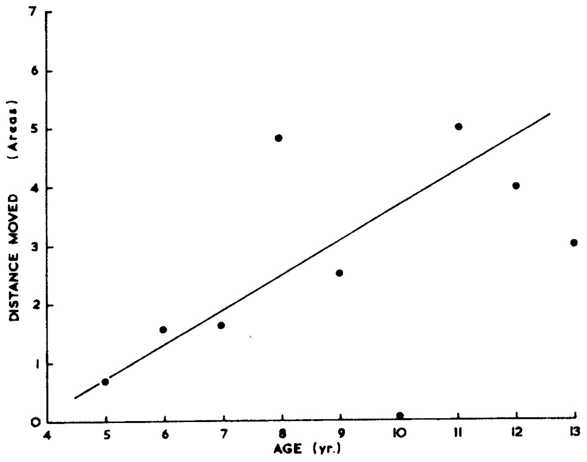

FIGURE 16

Comparison between the age at first breeding and the distance moved between the breeding and natal colonies; distance units are "areas" (see text).

In other words, when a young bird first returns to an island to breed, it usually returns to near its natal colony, but, if it does not become established as a breeder, it will move to another part of the island and possibly become established there at a later date. None of the 12 youngest breeders had moved more than one area from their natal colony.

b. *Comparison with breeding elsewhere.* At Terre Adélie, giant petrels may not return to the colony before their fourth or fifth year; there is one record of a 5 year old bird at a colony, but it was not breeding (Lacan and others, 1969). At Macquarie Island, birds aged 3½, 4 and 4½ years have been recovered on the island (Hitchcock and Carrick, 1958; Hitchcock, 1963). On South Georgia, eight such birds, five males (two aged 4 years, three aged 5 years) and three females (all aged 5 years) have been recovered (personal communication from W. L. N. Tickell). An additional two unsexed birds (both 3 years old) were recovered in March 1964 (Tickell, 1964).

Data on the age at first breeding are fewer. From Terre Adélie, four out of 68 chicks ringed in 1956 were recovered breeding, the youngest at 8 years old. The other three were 12, 13 and 13 years old (Lacan and others, 1969). Because of a 7 year gap in the occupation of the French station at Pointe Géologie between 1956 and 1963, it is possible that the youngest bird could have bred earlier. At Macquarie Island, no bird under 6 years old has been recovered breeding. Carrick and Ingham (1970) concluded that *M. giganteus* does not breed successfully until about 11 years of age, with a few birds breeding at 8 or 9 years.

In conclusion, it would appear that *M. giganteus* do not breed until they are 7 or 8 years old, and may not be successful until they are even older. Some of the birds can breed earlier, in their fifth year and perhaps even as early as their third or fourth year, although the evidence for the latter is based solely on sight observations. The males breed before the females and there would appear to be about a 2 year period between the birds' first return to the colony and first breeding.

c. *Comparison with other Procellariiformes* (see Table XXV). In some species, young birds visit the breeding colonies some years before the main return of the pre-breeding birds. In both the royal and wandering albatrosses, birds of 4 and 3 years, respectively, have been recovered at the breeding colonies, although it is more usual for birds to remain at sea until they are between 5 and 8 years of age (Richdale, 1950, 1952; Hitchcock, 1963; Purchase, 1969; Carrick and Ingham, 1970). In the Laysan albatross, birds of 2 and 3 years are recovered at the colony although the main group of birds does not return until their sixth year (Fisher and Fisher, 1969). Similarly, in the short-tailed shearwater, a few return in their second and third year, but the majority in their fourth year (Serventy, 1967).

Serventy (1967) showed that, in the short-tailed shearwater, females breed at a younger age than males (5·3 and 6·6 years, respectively), while Richdale (1957) and Fisher and Fisher (1969) suggested analogous situations in the royal and Laysan albatrosses. However, in the giant petrel, at least on Signy Island, the reverse appears to be the case, males breeding at a younger age than females. There are at present insufficient data from other species to say whether the situation in the giant petrel is unique. The only case

TABLE XXV

AGE OF RETURN TO THE COLONY AND THE AGE AT FIRST BREEDING OF SEVERAL PROCELLARIIFORMES

Species	*Pre-breeding*		*Breeding*		*References*
	1	2	3	4	
Diomedea exulans	2·8 yr. 4·5 yr.	5–7 yr.	8 yr.	10 yr.	9, 10, 11
D. epomophora	5 yr.	8 yr.	8 yr.		1, 13, 30
D. cauta	2·7 yr.	9 yr.*			17, 36, 37
D. melanophris	2 yr.	5 yr.	7–8 yr.		18, 19
D. chrysostoma	2 yr.	5 yr.			19
D. irrorata	3 yr.		6 yr.		1
D. nigreps			5 yr.		1
D. immutabilis	2 yr.	2–6 yr.	7 yr.	7–8 yr.	15, 16
Phobetria palpebrata			2 yr.		25
Macronectes giganteus	2·3 yr.	6–7 yr.	(?)3 yr.	7–8 yr.	
M. halli			7 yr.		11
Daption capensis	8 months 2 yr.		4 yr.	5 yr. Not before	2, 3, 4, 38
Fulmarus glacialis	3 yr.		6 yr.	8·4 yr.	32, 33
F. glacialoides	2 yr.				2
Pagodroma nivea	1 yr.				2
Puffinus l'herminieri		4 yr.			1
P. griseus			5 yr.	6 yr.	14, 26
P. tenuirostris	2 yr.	4 yr.		5–7 yr. (♂) 6–8 yr. (♀)	6, 30, 31
P. puffinus	1 yr.	2 yr.	3–4 yr.	5 yr. (♀) 6 yr. (♂)	5, 8
P. pacificus				8 yr. (one record)	35
achyptila turtur			5 yr.		26
Pelicanoides urinatrix	1 yr.		2 yr.		20, 21
P.u. urinatrix	8 months				34
Oceanodroma castro			4 yr. +		22
Hydrobates pelagicus	1 yr.		3 yr.		23
Oceanodroma leucorhoa	1 yr. 3 yr.		3 yr. 4 yr.	 5 yr.	7, 28 29
Pelagodroma marina			6 yr. (one record)		10

* Not known if breeding.

Columns:
1. The age of the youngest birds to return to the colony.
2. The mean age or age when the majority of birds return to the colony.
3. The youngest age at which a bird has been recorded breeding.
4. The mean age at which birds first breed.

References: 1. Harris (1969); 2. Lacan and others (1969); 3. Beck (1969); 4. Pinder (1966); 5. Harris (1966*b*); 6. Serventy (1967); 7. Gross (1947); 8. Lack (1966); 9. Hitchcock (1963); 10. Purchase (1969); 11. Carrick and Ingham (1970); 12. Tickell (1968); 13. Richdale (1950); 14. Richdale (1952); 15. Rice and Kenyon (1962); 16. Fisher (1967); 17. Hitchcock (1964); 18. Tickell (1969); 19. Tickell (1967); 20. Richdale (1965); 21. Richdale (1949*a*); 22. Allen (1962); 23. Davis (1957); 24. Robertson (1969); 25. Sorensen (1950*b*); 26. Richdale (1957); 27. Fisher and Fisher (1969); 28. Wilbur (1969); 29. Huntington and Burtt (1970); 30. Serventy (1956*b*); 31. Serventy (1957); 32. Fisher (1952*a*); 33. Dunnet (personal communication); 34. Kinsky (1963); 35. Bird Banders Association of Australia (1966); 36. Bird Banders Association of Australia (1969); 37. Bird Banders Association of Australia (1970); 38. British Antarctic Survey data.

where males probably breed before females is in the herring gull (*Larus argentatus*). Harris (1970*a*) remarked that "this situation is unknown in any other species of bird", referring to Lack (1968). A similar situation might occur in the black-browed albatross (*Diomedea melanophris*) and giant petrel in South Georgia; small samples show that males may return to the colony before females but no data are available for their respective ages at breeding (Tickell and Pinder, 1966; personal communication from W. L. N. Tickell).

Summarizing the situation in the Procellariiformes as a group, it would appear that there is a slight relationship between the size of the bird and the age at which it first breeds, with on average a gap of about 2 years between the time of the first return to the colony and first breeding. The value of 2 years' "prospecting" is that it allows the bird to find a mate and become established at a nest site.

Fisher and Fisher (1969) and Fisher (1971) have shown that in the Laysan albatross, birds ringed as nestlings have been recovered breeding near their natal area. Richdale (1965) obtained similar data in the diving petrels (*Pelecanoides urinatrix*), which were recovered breeding between 1·5 and 65 m. from their natal burrows. Unfortunately he did not give details of the age of first breeding for comparison with the distance moved from the natal nest. Serventy (1967) showed that short-tailed shearwaters older than 8 years, which had not become established on their natal islands, probably moved to new islands. Four birds were found on adjacent islands "obviously breeding" at ages ranging from 10 to 14 years, having last been seen on the study island at 7 years. The situation in the southern giant petrel may be similar in that movements away from the natal colony area are induced by the failure of the birds to secure a mate or site there. This too could also account for the increase of the fulmar in the Northern Hemisphere (Fisher and Waterston, 1941; Fisher, 1952*a*, *b*, 1966). The young birds could not become established on the colonies in which they were hatched, and were forced to move out and establish new breeding areas.

VIII. RE-LAYING AND TWO-EGG CLUTCHES

ABOUT 100 eggs were taken either for embryological examination or lost within 7 days of laying, and none was replaced (but a pair will accept a replacement egg if it is introduced immediately after the loss of the original egg). In one nest a second egg was laid, but it was incubated by a second pair of birds which had bred at an adjacent site about 2 m. away in the previous season.

During the present study, only eight (0·3 per cent) southern giant petrel nests with two eggs were found; of these, four were used in the subsequent year (three involving the same pair, the other at least one of the pair), when all of them then contained a single egg. In only one of the clutches did both eggs hatch and these chicks survived for about 50 days before both disappeared.

During December, in order to see whether *Macronectes giganteus* could incubate more than one egg, or raise more than one chick, a second egg was introduced into each of 16 nests, and accepted by the incubating birds. Data were also collected from five of the "naturally occurring" double clutches. The nests were visited twice weekly.

Details of the survival of the introduced eggs are shown in Table XXVI. No pair raised two chicks, although seven pairs successfully hatched two eggs, and the hatching success of 19 chicks from 32 eggs (59·4 per cent) compares favourably with that of the single-egg clutches. However, when the hatching dates of the single-egg clutches and the hatching dates of the first (or only) egg in the double clutches were compared, the mean hatching date of the latter was 7 days later than the single-egg clutch. Of the 19 chicks which hatched, six fledged, giving an overall breeding success of 19 per cent, much lower than the success (41 per cent) from the single-egg clutches. However, the number of chicks raised per pair was similar (double clutches 0·38, single clutch 0·41). Of the five clutches in which the two eggs hatched, three of the first chicks to hatch were squashed by the remaining egg, possibly the result of the parents continuing to incubate the egg at the expense of the chick.

Although none of the 16 nests in the present experiment provided twins which survived more than 14 days, one of the five "natural" double broods survived for just over 7 weeks. Of the other four clutches examined, three eggs were infertile, the remainder were either dead or retarded by between 20 and 30 days in their development.

The growth rate of the "twins" was compared with that of the two lightest chicks which survived in the main study area (Table XXVII). The weights show the greatest divergence, and when the twins departed the difference in weight between the two groups was 2·5 kg. The growth rates of the measured extremities

TABLE XXVI

HATCHING DATES (±1 day) FOR THE DOUBLE EGG CLUTCHES

Nest	*Hatching dates* *Egg 1*	 *Egg 2*	*Difference*	*Fate*
1	19 January	19 January	0	Both chicks disappeared between days 10 and 12
2	8 January	14 January	6	Chick (1) squashed Chick (2) fledged
3	22 January	Egg lost	–	Chick fledged
4	14 January	18 January	3	Chick (1) fledged Chick (2) squashed
5	24 January	Egg lost	–	Chick fledged
6	27 January	Egg lost	–	Chick lost
7	29 January	31 January	2	Both chicks disappeared by fourteenth day
8	12 January	Egg lost	–	Chick fledged
9	27 January	4 February	8	Chick (1) squashed Chick (2) died at 6 days
10	24 January	Egg lost	–	Chick lost
11	30 January	24 January	4	Chick (1) squashed Chick (2) died
12	16 January	20 January	4	Chick (1) fledged Chick (2) died at 4 days

Nests 13–16 both eggs lost.

TABLE XXVII

COMPARISON OF THE MEAN WEIGHTS AND SELECTED MEASUREMENTS BETWEEN TWO PAIRS OF GIANT PETREL CHICKS—A "NATURALLY OCCURRING" DOUBLE CLUTCH AND THE TWO LIGHTEST CHICKS WHICH SUCCESSFULLY FLEDGED IN THE STUDY AREA

Age (days)	*Weight* (kg.) *Foca Point*	 *Twins*	*Bill* (mm.) *Foca Point*	 *Twins*	*Wing* (mm.) *Foca Point*	 *Twins*	*Tarsus* (mm.) *Foca Point*	 *Twins*
16	1·2	1·2	49·1	48·9	61	57	36	35
30	1·9	1·7	59·8	56·4	95	87	46	41
36	3·2	1·9	64·0	60·0	115	99	54	46
40	3·7	2·3	69·0	62·9	130	118	61	51
48	4·2	2·5	73·3	67·6	162	134	68	56
52	5·4	2·9	81·3	72·6	219	178	76	60

showed a similar but far less marked difference. This suggests that the twins put more energy into the development of the body than in building up large fat reserves which could support them over a starvation period. It could be of value to the chick to risk a period of low nutrition, and by not unduly restricting its body development have some chance of surviving should conditions prove to be favourable.

It would appear that the species has difficulty in incubating two eggs. Although the hatching success per pair was similar to that of single-egg clutches, the hatching dates were later, the development of the embryos apparently taking longer. More data collected over several years from known birds are really needed before one can be categorical about the adults' ability to feed more than one chick.

Further experiments on other single-clutch sea birds have been discussed by Nelson (1964), Norman and Gottsch (1969) and Harris (1970*b*). The higher hatching success in the experimental double clutches, when compared with the "natural double" clutches, may be due to the introduced eggs being partially incubated when transferred. If chilling occurred, they could generate a small amount of energy allowing development to continue, although at a lower rate; the double clutches might well experience chilling soon after laying, markedly lowering the development rate and leading in extreme cases to embryo deaths.

IX. PLUMAGE COLORATION AND WHITE-PHASE BIRDS

Macronectes giganteus has two distinct colour phases: a dark phase, which at all colonies examined constitutes by far the greater proportion of the population; and a white phase, at one time thought to be a separate species, *Ossifraga alba* Potts 1874. Although the white birds usually have a few dark feathers scattered throughout their white plumage, they are easily distinguished from the dark birds. White-phase chicks have white natal down and are distinguishable from the dark-phase chicks within about 48 hr. of hatching. In addition, pure white individuals, complete with pink feet, and no brown feathers but with dark-coloured eyes, are found. These constitute about 0·3 per cent of the Signy Island population.

It has generally been accepted that the proportion of white birds increases with latitude, and data, based on pelagic observations from the *Discovery* expedition, are quoted to support this view (Wilson, 1907). These data give a far higher proportion of white individuals (20 per cent) than has been found elsewhere either at sea or at breeding colonies (Table XXVIII).

Inspection of this table shows that the incidence of white-phase birds is lower not higher at breeding colonies at or near the Antarctic continent. In fact, the data presented below suggest that the Scotia arc, perhaps even the South Orkney Islands, has the highest incidence of white-phase breeding birds. The data for the South Orkney Islands vary: Clarke (1906) listed 2 per cent white birds on Laurie Island, while Ardley (1936) gave 9·5–10 per cent for the South Orkney Islands as a whole. When the Falkland Islands Dependencies Survey had a station on Laurie Island, Robin (1947) recorded 5 per cent from a colony there. The Signy Island data are more complete; there are 4 years' data when over 200 adult birds were ringed, and the mean proportion of white-phase birds for these years is 7·82±1·09 per cent (Table XXIX).

Clarke's low value can be interpreted in three different ways. The number of white-phase birds in the South Orkney Islands has increased markedly since 1903; the *Scotia* biologists only counted completely white individuals; only a small colony was counted.

The evidence suggests that either the second or the third explanation is the true one. Since 1958, there have been no significant differences in the proportion of white-phase chicks ringed on Signy Island (Table XXIX) and, although the data for adult birds are less complete, the four counts since 1959 appear to show no real difference from those of 1933 (Ardley, 1936). Robin (1947), when listing colour phases at Cape Geddes, gave 2 per cent pure white and 3 per cent white with dark feathers.

The genetics of the white-phase birds have not previously been investigated. During the present study, 16 pairs with at least one white parent of known sex were studied. No dark chick was ever found where both the parents were white, and white chicks always had at least one white parent. (In over 250 nests examined no white chick was produced where both parents were dark phase.) The sex of the white parent appeared not to be important (Table XXX). Seven of the above pairs which bred chicks in 1967 did so again in 1968; of these, four pairs produced chicks of the same colour phase (three brown phase and one white phase), and three pairs produced chicks of the other colour phase, two pairs producing brown-phase chicks compared with white phase, and one producing a white-phase chick compared with a brown phase from

TABLE XXVIII
PROPORTION OF WHITE-PHASE BIRDS IN VARIOUS BREEDING LOCALITIES

Breeding location	*White phase*	*Reference*
Marion Island	0	Rand (1954)
Campbell Island	"Rare"	Bailey and Sorensen (1962)
Iles Crozet	0 (sample 200)	Falla (1937)
	1·5 per cent (33 breeding pairs)	Voisin (1968)
Falkland Islands	2·5 per cent	Bourne and Warham (1966)
	2·0 per cent	Bennett (1926)
Heard Island	0·5 per cent	Falla (1937)
		Downes and others (1959)
	0·1 per cent	Howard (1956)
	7·0 per cent	Downes and others (1954)
Iles Kerguelen	0·0 per cent	Falla (1937)
Macquarie Island	5·3 per cent	
	7·9 per cent (juvenile)	Howard (1956)
	8·7 per cent	Warham (1962)
	10·0 per cent	Falla (1937)
South Georgia	0·5 per cent	Mansfield (1951)
	2·0 per cent	Wilkins (1923)
	2·0 per cent	Murphy (1936)
	0·1 per cent	Tickell (personal communication)
South Sandwich Islands	5·0 per cent	Tilbrook (personal communication)
South Shetland Islands	12·5 per cent	Bennett (1926)*
	9·0 per cent	Tufft (1956)
	1·8 per cent	
	3·0 per cent (juvenile)	Araya and Aravena (1965)
Avian Island	*c.* 4·0 per cent	Willey (personal communication)
Pourquoi Pas Island	1·7 per cent	Imray (1957)
Antarctic continent		
Terre Adélie	3·8 per cent (adult)†	Prévost (1953)
	1 in 69 (juvenile)	Prévost (1958)
Rookery Island (Mawson)	None seen in four visits	McGregor *in* Ingham (1959)
Nellie Island (Windmill Islands)	0 in 250 nests	Law (1958)
South Orkney Islands (excluding Signy Island)	9·5 per cent	Ardley (1936)
	2·0 per cent	Clarke (1906)
	5·0 per cent	Robin (1947)

* Non-breeding count. † Birds not breeding.

the previous year. The data suggest that the incidence of white phase in the southern giant petrel is controlled by one or more recessive genes.*

The data from the present study show no selective mating or sexual selection for colour to maintain sexual dimorphism (Table XXXI). The expected data are based on the proportion of white adults in the population and the total number of nests in the study area each year.

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* Shaughnessy (1970*b*) has published his findings from Macquarie Island. With a much larger sample (208 pairs), he found two white chicks from a dark × dark mating and one dark chick from a white × white mating. He assumed these were not the true offspring of the pair but the result of fostering. Eliminating them from his calculations, he found the data were in agreement with the hypothesis that dimorphism was controlled by two autosomal allelic genes in which white is dominant to dark.

TABLE XXIX

PROPORTION OF WHITE-PHASE CHICKS AND ADULTS RINGED ON SIGNY ISLAND

Nestlings Season	Per cent white	Adults Season	Per cent white†
1958	9·68	1959	6·80
1959	8·40	1961	7·90
1960	9·55	1962	7·28
1961	8·84	1969	9·30
1962	10·00		
1963	9·24		
1964	5·88*		
1965	10·54		
1966	—		
1967	8·43		
1968	9·66		
1969	10·80		
1970	10·09		
MEAN	9·37±0·79		7·82±1·09
	$t = 3{\cdot}459$		

* Only a small number of chicks ringed.

† Adult figures taken only from years when over 200 adult birds were ringed.

TABLE XXX

COLOURS OF CHICKS FROM MATINGS OF BROWN MALE × WHITE FEMALES, WHITE MALES × BROWN FEMALES AND WHITE MALE AND FEMALE

Chick colour	White parent Male	Female	Pair
Brown	5	4	0
White	6	7	1

TABLE XXXI

EXPECTED AND OBSERVED MATINGS OF BROWN × WHITE INDIVIDUALS IN FOCA POINT COLONY ASSUMING RANDOM MATING

Year	Observed	Expected
1966	5	6
1967	17	17
1968	20	19

The suggestion of Murphy (1936), supported by Bourne and Warham (1966), that the white-phase giant petrels tended to have a more polar dispersal has been discussed elsewhere and would appear not to be the case (Hudson, 1968; Conroy, 1971; Shaughnessy, 1971). On Signy Island the proportion of white-phase chicks recovered in the low latitudes is not significantly different from the proportion originally ringed on the island (10·86 per cent and 9·64 per cent, respectively).

There may be a differential mortality rate between the two phases. At Signy Island, the South Shetland Islands and Macquarie Island, the proportion of white chicks in the population is greater than the proportion of white adults (Table XXXII; Howard, 1956; Araya and Aravena, 1965), but the data from Terre Adélie, based on a smaller sample, do not follow this trend (Prévost, 1953).

TABLE XXXII

PROPORTION OF WHITE-PHASE ADULTS AND CHICKS IN THE POPULATIONS OF GIANT PETRELS FROM VARIOUS BREEDING LOCATIONS

Breeding colony	*Per cent white* *Adult*	 *Juvenile*
Macquarie Island	5·30	7·90
South Orkney Islands (Signy Island)	7·82	9·57
South Shetland Islands (Nelson Island)	1·80	3·02
Terre Adélie	3·80	1·45

Examination of the Signy Island data shows that 291 dark- and 46 white-phase juveniles have been recovered whose fate was recorded (dead or alive). Of these 41·3 per cent of the white juveniles were recovered dead, compared with 33·7 per cent of the dark-phase chicks; the difference is significant ($\chi^2 = 6{\cdot}973$, $p = 0{\cdot}01$). On Macquarie Island, Shaughnessy (1970*b*) found no evidence of differential mortality of chicks while they were on the nests. At present no data are available to determine whether there are any differences in adult survival of the colour phases.

Matthews (1929) raised the question of an intermediate colour phase—a very light-headed bird. This has been discussed by Lowe and Kinnear (1930) and Murphy (1936), and is now accepted that these differences are the results of ageing in the "dark phase". The older the bird becomes, the lighter the plumage (Warham, 1962; Carrick and Ingham, 1970). It has been established that the heads of both *Macronectes giganteus* and *M. halli* lighten as the birds get older and that the near-black plumage of the fledgling becomes lighter with age. At present there are insufficient recoveries of known aged birds from any one colony to try and relate the plumage to age (cf. the wandering albatross (Tickell and Gibson, 1968; Tickell, 1969)).

X. FOOD AND FEEDING

1. *Diet of adult Macronectes*

The diet of the giant petrel is extremely varied, reflecting the birds' scavenging habits. 71 food samples, 47 regurgitated by live birds and the remainder from the stomachs of dead birds, were examined (Table XXXIII). The relative frequencies of food items in the two types of sample are similar. This method of analysis is not quantitative; the penguin feathers could have come from one or more birds, and the remains of some food items are more persistent than others. Eye lenses, trachea rings and squid beaks are more likely to be found than other remains which may be completely digested. This table is, however, a qualitative list of the dietary items. Penguins were represented by trachea, feathers, eye lenses and occasionally flesh; squid remains found were tentacles and beaks (up to 16 being counted in one sample).

Seals form an important source of food at Signy Island. Between August and November, when the

TABLE XXXIII

OCCURRENCE OF FOOD ITEMS IN A SAMPLE OF 71 ADULT GIANT PETRELS (*Macronectes giganteus*) ON SIGNY ISLAND

Food items	*Frequency*		*Food items*	*Frequency*	
	Number	*Per cent*		*Number*	*Per cent*
Penguin	60	85	Fish	3	4
Squid	51	72	Vegetable material	3	4
Seal	15	21			
Other birds	9	13	Synthetic material	3	4
Krill	20	28	Unidentified material	9	13
Other Crustacea	4	6			

Weddell seals (*Leptonychotes weddelli*) are pupping, birds are usually seen in ones and twos feeding at pup carcasses. Seals are eaten both on land and at sea. Dead seals in the summer appear to attract more birds than in the winter. In April 1967, about 100 giant petrels were feeding on an elephant seal (*Mirounga leonina*) carcass in Borge Bay (an area where normally only two or three birds were seen daily), while during the winter, even with three or four dead pups in the area, rarely were more than a dozen birds seen. Seals are usually eaten by the bird tearing small holes in the skin and putting its head directly inside the body cavity which results in very bloody headed birds. A stranded fin whale (*Balaenoptera physalus*) was devoured by the giant petrels, the fresh carcass, 5 m. long, was first discovered in early January 1969, and by the beginning of February, all the flesh had been eaten.

In addition to the food items listed above there are other observations on the giant petrel's diet on Signy Island. D. W. Brown (personal communication) saw a giant petrel kill and eat a Wilson's petrel which had previously been forced on to the sea by a skua. Legs and feet of prions (*Pachyptila* spp.), probably dove prions (*Pachyptila desolata*), have been found around nests. The legs and webs of a silver-grey petrel (*Fulmarus glacialoides*) and a cape pigeon were found at nests. In September 1968, 8 or 9 giant petrels were found feeding on a jellyfish (*Desmonema gaudichaudi*) (personal communication from M. G. White). Among the interesting large amphipods regurgitated was a specimen of *Eurythenes magellanicus* (M. Edwards) which had originally been identified from the stomach of a fish caught near Cape Horn (M. Edwards *in* Barnard, 1932).

Although frequently found in the guts of giant petrels, no live penguins were ever seen being attacked at Signy Island, but occasionally they were seen at freshly dead carcasses at the edges of colonies (personal observation; Sladen, 1958). There is, however, one record of a giant petrel attacking a newly fledged Adélie chick after it had taken to the water (Richards, 1959), while van Zinderen Bakker (1971*b*) and Warham (1967*b*) saw giant petrels attack and kill sick and injured penguins on the surface of the sea. By contrast, in other penguin species, there have been reports of giant petrels isolating young king (*Aptenodytes patagonica*), emperor (*A. forsteri*) and royal (*Eudyptes chrysolophus schlegeli*) penguins from the crêche and killing them (Stonehouse, 1960; Prévost, 1961; Warham, 1962; Arnaud, 1964; Guillard and Prévost, 1964). At Ongulkalven (Syowa station), Matsuda (1964) recorded giant petrels feeding on Adélie penguin eggs, although the accompanying photograph shows a skua and not a giant petrel. Verril (1895) recorded that they will enter rookeries and carry off young penguins on Gough Island, and van Zinderen Bakker (1971*b*) reported that on Marion Island a giant petrel tried to pull a penguin chick from under a sitting adult.

It is difficult to ascertain how squid come to be caught. Sightings of squid on the surface are few and, although there are records of squid being stranded on the beaches of the South Orkney Islands, these are insufficient to form such a numerous item in the diet of the birds. During an afternoon in March 1969, a flock of about 12 giant petrels about 1·5 km. offshore were disturbed feeding on a nearly dead squid; it is possible that the squid was moribund before coming to their attention. A moribund squid found on the surface has quite easily been lifted into a boat (personal communication from R. M. Laws). The squids are active near the surface at night and may be taken at this time. Some squid may be killed by other animals such as whales or seals and so be available during the day. Gibson and Sefton (1955) discussed this method of killing squid by porpoises and how the wandering albatrosses fed on the carcasses.

Seals and whales appear to form an important part of the giant petrels' diet elsewhere. A decline in the elephant seal population is inferred to have led to the extinction of the giant petrel population on Tristan da Cunha (Elliott, 1957),* while around whaling stations at South Georgia, Matthews (1929) suggested that during the winter, when whaling had ceased, many giant petrels died of starvation.

From other localities giant petrels have been reported feeding on small and young birds, such as diving petrels and prions at Heard Island (Downes and others, 1959), sooty shearwaters and prions at Macquarie Island (Warham, 1962), and young wandering albatrosses on Gough Island (Verril, 1895). They have been recorded feeding on terns (*Sterna* sp.). Wetmore (1923) and Buller (1873) reported them taking prions at sea. The stomach of a giant petrel killed along the coast of South America contained the remains of a dead shag (*Phalacrocorax* sp.) (Murphy, 1936). A giant petrel has been seen robbing a Dominican gull (*Larus dominicanus*) of a dead petrel (Ramsay, 1957) and on Gough Island they will pull petrels from burrows (Verril, 1895). In the Falkland Islands, the birds attack fallen and dead sheep (Vallentin, 1924), while from Australia, Bampton (1937) reported a giant petrel attacking a cocker spaniel which had swum out to meet it, the ensuing fight lasted about 5 min. during which the bird tried unsuccessfully to keep the dog's head under water. In temperate regions the birds are attracted to sewage being discharged near cities (Hindwood, 1955; Fleming, 1957; McIlwaine, 1963).

2. *Diet of the chick*

During the three summer seasons, 96 regurgitated food samples were collected from chicks (Table XXXIV). It is clear that krill (*Euphausia superba*) is found in a larger proportion of chicks than adults, and when the food samples from chicks of different age groups are compared krill appears to be most important in the days immediately following hatching. 66 per cent of the krill samples were collected within the first 30 days of chick life.

TABLE XXXIV

OCCURRENCE OF FOOD ITEMS IN 96 GIANT PETREL CHICKS (*Macronectes giganteus*) ON SIGNY ISLAND, AND THEIR DISTRIBUTION IN RELATION TO THE AGE OF THE CHICKS

Food items	*Chick's age* (days)						*Frequency*	
	0–10	11–20	21–30	31–40	41–50	50+	*Number*	*Per cent*
Penguin	7	10	12	9	11	14	63	67
Squid	1	3	8	4	2	12	30	32
Seal				2	2	5	9	10
Other birds			1	2	1	2	6	7
Krill	14	17	10	8	10	2	61	65
Other Crustacea		1	1	1			3	4
Fish				1		1	2	3
Vegetable material		1	1	2		3	7	7
Other material			1	1	2	2	6	7
Sample size	16	22	14	13	14	17		

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* Swales (1965) thought that the disappearance of the giant petrel from Tristan da Cunha is due to changes in climate and vegetation or "competition".

XI. DISCUSSION AND CONCLUSIONS

1. *Attendance of nestlings at colony after fledging*

There have been reports of giant petrel and other Procellariiformes chicks remaining around the colony after they have left the nest. At Heard Island the young giant petrels are often seen on the beaches after leaving the nest (Downes and others, 1959). In the North Atlantic fulmar, Campbell (1970) found that the chicks remain around the colonies after fledging, and contributed to a marked increase in the number of birds counted at the colonies at that time. Likewise, Moss (1965) attributed the increase in fulmars seen after the fledging period to the young of the year. Richdale (1965) reported that the young diving petrels may remain for 1 or 2 days, while Laysan albatross fledglings may remain around the colony for 4 and 5 days and even return after going to sea to feed (Fisher and Fisher, 1969). Great shearwaters on Tristan da Cunha do not leave the island immediately they fledge and there is "a fair amount of coming and going between the island and the sea" (Rowan, 1952). The advantage of this is that the fledglings will gain experience in flying and strengthen their flight muscles, which might increase their subsequent survival. While around the island, the chicks will probably continue to live mainly off their fat reserves. (There is little food on or around the Antarctic islands in early winter, and there is no observation of a chick, once it has left the nest, being fed by its parents.) The length of time that a juvenile can remain around the colony will depend upon the fat reserves, and the "stimulus" which causes it to leave the Antarctic for the Southern Ocean. This stimulus could well be hunger, when the fat reserves reach a threshold level.

With the onset of winter, the young cannot remain around the island. During May, the weather deteriorates, and the chicks which fledge earlier can spend more time, and being heavier, have more fat reserves to remain near the island than those which fledge later in the season. If by having the extra days of exercise survival is enhanced, it would clearly be advantageous to fledge as early as possible. Unfortunately there are no data on chicks subsequently recovered breeding on the island comparable to those of Perrins (1966), who reached similar conclusions on the Manx shearwater.

2. *Dispersal of adults and winter sightings of birds at the breeding colonies*

Although there have been several hundred recoveries of juvenile giant petrels, there have been very few recoveries of adult ringed birds in latitudes far from their natal colonies (Appendix III). Only three ringed breeding birds have been recovered from Signy Island. The scarcity of adult recoveries from the low latitudes could be due to at least two factors.

First, the adult birds may not disperse to such low latitudes as the juveniles, and if so, since the land area south of lat. 40° S. is small, and that inhabited even smaller, when compared to the expanse of the Southern Ocean, the chance of recovery from these higher latitudes is less. There is slight evidence to support this from the data of Sladen and others (1968, tables VIII and XI) for the black-browed albatross and the giant petrel. Tables XXXV and XXXVI here are drawn from these data, and show that it is the younger birds of both species which are found in the more northerly latitudes. Unfortunately there are no data

TABLE XXXV

LATITUDINAL DISTRIBUTION OF RECOVERIES OF GIANT PETRELS RINGED AS CHICKS FROM VARIOUS RINGING LOCALITIES IN THE ANTARCTIC AND THE AGE OF RECOVERY (AFTER SLADEN AND OTHERS, 1968)

Age (months)	*Latitudinal range of recovery* (°S.)							
	10–15°	16–20°	21–25°	26–30°	31–35°	36–40°	41–45°	46–50°
0–6	3	2	3	6	38	8	2	
7–12			1	6	15	18	4	1
12–18					4	3		
19–24					1			
24+						1		1

TABLE XXXVI

LATITUDINAL DISTRIBUTION OF BLACK-BROWED ALBATROSSES RECOVERED AND THE AGE OF RECOVERY (AFTER SLADEN AND OTHERS, 1968)

Age (months)	*Latitudinal range of recovery* (°S.) 0–5°	6–10°	11–15°	16–20°	21–25°	26–30°	31–35°	36–40°
0–6	1	1	3	0	9	7	20	6
7–12					4	5	14	1
13–18					2	1	22	4
19–24							6	
24+							10	4

available for adult birds, but when the data for the wandering albatross are analysed (Sladen and others, 1968, table VII), there is a preponderance of adult recoveries, and the latitudes at which these are recovered are on average farther to the south than the positions of the four juveniles listed. However, the data are again very limited. Other sea birds in which the adults do not range so far as the juveniles are the North Atlantic fulmar (personal communication from G. M. Dunnet; Fisher, 1952*b*), the kittiwake (Coulson, 1963) and black-browed albatross (Amiet, 1957). In petrels with a trans-equatorial migration, the situation is different, both adults and juveniles following the same pattern. Examples are the short-tailed shearwater (Marshall and Serventy, 1956) and probably Wilson's petrel (Roberts, 1940*a*; Beck and Brown, 1972).

Secondly, the older birds are more experienced than the young birds and are less likely to succumb to storms and be washed or blown ashore on to the beaches, where many are recovered. Again, looking at the data of Sladen and others (1968), there is some evidence that the older birds are less likely to be recovered ashore (Table XXXVII). Only 40 per cent of all black-browed albatross recoveries older than 12 months were recovered on land compared with over 70 per cent of those under 12 months. Thus, if the situation in the southern giant petrel is similar to that of the black-browed albatross, few adults have been recovered away from their breeding colony because the adults do not disperse as far to the north. They are more experienced and less likely to be caught or blown ashore than first-year birds.

TABLE XXXVII

DISTRIBUTION OF RECOVERIES OF BLACK-BROWED ALBATROSSES AT LAND AND AT SEA, AND THE AGE OF RECOVERY (AFTER SLADEN AND OTHERS, 1968)

Age (months)	*Number recovered*	
	On land	*At sea*
0·6	48	18
7–12	31	17
13–18	25	27
19–24	5	10
24+	7	20

χ^2 values for all age comparisons are significantly different from a 50/50 ratio except for the age group 13–18 months.

3. *Return of adults to the colony*

Why the majority of southern giant petrels return to their colonies in August is not known. Although there is evidence that it may be linked with an increased availability of food, this may be coincidence. At

Pointe Géologie they re-appear as the emperor penguin chicks hatch and during their early development many may be taken by giant petrels (Prévost and Sapin-Jaloustre, 1965); on Signy Island, where they feed on pup carcasses, the bulk of the giant petrels return at the time the Weddell seals pup. However, when they return, at least on Signy Island, the birds are at their maximal weight; there are never as many birds around the carcasses during the winter as there are during the summer and in some years few pups die.

It may be that a pre-egg period at the colony of up to 12 weeks is necessary to bring some birds into breeding condition.

Winter sightings of giant petrels at other breeding localities are well documented. North of the Antarctic Convergence, birds have been seen all year round at Marion Island (Crawford, 1952) and Macquarie Island (Warham, 1962), where ringed birds have been caught during the winter months, but their previous season's breeding status was not known (Hitchcock and Carrick, 1958; 1960). Data from south of the Antarctic Convergence are similar. During the wintering of *Scotia* at Laurie Island, giant petrels were seen all year round, numbers dropping to a minimum in May and June (Clarke, 1906). In recent years at Pointe Géologie the birds appear to have been absent during May and June (Mougin, 1968), but both Prévost (1953) and Cendron (1953) reported that they were seen during these months. The absence of birds during the early winter is probably due to a decrease in the number of breeding birds at Pointe Géologie since the work of Prévost. At Avian Island, the frequency of winter sightings is similar to that at Signy Island (personal communication from I. Willey). Both the French and Swedish expeditions to the Antarctic Peninsula reported the birds throughout the year, although neither of these expeditions wintered near a known breeding colony (Andersson, 1908; Gain, 1914).

4. *Pre-breeding behaviour, keeping company and the pair-bond*

During the pre-breeding period, a great deal of attention is paid to the nest site. The male is usually the first to arrive and spends more time at the nest site than the female. The earlier arrival of the male has also been described in Buller's mollymauk (*Diomedea bulleri*), wandering, royal and Laysan albatrosses (Richdale, 1949*c*, 1950; Rice and Kenyon, 1962; Tickell, 1968; Fisher and Fisher, 1969). Site tenacity is not related to the dangers of the rightful owners being usurped by other birds in their absence; in fact the evidence is quite the contrary; once a pair have become established they have the first option on the site, and the male bird can evict, without any apparent force, other males which might sit on the nest in his absence. Similarly, in the North Atlantic fulmar established birds were never challenged over the right of ownership (Fisher, 1952*a*) and in the royal albatross the resident bird has no fear of losing his nest site because, like the southern giant petrel in the present study, he can evict any transgressor (Richdale, 1950).

A possible function of the maintenance of the pair-bond from year to year is that it may allow the birds to come into breeding condition more readily and lay earlier than if they had to form a new pair every year. The available data on laying and hatching dates of eggs from pairs breeding for the first time and from established pairs, show that, on average, the latter lay and hatch their eggs at an earlier date (Table XXXVIII). This means that the chicks will fledge earlier and, as suggested on p. 39, may have a better chance of survival and be less likely to be exposed to as much snowfall and drift as birds which fledge later.

In the pre-breeding period a bird can return to its nest to await the return of its mate and, in the absence

TABLE XXXVIII

COMPARISON OF THE MEAN LAYING AND HATCHING DATES OF NEWLY FORMED PAIRS AND THE FOCA POINT COLONY

1967 chicks	New pairs (4)	Mean hatching 20 January (19·5±3 days)
	Foca Point colony	Mean hatching 13 January (13·1±4·6 days)
1968 chicks	New pairs (5)	Mean hatching 17 January (17·4±3·6 days)
	Foca Point colony	Mean hatching 12 January (11·7±3·8 days)
1968 eggs	New pairs (7)	Mean laying 19 November (19·1±3·6 days)
	Foca Point colony	Mean laying 13 November (13·3±4·9 days)

of the mate, will keep company in the nest area with other giant petrels of the opposite sex. But should the mate return, the old pair-bond is re-established; there are no records of divorce in over 150 known pairs in the present study.

There is a selective value in the giant petrel's passiveness to birds of the opposite sex which allows unmated birds to keep company with each other, and, in the absence of the mate, a new pair-bond may form.

Although the pair breed together from year to year, it is unlikely that they remain paired at sea. (Richdale (1947) produced slight evidence that this might be the case in some species such as the royal albatross.) Although birds arrive at the breeding ground paired, it does not mean they have remained so during the non-breeding season. Rather in migratory species, the stimulation which causes the birds to return to their breeding colonies would be sufficient to bring a pair back about the same time. It is more likely that the males and females return independently and the arrival of a pair together at a nest site is coincidental. In the present study there is only one case, in over 20, where both birds appeared together at the nest. The nest site of the previous year serves as a focus to which the pair return after their sojourn at sea. If a new site is chosen, it is likely that this has been selected in the previous autumn. Data show that eight of the nine pairs which changed nests were failed breeders, and there are records of three of the pairs at their new sites in the autumn. (In the case where a successful pair changed site, they moved to an adjacent nest 3 m. away, compared with an average distance of 59 m. moved by failed breeders.) This has been further discussed by Lack (1940) and Richdale (1949*b*).

When a new pair-bond forms is not known. For penguins, Richdale (1946) concluded that the moult period was the most important time for new pairs to form.

In the giant petrel there are two periods when non-breeding birds (the prospecting population) take an interest in the nest: autumn and early spring (Plate VIIIa). During the autumn there are pre-breeding birds as well as failed breeders in this prospecting population (identified by their rings), while in the spring the population consists almost entirely of breeding birds, some having already paired while others await the return of their mates. Both the spring and autumn prospecting populations contain birds which have lost their mates.

For a new bond to form, a pair must meet, find a nest site and have sufficient time to get through the routine necessary for successful egg-laying.* Birds which have lost their mates are familiar with pre-breeding behaviour and experienced in breeding. If a pair of such birds meet early in the season, it is possible that they can successfully lay in the current breeding season. The data show that new pairs are later in laying than established pairs (Table XXXVIII). There must be a time during the pre-egg period after which, even if a pair is formed, the chances of successfully laying an egg are reduced. When this time comes the remaining unmated birds leave the area and hence the decline in numbers towards October (Fig. 3).

Pre-breeders have no experience of breeding and it is possible that they would not have sufficient time to return to the colony in spring, find a mate, a nest and successfully breed in that season; it may be more than one season before this happens. Tickell and Pinder (1966) have shown that, in the wandering albatross, pre-breeders may need five seasons before successfully finding a mate. However, if on its arrival at the colony in the spring a pre-breeder already has a mate and a nest site, it might have enough time to successfully lay an egg. By visiting the colony during the autumn a pre-breeder may find a prospective mate and nest site for the following season.

Likewise new pairs formed between established breeders during the autumn also have a better chance of success in the following breeding season.

The return of pre-breeders towards the end of the breeding season has been described in several species of bird including the Laysan albatross (Fisher and Fisher, 1969), the short-tailed shearwater (Serventy, 1967) and the kittiwake (Coulson and White, 1960). Autumn nest activity has been seen in the gentoo penguin (Warham, 1962), chinstrap penguin (*Pygoscelis antarctica*) (Bagshawe, 1938), the cape pigeon, snow petrel and North Atlantic fulmar (personal observation).

Spring prospecting populations have been observed in the snow petrel (paper in preparation by Conroy and Beck), cape pigeon (Pinder, 1966) and dove prion (Tickell, 1962); in the Wilson's petrel, there was a drop in the numbers of birds in the prospecting population towards the end of the pre-egg period (Beck and Brown, 1972). In the North Atlantic fulmar, Coulson and Horobin (1972) reported that non-breeders may visit the colony very early in the year, departing long before egg-laying. Keeping company ("flirtation",

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* Successful egg-laying involves laying early enough in the breeding season so that the chick can successfully fledge in April–May.

Richdale (1946)) in the absence of one's mate is common in several groups of birds, dove prion, snow petrel, cape pigeon and North Atlantic fulmar (personal observation), the diving petrel (Richdale, 1965), the gentoo, chinstrap, Adélie and yellow-eyed penguins (Bagshawe, 1938; Sladen, 1955; Richdale, 1946), also the great crested grebe (*Podiceps cristatus*) (Huxley, 1914) and black-tailed godwit (*Limosa limosa*) (Huxley and Montague, 1926).

Diurnal activity has been described in the North Atlantic fulmar in both Jan Mayen (Cullen, 1954; Moss, 1965) and in Britain (Coulson and Horobin, 1972). In the latter study they found that as egg-laying approached so there was an increase in the number of nests occupied at night.

5. *Pre-laying exodus*

A pre-laying exodus has been recorded in several Procellariiformes and it is interesting that it occurs mainly in those species which have a long pre-laying period ashore.

In the North Atlantic fulmar, which can have a pre-egg period lasting up to 6 months (Dott, 1968), there is an exodus lasting about 3 weeks (Dunnet and others, 1963).

The Manx shearwater on Skokholm has a pre-egg period of about 12 weeks, and pre-laying exodus of about 10 days (Harris, 1966*a*). The pre-egg period in the short-tailed shearwater lasts 10 weeks, and there is a very marked exodus lasting about 3 weeks (Marshall and Serventy, 1956). In the dove prion on Signy Island, Tickell (1962) described a pre-egg period of about 2 months, with an exodus only in the female. Likewise, in the cape pigeon, whose return can be governed by the sea-ice conditions but is usually between August and September, the female is away for 2–3 weeks prior to the eggs being laid in mid-November (Pinder, 1966). A short exodus has also been recorded in the silver-grey petrel at Terre Adélie (Mougin, 1967) and the diving petrel (Warham, 1964), although Richdale (1963) made no mention of an exodus in his study of the latter. Zino (1971) reported exodus in Cory's shearwater (*Calonectris diomedea*). Among the albatrosses, Richdale (1950) said that in Buller's mollymauk the female on average is seen 8·17 days (range 0–23 days) before the egg is laid; there is no information about the female leaving the colony again after her appearance and laying of the egg. Similarly, no exodus is recorded in the black-footed (*Diomedea nigreps*) and Laysan albatrosses; in both these species the birds do not return to the colony until just before the egg appears (Rice and Kenyon, 1962). In the royal albatross, where on average the pre-egg period lasts 33 days, Richdale (1950) found that the females were seen only intermittently prior to egg-laying. Their erratic sightings at the colony could well result from a type of exodus. Tickell (1968) found similar situations in the wandering albatross, where the pre-egg period was 27 days, but the sightings of females were very erratic and constituted less than 20 per cent of the observations of the population at that time. While on Marion Island, van Zinderen Bakker (1971*c*) reported an actual exodus of the female wandering albatross, which returned 1 or 2 days before the egg was laid.

If the function of the pre-laying exodus of the female is to allow her to build up a food reserve for egg production, it is possible that the species which show no exodus already have accumulated this reserve. This could account for the difference in arrival time of the males and females in some species, such as the Pacific albatrosses (Rice and Kenyon, 1962). By having built up this reserve, the female can return to the colony, re-form the pair-bond, copulate and lay her egg before having to return to the sea. In those species which return several weeks before the egg is laid, the female may not have built up enough food reserves to last her throughout the pre-egg period and have to return to sea before she has enough food to lay her egg. Although the female giant petrel's weight is fairly constant during the pre-egg period, she returns to sea to feed, and may need a more steady and undisturbed period of feeding to attain optimum condition.

The laying data for the cape pigeon and snow petrel at Signy Island show a similar synchrony (Pinder, 1966; paper in preparation by Conroy and Beck). The arguments for synchronous laying in the giant petrel on Signy Island are similar to those already expressed for these species (Beck, 1970). It would appear that laying has evolved to occur at the most opportune time, relative to the environmental conditions. The weather conditions for the years shown in Table X include a representative sample of spring conditions that the birds are likely to meet, and the laying period is not too greatly affected by local annual changes in weather. Richdale (1949*b*) also stressed the importance of laying synchrony in birds, such as petrels and penguins, which have a long breeding cycle. This is especially true in the high latitudes where there is a relatively short period of time available for breeding.

6. *Re-laying and two-egg clutches* (Plate VIIIb)

During recent years hypotheses relating to the evolution of a single-egg clutch have been developed. Wynne-Edwards (1955, 1962) argued that the single-egg clutch had evolved because these species were long lived, and the production of only a single egg, which, if lost, is not replaced, reduces the dangers of over-population. He argued that the "cost of egg replacement would presumably be trifling" taking as his standard the gannet (*Sula bassana*). Lack (1954, 1966, 1967, 1968) disagreed with this, arguing that a single-egg clutch has evolved because the female cannot find enough food to produce more than one egg, or else the pair will have difficulty in finding enough food to feed more than one chick. He believed Wynne-Edwards was wrong to describe the eggs of the Procellariiformes as "relatively small" and that the available evidence strongly suggests the opposite (Lack, 1966). The egg/female weight ratio of the smaller members of the Procellariidae and the Hydrobatidae, such as the Leach's storm petrel, short-tailed shearwater and Manx shearwater support this view but in the larger members of the Procellariiformes, particularly the Diomedeidae the egg/female weight ratio is rarely above 10 per cent (data from Lack, 1968, appendix 17). It is only in some of the smaller members of the Procellariiformes that the ratio approaches 15 per cent or more.

In the following discussion on re-laying and two-egg clutches each topic is discussed separately, because two-egg clutches could occur by the simultaneous fertilization of two oocytes at the same time (Serventy *in* Warham, 1962). It appears that at least in some of the petrels, such as Gould's petrel and the short-tailed shearwater, there is a very rapid regression in the testes between fertilization and egg-laying, making a second successful copulation practically impossible (Hindwood and Serventy, 1949; Marshall and Serventy, 1956).

Two-egg clutches have been reported in giant petrels from other locations, namely Marion Island (Rand, 1954), Laurie Island, where Clarke (1906) attributed the two eggs to different females, and on Macquarie Island where 0·14–0·18 per cent of the nests had two eggs (Warham, 1962). Warham argued that they were laid by the same female, and that two-egg clutches were possible because the territoriality of the giant petrel prevents any other birds approaching the nest; because it is impossible that a bird could leave the nest for any length of time without the egg being destroyed, and because of the discovery of a white-phase adult brooding two similar white-phase chicks.

In general, giant petrels are tenacious to their nest sites, but there are cases when incubating birds will allow other birds to sit alongside them and, although skuas are very quick to spot any abandoned eggs, there were, in the present study, records of giant petrel eggs being deserted for 1–12 hr., sufficient time for a second female to come along and lay in the nest. Perhaps Warham's strongest argument for two eggs being laid by the same female is that case when both of the chicks in the nest were white. Tickell and Pinder (1966), without examining the genetics of the white phase, argued that the chicks could have been the result of a single white male fertilizing two brown-phase females and allowing both to lay in the nest. However, the probability that the genetic complement of the three birds was such that the two chicks are white is less than half the probability of getting two white chicks from the same two parents (probabilities 0·1 and 0·25) (personal communication from D. P. Fox).

In other Procellariiformes two-egg clutches have been reported (see below for references) and the arguments for and against one or two females being responsible for the eggs are, in most cases, very circumstantial.

Fisher (1952*a*) reported an interesting case of two-egg clutches in the North Atlantic fulmar. In subsequent seasons one of the eggs was of an elongated shape and from this Warham (1962) concluded that "these evidently represented laying of two eggs by the same female".

Looking at other members of the Procellariiformes, including species which are surface nesters, there are several species where, on occasions, more than one pair have been involved at a site in a single season. In the North Atlantic fulmar, two pairs, positively identified by their colour rings were found incubating a single egg at the same nest in two successive years (personal observation), and Dott (1967) reported three fulmars sharing parental duties at a nest. In the cape pigeon, one two-egg clutch was found where four birds were involved in the early part of the incubation (Pinder, 1966). In the Madeiran storm petrel (*Oceanodroma castro*), visiting birds have been recorded at nests with incubating birds in the burrows (Allen, 1962).

It has been shown in other species of bird, such as the yellow-eyed penguin (Richdale, 1957) and the kittiwake (Coulson, 1963), that the eggs of birds breeding for the first time are longer than those of the older birds. This is caused, it is thought, by the lack of elasticity in the oviduct of the young bird, and the female fulmar responsible for the long egg in the above case could well have been a young bird.

Possible confirmation that females, in one species of Procellariiformes, can lay two eggs has been found on Macquarie Island. Initially, Carrick and Ingham (1970) provided circumstantial evidence that some wandering albatrosses consistently produced two-egg clutches. Further work by K. R. Kerry using a chemical technique is in progress and initial results appear to support this hypothesis that some females do lay two eggs (personal communication from G. W. Johnstone).

Re-laying has been reported in several members of the petrel family. Second and even third layings have been reported for *Macronectes* sp. from Gough Island (Verril, 1895), and re-laying has also been reported in Leach's storm petrel (Wilbur, 1969). A doubtful record has been given by Davis (1957) for the storm petrel. In the cape pigeon, Mougin (1968) produced circumstantial evidence which suggested re-laying but, bearing in mind the finding of four cape pigeons at a nest on Signy Island, there is the possibility that the second egg was laid by a second female. The strongest evidence for a replacement egg being laid comes from the Manx shearwater (Harris, 1966*a*).

Re-mating does not seem to be likely, in view of the findings of Marshall and Serventy (1956) and Hindwood and Serventy (1949), who showed that in two species of petrel (the short-tailed shearwater and Gould's petrel) there was rapid regression of the testes between fertilization and egg-laying. If this is representative of the whole family, it would mean that for the male bird to be able to re-mate with his partner following the loss of the egg, spermatogenesis would have to re-occur, bringing the testes to a state capable of fertilization. The time this would require is not known and it might result in an egg being laid after the end of the "normal" laying period. The resultant fledgling might have a very poor chance of survival (compare the situation in the Manx shearwater (Perrins, 1966)). If this is so, there appears to be little selective value in the evolution of a mechanism to produce replacement eggs.

The present data on replacement clutches and re-laying in the Procellariiformes are insufficient to permit an accurate assessment of the situation. However, if re-laying does occur, it is very unusual.

XII. SUMMARY

SOUTHERN GIANT PETRELS (*Macronectes giganteus*) at Signy Island, South Orkney Islands, show sexual dimorphism and, using the bill length and depth, a discriminant function can be calculated and used to sex birds in the field. Birds seen around the colonies during the winter include the breeding population. There is a sharp decline in numbers from April until July, with the majority of the birds returning to the colonies in August.

The pair-bond is usually established at the old nest site, with the old mate, but in the absence of the latter a bird will keep company with other birds. There is a short pre-laying exodus, lasting about 2 weeks, which appears to occur only in the female.

Egg-laying is fairly synchronous, the first eggs being laid during the first week in November and lasting about 3 weeks. Incubation is by both sexes and lasts about 61 days, the eggs hatching in January. The nestling period lasts on average 117 days.

The pre-breeders return to the colony about their fifth year, although birds in their third year have been recovered. The first confirmed record of breeding is a 5 year old male, although sight records of colour-ringed birds suggest that birds may breed as early as their third year. Males appear to breed at a younger age than females.

Body moult starts during incubation, but primary moult in breeding birds is arrested for several weeks, at least until the nestlings have laid down fat reserves. Failed breeders start moult before successful breeders, wing gaps appearing in their primaries within 3 weeks of the loss of their chick or egg. Primary moult probably lasts about 95 days.

The breeding success during 1968 was estimated from four different colonies and was found to be highest in the colony subject to least skua predation.

The incidence of white-phase birds in the population appears to be under the control of one or more recessive genes and is not sex linked, nor is there any selective mating to maintain the white phase within the population. Such ringing data as are available suggest that there is a differential mortality between the two colour phases of juveniles.

There is no evidence to suggest that *M. halli* is found on Signy Island. The Signy Island data are compared with the studies elsewhere, attention is drawn to similarities and differences are discussed.

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APPENDIX I

THE SPECIES OF *Macronectes* BREEDING ON SIGNY ISLAND

Throughout the winter and spring (August until November), the breeding colonies of the island were examined to see if there were any birds breeding earlier than the main population. None was found. No birds on the island were seen with a "yellow-lemon" bill, characteristic of *Macronectes halli*, at least on Macquarie Island and Iles Kerguelen (Mathews, 1912; Bourne and Warham, 1966; Johnstone, 1971).

Based on the above observations, it is assumed that there is only one species of *Macronectes* breeding on Signy Island, namely *Macronectes giganteus.*

APPENDIX II

SEXING ADULT BIRDS BY THEIR INCUBATION SPANS (TABLE XXXIX)

It is not always possible to see a female lay her egg. However, in birds, such as the giant petrel, which have lengthy incubation spans, it should be possible to sex a bird by reference to the early incubation spans. The male usually relieves the female a few hours after the egg has been laid. In the present study 59 per cent of the females were relieved within 24 hr., although a female may sit as long as 8 days before relief. By comparison, the male's first incubation span is fairly long, averaging 8 days (range 6–11 days). No female was recorded as relieving her mate within 7 days of the egg being laid, the mean period being 10 days (range 7–19 days).

It is argued here that the female will probably not return to the nest until a week or more after the egg has been laid, and that any change-over which occurs before this time is the first relief of the female following egg-laying. To reduce the potential error introduced by a female returning earlier than a week, it was assumed that if a change-over occurred within 4 days of the egg being laid, the relieved bird was the female. 4 days was taken as the value because it is the sum of the mode of the first female span (1 day) and half the shortest recorded first male span (3 days).

This was tested by measuring the birds and applying the discriminant value calculated for each; all fell within the range of their allotted sex values.

TABLE XXXIX

LENGTH OF THE INITIAL INCUBATION SPAN IN THE GIANT PETREL ON SIGNY ISLAND, NOVEMBER 1968

Number of days before male took over incubation	*Number of nests*	*Per cent of nests*
1	22	59·46
2	6	16·22
3	4	11·11
4	3	8·11
5	1	2·70
8	1	2·70

APPENDIX III

CALCULATION OF THE LENGTH OF THE PRE-LAYING EXODUS

Until the week ending 14 November the number of marked females observed in the study area was approximately the same as the number expected from the ratio of males to females, but thereafter there is a progressive difference between the values. In order to estimate the duration of the pre-laying exodus of the female, the number of females observed in the colony was expressed as a percentage of the expected number of females. Thus, percentage of females still in colony (A) = ($O \times 100$)/E, where O is the number of marked females counted and E the number of marked females expected to be counted in the colony. The percentage of females away from the colony was then ($100-A$) per cent. Values for ($100-A$) per cent were calculated for the data in Table VII. Prior to 14 October, it is assumed that all of the females were present in the colony at the time of counting. The data on the weekly percentage of eggs laid during November 1968 have also been plotted and show a much steeper curve (Fig. 17).

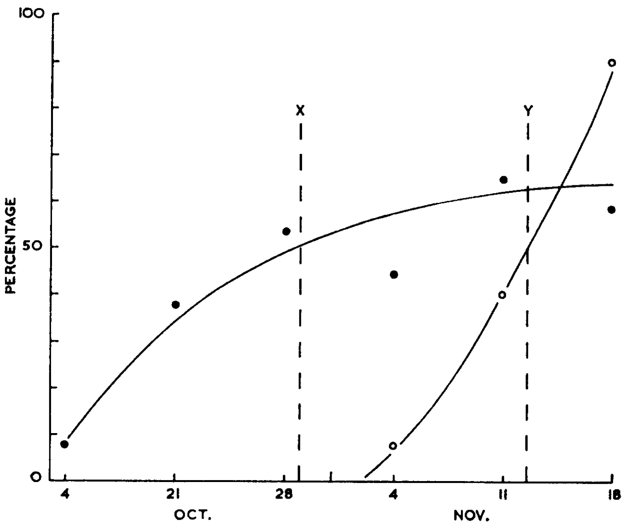


FIGURE 17

Comparison between the possible percentage pre-laying exodus of female *M. giganteus* from the study area and the number of eggs laid in the study area.

- ● Percentage females absent; X, 50 per cent females absent.
- ○ Percentage eggs laid; Y, 50 per cent eggs laid.

The first females appear to leave the island during the week ending 21 October and the start of the exodus is taken as the middle of that week, 18 October. The first egg was laid on 4 November and, if the first females to leave the island are the first females to lay their eggs, the pre-laying exodus would last approximately 16 days (±3 days) assuming that 24 hr. elapse between the return of the female to the island and the appearance of the egg.

A more accurate estimate may be obtained by comparing the date when 50 per cent of the females appear to have left the island (i.e. approximately 31 October) with that when 50 per cent of the eggs have been laid (approximately 12 November). This gives an estimate for the pre-laying exodus of approximately 12±3 days.

It is concluded that the average pre-laying exodus in the southern giant petrel on Signy Island is probably about 12 days.

APPENDIX IV

RECOVERIES OF ADULT BIRDS IN LOW LATITUDES AWAY FROM THEIR COLONIES

The majority of ringing recoveries from low latitudes have been birds in their first 2 years of life; few older birds have been recovered away from the breeding colonies.

During the past 3 years, six birds older than 5 years of age have been recovered away from Signy Island; four were ringed as adult birds, and two others as nestlings. Of the adult birds, No. 5022741, breeding on Signy Island in February 1967 was recovered in New South Wales in June 1967; it was breeding on Signy Island in January 1969 and again recovered in New South Wales in August 1969. No. 5014672, breeding on Signy Island in January 1968, was shot in Wellington Harbour, New Zealand, in September of that year. The two remaining recoveries had been ringed as adults in 1962, but had not been subsequently seen until they were recovered off South America and New Zealand. Two nestlings were recovered off New Zealand and South Australia when 7 and 8 years old, respectively. Recoveries of adult birds from other breeding colonies are very few. From Macquarie Island, an adult bird, thought to be a failed breeder, was recovered on the Antarctic mainland at Cape Crozier, as were two 6 year old Macquarie Island nestlings, the first evidence of birds dispersing south from their native colonies (Carrick and Ingham, 1970). There is also a record of *M. halli* being recovered in New South Wales and later breeding at Macquarie Island (Bird Banders Association of Australia, 1970).

Recoveries of birds in succeeding years at areas other than their breeding grounds come from both New South Wales and New Zealand. The case of No. 5022741 mentioned above is the first record of a double recovery of a breeding bird in different years away from its breeding colony. The New South Wales study group ringed an adult giant petrel off Malabar in 1962; it was recovered dead in the same area in the following year, although the possibility that the bird had died in 1962 and remained mummified for a year cannot be ruled out (Bird Banders Association of Australia, 1963).

The New Zealand recoveries are of live birds and have been listed by Kinsky (1957, 1960). A bird ringed at Torry Island in July 1958 was found breeding at Wilkes Land in December of the same year (Kinsky, 1959).

APPENDIX V

PARASITES

Of 32 birds (21 adults, 11 nestlings) examined for external parasites, all the adults were found to have feather lice (Mallophaga). These were identified as *Paraclisis obscura* (Rudow 1869) by Dr. T. Clay at the British Museum (Nat. Hist.). The lice were found mainly on the abdomen, neck and head region; few were found on the back, and none on the wings or tail. None of the chicks examined (aged 80–90 days) was found to have any lice.

No other external parasites were found and no parasites were found in 14 nests, of both stones and moss, which were examined in March 1969. Giant petrels collected in Western Australia were also infected by *Decophoroides hunteri* (Harrison) (Glauert, 1949). Fleas (*Siphonoptera*) have been found on giant petrels at both Iles Kerguelen and Macquarie Island. *Parapsyllus cardinis* Dunnet 1961 was found on the Macquarie Island birds where it also occurs on white-headed petrels (*Pterodroma lessoni*) and dove prions. *Parapsyllus magellanicus heardi* de Meillon 1952 was found on Iles Kerguelen birds and also on several other species of petrel and penguin. Although *P. m. heardi* is also found at Macquarie Island, it has not been found on the giant petrels there (Dunnet, 1964).

From *Macronectes giganteus* on Signy Island, V. W. Spaull (personal communication) found *Seuratia* sp. (Nematoda) in the inner layer of the gizzard, while I. Williams (personal communication) found the following Cestoda in the guts: *Diphyllobothrium ditreum* (Creplin 1825), *Tetrabothrius heteroclitus* (Diesing 1850) and *Parorchites zenderi* (Baird 1853). *Tetrabothrius* sp. has also been found in *Macronectes giganteus* on Heard Island (Prudhoe, 1969).

APPENDIX VI

PREDATORS

At their breeding colonies, adult giant petrels appear to have no predators. Elsewhere, there are two predators, neither of which exact a major toll on the birds.

Hamilton (1939) reported that leopard seals (*Hydrurga leptonyx*) may take giant petrels on the water. In the lower latitudes, Man also is responsible, directly or indirectly for the deaths of giant petrels, particularly young birds. Of 326 young birds recovered, whose fate has been recorded (i.e. recovered dead, alive or killed), 38 were known to have been killed by Man, and of the remaining 288, 199 were recovered dead, and some of these too may well have been originally killed.

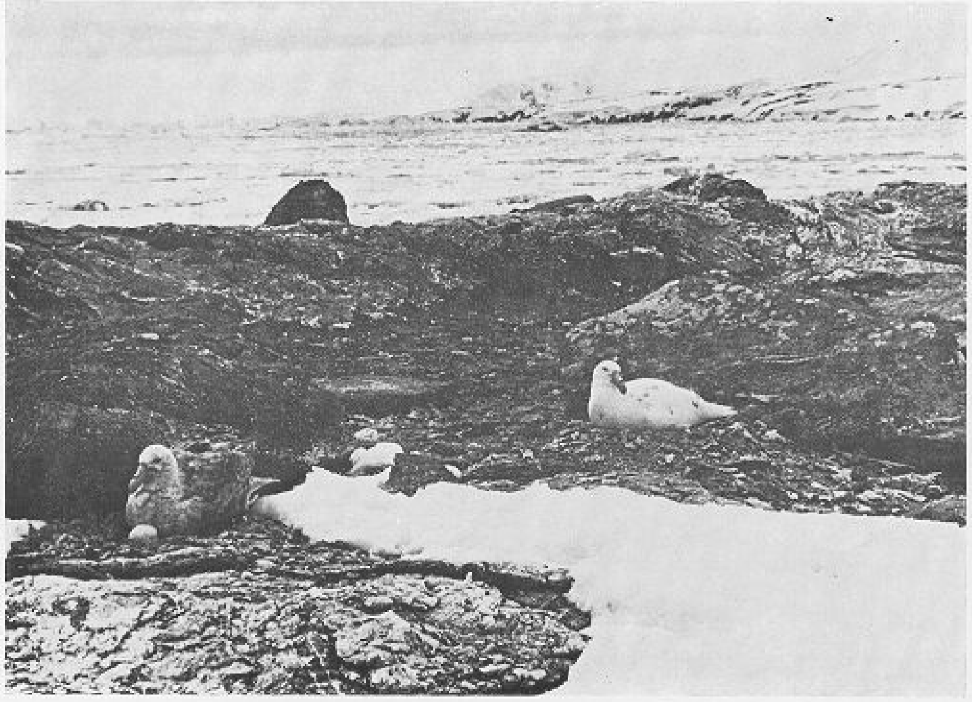
On the Falkland Islands, Man also collects giant petrel eggs, either as food or destroys the eggs because of the alleged damage the adults cause to sheep (Cott, 1954).

Deserted young giant petrel chicks on Signy Island fall prey to skuas, sheathbills and possibly other giant petrels. In addition to these predators, on Macquarie Island wekas (*Galliralllus australis*) may carry off young chicks (Law and Burstall, 1956).

PLATE I

a. The two colour phases of the giant petrel breeding on Signy Island.

b. Typical nesting terrain of the giant petrel on Signy Island.



a

b

PLATE II

a and b. The study area on Signy Island in winter.

c and d. The study area on Signy Island in summer.

a

b

c

d

PLATE II

PLATE III

a. Using a puffin hook to lift a sitting bird to check the ring combination and nest contents.

b. Measuring the length of an adult giant petrel's bill in the field.

a

b

PLATE IV

a. Typical nest of stones of the giant petrel on Signy Island.

b. Nest of the giant petrel on South Georgia among tussock grass.

(Photograph by I. Everson.)

PLATE IV

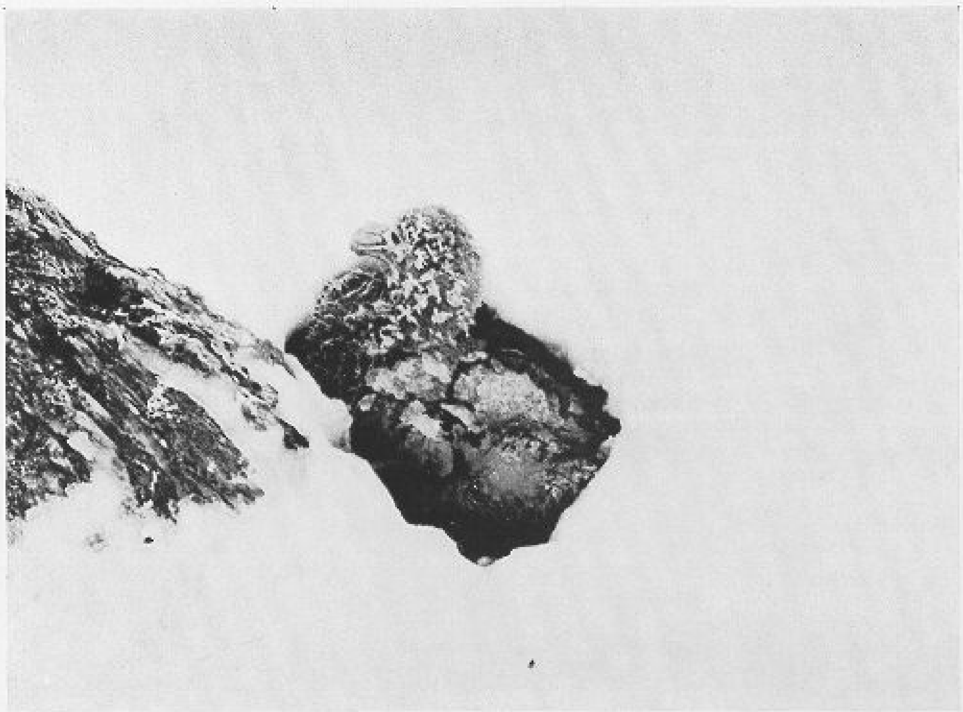
a

b

PLATE V

a. The nest of a 30 day old chick after 2 days of heavy snowfall where there is no record or sign of parents visiting the nest. The bird is almost snowed over and the down is ice-covered.

b. The nest of a 35 day old chick after 2 days of heavy snowfall with parent in attendance. The bird is not snowed over and the down remains ice-free.



a

b

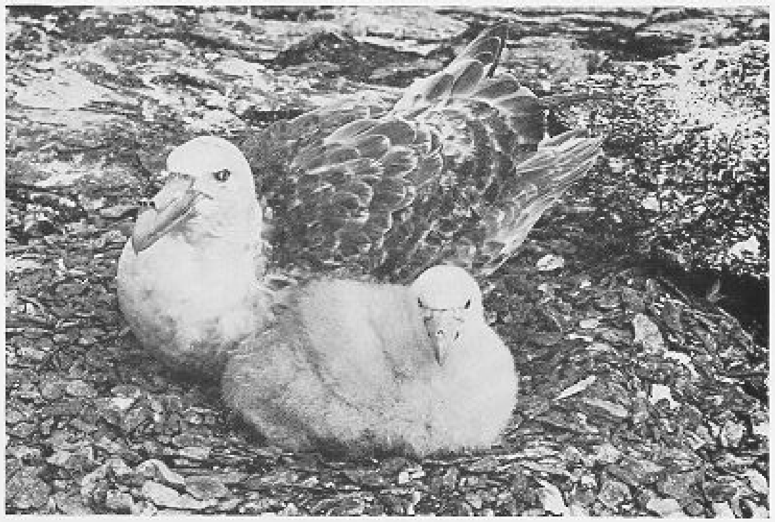
PLATE VI

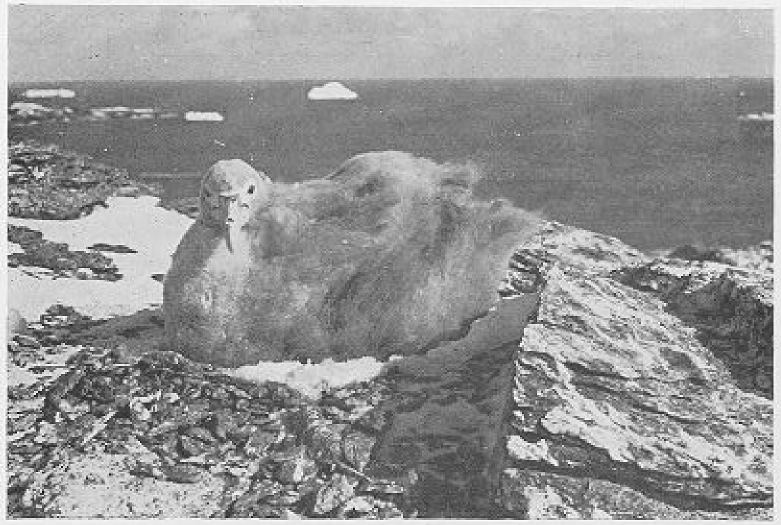
Giant petrel chicks at different stages of development.

a. 7 days old.
b. 21 days old.
c. 40 days old.
d. 95 days old.

PLATE VI


a


b


c

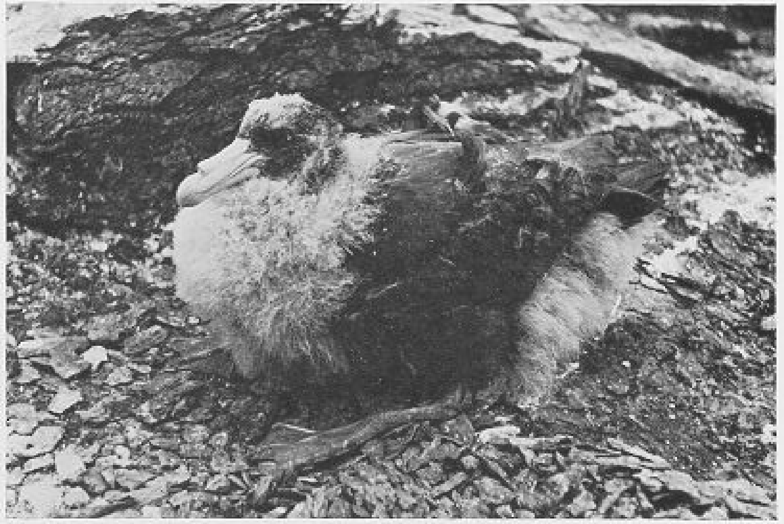
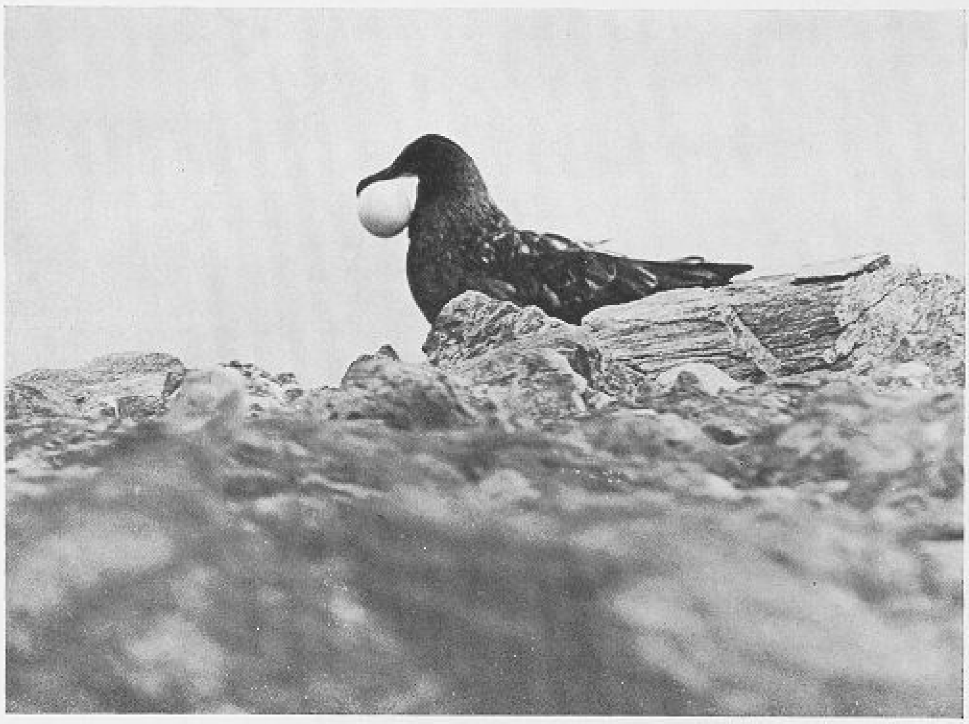

d

PLATE VII

a. Brown skua at a giant petrel egg.
b. Brown skua removing a giant petrel egg.

a

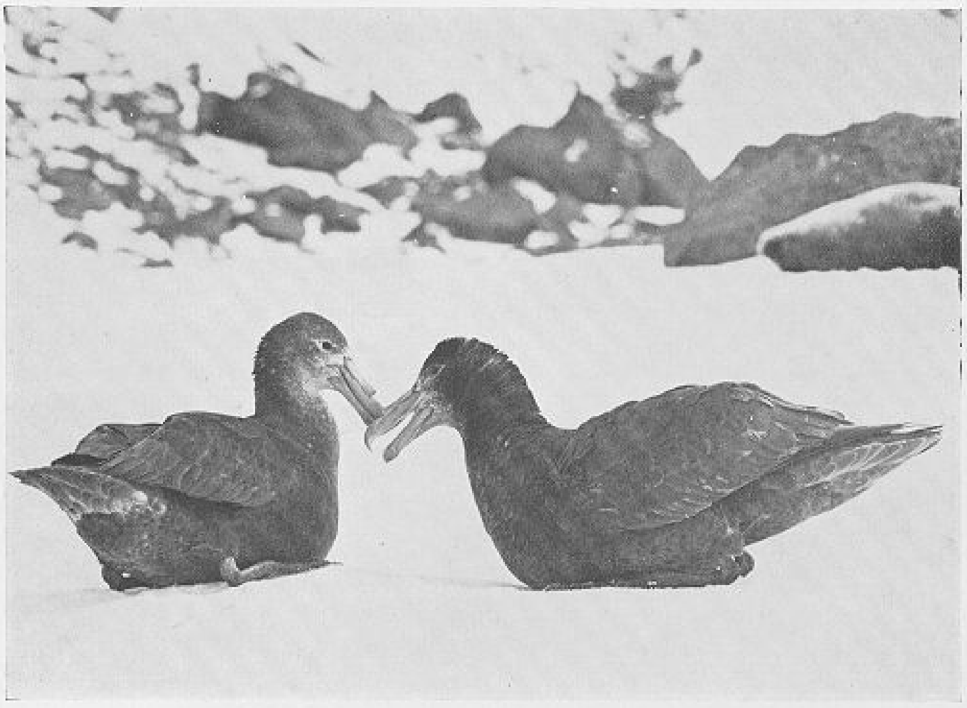


b

PLATE VIII

a. Pair of immature giant petrels billing on a snowed-over nest site in late autumn.

b. A two-egg clutch found in the main study area on Signy Island.



a

b