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THE BIOLOGY OF THE GIANT PETREL *MACRONECTES GIGANTEUS*

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THIS account of the Giant Petrel (*Macronectes giganteus*) is based on investigations on Macquarie Island from 29 December 1959 to 12 March 1961 while the author was biologist to the 1960–1961 Australian National Antarctic Research Expedition (ANARE).

Macquarie Island (latitude 54°30' S; longitude 159° E) is about 1,300 km (800 miles) south of Tasmania and just north of the Antarctic Convergence. It lies approximately north and south and is about 34 km (21 miles) long by 4.8 km (3 miles) wide. A narrow beach terrace borders much of the coastline, but inland the ground rises steeply in scree to a plateau averaging about 260 meters (800 feet) above sea level. There are no trees, and the vegetation is composed mostly of mosses, Maori Cabbage (*Stilbocarpa*), and tussock grasses (*Poa* spp.); there is very little growth on the exposed parts of the plateau. The climate is wet with much mist on the high ground, and, as the island lies in the west wind belt, gales are frequent at all seasons. The mean monthly temperatures range from 3° C (37° F) in June to 7° C (44° F) in January, and even in winter snow seldom remains for long on the ground at sea level. A general account of the island and of ANARE activities there has been given by Law and Burstall (1956).

Macronectes giganteus is a large petrel of the sub-Antarctic zone. It is a surface nester; too large for natural enemies to attack it when ashore, it is active on land by day. Most recent studies of the species are concerned with migration of juveniles as revealed by the recoveries of birds banded as nestlings. On Macquarie Island 7,366 chicks and 1,157 adults have been banded up to March 1961, including 2,946 chicks during the course of the present work. Recoveries have been discussed by Howard (1956) and Ingham (1959). Sladen and Tickell (1958) and Tickell and Scotland (1961) have dealt with recaptures of birds marked by the Falkland Islands Dependencies Surveys. Murphy (1936: 584–596) summarized



Giant Petrel on nest with two-egg clutch.

what was known of the species at that time. Various voyagers, *e.g.*, Biermann and Voous (1950: 35–39), recorded the distribution of the Giant Petrel at sea. Falla (1937: 137–145) described observations made at Macquarie Island, Kerguelen, at sea, and on the coast of Antarctica. Downes *et al.* (1959: 69–78) have published observations made at Heard Island.

Several members of the ANARE parties contributed to the present study. Messrs. K. Watson and A. Evans helped with the banding of the chicks in 1961, a project that would have been impracticable single handed, and Messrs. J. McNally and A. Thomas also assisted. Dr. R. Carrick, Dr. D. L. Serventy, Mr. S. Davies, and Miss S. A. Ingham kindly read the rough draft, and the latter's summaries of the biological logs of previous parties have been of help for comparative purposes. Mr. W. B. Hitchcock provided the banding data. The paper has also been improved as a result of a helpful discussion with Dr. R. A. Falla.

THE ANNUAL CYCLE

Most Giant Petrels at Macquarie Island laid their eggs from about 5 to 11 October. A minority laid earlier—mostly from 21 August to 10 September. These did not nest colonially like the later breeders, but rather as solitary pairs or in small, very scattered groups. Such early nesters hatched their eggs from about 19 October to 6 November, and their chicks flew from about 1 February to 5 March. Most of the colonial pairs hatched their eggs between 5 to 20 December, and their chicks first flew between 26 March to 30 April.

Long before the last chicks left there was an outburst of nest building, either at the edges of the colonies or in entirely new places. This was seen during the first week of February and was attributed to submature birds. Thus on 6 February 1961 a small party of Giant Petrels was disturbed from a group of four freshly made nests. The birds were in dark gray-brown plumage, had dark heads, and were away from any established rookery. During the next three weeks a revival of nest building was noted at many places, but especially around the edges of existing colonies. This activity may have begun as early as 16 December. On 28 February six new nests were found whose occupants were mostly rather dark-plumaged birds. They were in pairs, braying and displaying mutually. Dark or freckle-headed petrels predominated among the other autumnal nesting parties, and the absence of light-headed birds strongly suggested that such autumn nest makers belonged to a subadult class of the Giant Petrel community. They could hardly have been breeding birds because successful pairs were still busy feeding chicks. The only other

bird that frequently makes nests in the autumn at Macquarie Island is the Gentoo Penguin (*Pygoscelis papua*), which is present throughout the year.

Some breeding stations of the Giant Petrel, such as those on islands off Antarctica, are deserted during the southern winter, but at Macquarie Island the rookeries were occupied at all seasons. Successful breeders may have gone to sea after the departure of the chicks, but the colonies were soon reoccupied by adults and continued to be used during the winter. At that season many Giant Petrels sat in pairs in the colonies by day and engaged in energetic mutual display. Such activities were seen even when the ground was under snow, and pale-headed birds predominated. This indicates that they were all mature individuals, a hypothesis supported by the capture on 2 June of a bird that had been banded on its nest at the same colony in November 1954 and by three similar recoveries on 25 July 1959 by S. Csordas.

Four Giant Petrels banded as chicks have now been recovered on the island, three during the course of the present study:

130-03555, a white-phase bird banded 13 March 1955 and shot on 5 August 1958, three years and five months after banding.

130-00160, banded 24 February 1957 north of Aurora Point and shot when a dark-eyed, dark-brown bird at Bauer Bay on 30 August 1960, three years and six months later.

130-08175, banded 22 February 1956 at Major Lake, was caught and released at Hasselboro Bay on 4 October 1960, four years and seven months after banding. It was described by its captors as a "uniformly grey bird."

130-02806, banded 24 February 1957 north of Aurora Point, was caught and released on 10 March 1961, four years later on a rookery near Douglas Point. It was then a dark-eyed, dark gray-brown bird with a dark head and may have been one of several autumn-nesting birds on this rookery.

The last of these recaptures, and the absence of other birds banded as chicks on the colonies, suggests that the Giant Petrel does not breed until at least five years old; this is in agreement with Downes *et al.* (1959: 75), who came to the same conclusion from the lack of recoveries of chicks at Heard Island. Tickell and Scotland (1961: 261) report a banded bird nesting at eight years old but give no details of its age at first breeding or of its sex or plumage.

POPULATION AND NEST SITES

A census of breeders was attempted during January and February 1961 when all the rookeries were inspected and the chicks banded. A total of 2,846 were marked with bands issued under the Australian Banding Scheme and inscribed "Write Wildlife CSIRO Canberra Australia." Twenty-one

other chicks too small to band were also counted. There were more than these 2,867 chicks on the island, as a few isolated nests on both west and east coasts were known to have been overlooked; a yard-by-yard search of the rugged tussock-clad rocks along the indented coastline was impracticable. It is estimated that not more than 150 such nestlings were missed. *Per contra*, some of the counted chicks must have died through various natural causes after banding. In all, the chick production for the 1960–1961 season is believed to have been about 3,000 birds.

Assuming that the breeding success of Giant Petrels was 57 per cent that year, then about 5,300 eggs were laid during the season, the product of 10,600 breeding birds. However, from the data available, the breeding success could have been nearer 70 per cent, which gives only 8,600 breeding birds. The total population, allowing for all classes of nonbreeders, was certainly much greater than this.

The petrels bred in 70 colonies. All but one of these colonies were on the west side of the island where they were exposed to the strong prevailing winds. Most were quite small, producing an average of 41 chicks. The three largest held 167, 160, and 126 young birds, the smallest only four to six at the time of banding.

The greatest concentrations of rookeries in both the 1959–1960 and 1960–1961 seasons were in the area of Caroline Valley in the southwest corner, where 606 chicks were counted, and along the coastal rocks between Mawson and Aurora points, where there were 940 chicks during the census. Previous records suggest that these have always been the best breeding areas. Complete details of the 1960–1961 colonies are deposited at ANARE headquarters in Melbourne.

From previous plots showing the sites of some of the breeding colonies it is clear that the locations of many of the larger and more accessible rookeries are relatively permanent. Several were evidently on the same sites in 1952 and 1954 as in 1958–1961. A more complete mapping by K. Keith in 1956 reveals that 12 of the larger colonies were in the same places then as they were during my stay on the island. Some shifting occurs; large colonies may split into two, and small ones may coalesce. In the region of Major Lake the sites of the rookeries have changed several times between 1952 and 1960. One colony near Mawson Point in which about 20 chicks were reared in the 1959–1960 season was not re-occupied the next year; instead a new site was used about 400 meters to the south, apparently by the same birds.

The faithfulness of Giant Petrels to a particular rookery or breeding area was shown by six recaptures of breeding birds during 1959–1961 at the same colony or in the same general area where they were banded as

adults several years before. Most adults recaptured before 1960 were also found where banded, but a few records suggest shifts of one to three km.

Postbreeding occupation of the rookeries, apparently by the mature birds, must tend to stabilize the sites from year to year. It may also tend toward the continued use of the same nest by the same pair during successive seasons. Many of the early solitary breeders did not choose the same places in successive seasons, but such birds were not seen near their nests during the winter months. Repeated use of the same nests by the same pairs is usual in burrowing petrels and occurs in at least one surface nester—*Fulmarus glacialis* (Carrick and Dunnet, 1954).

DISPLAY

Giant Petrels are easily frightened by man. For close observation concealment or long-range viewing was necessary, and much of the following information on behavior was obtained by observation from blinds. Written records were supplemented by a frame-by-frame study of motion pictures.

Threat

Aggressive posturing was the most common type of display. Threatening occurred among birds in rookeries and among members of parties gathered around food either on land or sea. It was not always clear just where threat ended and courtship or greeting ceremony began, and many threats began mildly and ended in combat.

A low-intensity attitude used by birds on their nests to discourage intruders involved braying cries and head-swaying movements in which the neck was upstretched and the nape feathers ruffled. If this was ineffective, sitting birds lunged forward and struck with their bills. Well-grown chicks also threatened in this manner.

Much more impressive was the forward-threat posture, a grotesque attitude often seen among birds attempting to feed on a dead seal (Figure 1). The threatening bird squatted, stood, or ran with its tail fully expanded and tilted so that the tip was directed forward. The neck was arched, the nape feathers much ruffled, and the bill lowered. The outstretched wings were also arched, and their tips might trail on the ground. The posturing bird either faced its rival or had its back to it with the tail uplifted.

This forward threat seemed to reflect the bird's intention to attack. Such display was seldom ignored by the rival (usually a dominant bird on a seal carcass). The response of such a "sealmaster" was the upright-threat attitude described below followed perhaps by attack. Particularly noteworthy was the effectiveness of forward-threat display in inducing



Figure 1. Forward-throat posture of Giant Petrels feeding on a dead seal.

attack at a distance; dominant birds were seen to stop feeding and to drive off potential rivals displaying 20 meters away. Furthermore, the fact that the threatening petrel presented only the underside of the fanned tail did not reduce the vigor with which it was attacked. It seemed rather that the uplifted tail released aggression in the "sealmaster," but no experiments were made to test this belief. Petrels that fed with their heads and necks immersed within a seal kept their tails cocked high. Such birds seemed very conscious of the weakness of their position; they were nervous and were quick to switch to attack when threatened.

In disputes over food it was not always the feeding bird that was the more aggressive; often the forward-threatening petrel dashed toward the carcass to fight the dominant bird. The latter either retained its position and the disputant retired or the new bird won and reigned in the other's place. Sometimes threats alone sufficed to evict a "sealmaster," and there was no fighting. The changeover of feeding birds appeared to be continuous. As the dominant ones became satiated, their belligerence dwindled, and they were replaced by more vigorous or hungrier birds. None was ever seen to displace another without first adopting the forward-threat posture.

The upright-threat attitude is illustrated by Downes *et al.* (1959: 76). As in forward threat, the wings were spread and bowed, the tail fanned and uptilted, and the nape and back feathers extensively ruffled. Now, however, the neck was vertical, the head held high, and the bill at about 45°. The head was waved vigorously from side to side, rapidly or slowly according to the individual, so that the bill almost touched the bend of each wing. At the same time an expiratory neighing cry was made, wavering in time with the head oscillations.

This display occurred when a bird seemed to be trying to repel several others, whereas forward threat seemed to be directed at a single rival. Upright threats were often used by Giant Petrels immediately after alighting in a rookery, perhaps because they had difficulty in landing on "neutral" ground. The display was also used almost invariably by the victor of a fight over food or by a victorious "sealmaster" that returned to a carcass to find several bystanders feeding in its absence. Adoption of the upright-threat posture appeared to reestablish the dominant bird's claim to the feeding place.

When fighting, the birds' beaks often became interlocked. The adversaries then grappled together, breast to breast, straining upwards. Sometimes one grasped the other's nape and hung on tenaciously. A bird that obtained such a grip usually became the victor. Many fights were seen without any wounds being apparent, but the severity of some struggles suggested that serious injuries must sometimes result.

Both forward and upright threatening with uptilted tails occurred at sea when mobs of birds were attracted to a carcass. In forward threat the neck lay on the surface, and attack followed a violent dash across the water. In upright threat the birds kept their heads high and waved them from side to side just as on land.

During banding operations many adults were found with their chicks, and some remained with them. They had to be pushed off the nests before the chicks could be banded. Most parents merely gave low-intensity threats and returned when we moved off, but one male that had shown little alarm when its own chick was handled, suddenly attacked the bander as he was engaged with the next chick. Such aggression toward man was quite exceptional.

Mutual Display

This sexual display was seen throughout the year. It occurred during the winter reoccupation of the rookeries, before egg laying, in the breeding season, and during the autumn nest-building phase. The actions used were very similar to those described for *Fulmarus glacialis* and *F. glacialisoides* and involved billing, mutual nibbling of heads and necks, and bowing. Such displays often involved only two birds of opposite sex, but three or more members of small groups would display among themselves in this way. Much mutual display during and immediately after nesting seemed to be between adult nonbreeders.

The birds of a pair generally sat close together and either sex initiated the display. Typically, one lifted its head and pointed the partly opened bill skywards before turning it down toward its companion, leaning forward, and, with a swaying action of the head, reached toward the other's head and neck. Both then wobbled and stretched out their heads, and a soft braying call was heard. Their tails were often spread and wagged from side to side but were not uptilted. Their bills were slightly ajar, but their napes were not ruffled. Head wobbling often led to mutual preening of heads, throats, and flanks when feathers were sometimes dislodged. The birds' beaks often touched, and each bout of activity lasted about 10 seconds. One pair on 26 July 1960 performed 22 times between 09:21 and 09:58 hours. At intervals one bird, often the female, tucked its beak into the scapulars as if it were sleeping.

Before egg laying, paired petrels generally kept together in one spot, but some wandered and displayed mutually in various places. Such wanderers often returned to one particular site; presumably this was where they would nest.

Head waving was frequently seen when a Giant Petrel was approached by another, not necessarily by its mate, and such actions appeared to

form a greeting ceremony since mutual preening and billing often followed. Mutual display was also seen among birds resting on the beaches while waiting to feed at a dead seal.

Coition

Coition was first seen on 24 August and last seen on 1 October. On both these occasions the females were already covering eggs. On 1 October, when her egg was not more than one day old, a sitting female was the object of preliminary circling by a male thought to be her mate. The female sat low in her nest, bobbing her head slightly and making a short, mewling cry. At intervals the male dipped his beak toward her; she swivelled around to face him, and occasionally she tried to peck him. Eventually he climbed onto her back and stayed there for five minutes, trying to strop his bill across hers in the manner described below; but she was unresponsive and he had to stop.

More usually, once the male had mounted, he held his bill vertically, pointing downward, and, by a series of swinging movements to either side, wiped his bill across that of his mate. Their beaks touched three or four times per second, and the resulting clicks were quite audible from 100 meters away. The male's tail was swung from side to side, and at intervals the female gently thrust her opened bill upwards into the feathers of his throat, breast, or flanks. Most males only opened their wings slightly during these preliminaries, but toward the climax extended them to either side. The bill movements then ceased, and the male reached forward and remained quite still while he swung his tail sideways to bring the cloacae together. Some attempted copulations lasted for 5–10 minutes, but it was not possible to distinguish between effective and ineffective matings.

The seldom described copulation of the Atlantic Fulmar (Fisher, 1952: 333) is apparently rather similar except that beak actions of the males are not recorded; in *Fulmarus glacialiodes*, however, they do occur (Prévost, 1953b).

Aerial Display

This was the most puzzling of the Giant Petrel's displays. It was seen in every month and did not seem to be more frequent at any season or at any time of day (*vide* Murphy, 1936: 593). The performance resembled the upright-threat display and was used both by single birds far from other Giant Petrels and when two were flying close together.

Most such displays began when a flying bird rose a few meters on stiff, somewhat drooped wings, and then descended in a short curve. The action was rather like that of a displaying turtle dove. The petrel's neck

and head were stretched and raised, the nape feathers ruffled, and the tail fanned. Often the legs were lowered and the webs expanded. As the bird glided along, its head was waved from side to side and the usual neighing cry was heard.

In a few instances aerial display appeared to be the culmination of a short chase. If so, it was usually the hindermost bird that displayed, although both might do so. Single birds were seen to display, and after a wide circuit over the coastal terrace, repeated the performance when they reached the same place as before. Such birds might be over rookeries, but often no possible point of interest could be seen; *e.g.*, one petrel displayed vigorously when about 100 meters up and directly above the writer.

A small group of Giant Petrels was feeding on a dead rabbit on 29 March 1960. Several others circled above, and as they flew past drooped their wings, lowered their feet, swayed their heads, and brayed. Here aerial display seemed to be associated with threat.

Quite distinct was the mild chasing that occasionally involved two birds when one followed another for a few hundred meters. Close pursuits or synchronous flights such as occur among petrels of the genus *Pterodroma* or among *Phoebetria* albatrosses were never seen in *Macronectes*.

THE NEST AND INCUBATION

The kind of nest at Macquarie Island varied with the situation. Solitary nests, and those in colonies among coastal rocks or tussock, were built of grass and were mostly quite large. Those on the open moss consisted of depressions lined with plant debris and grasses, while those on the plateau, which were very exposed, were saucerlike hollows containing little or no nest material. Usually at such sites there were no plants nearby except mosses or *Azorella*, and any vegetation that was brought in would soon disappear in the strong winds. Such situations appear to resemble the nest sites on Kerguelen reported by Paulian (1953: 163). No solitary nests of the early breeders were found on the plateau; all these nested near the sea, mostly in relatively sheltered places among rocks and tussock grass.

How the nesting hollows were made was not discovered, but the birds before egg laying collected grasses that they dropped to one side and later added to their nests. Some birds tore blades from the *Poa* stools; similar behavior was noted among the autumn-nesting birds. During incubation the petrels added to their nests any fragments of vegetation within reach.

Because no birds were color marked before egg laying, it was impossible to discover whether there was a prelaying exodus such as occurs with some burrowing petrels and with the fulmars *Fulmarus glacialis* and *Daption capensis*.

Many incubating Giant Petrels deserted their eggs when closely approached. Such eggs were quickly taken by the skuas. For information on incubation, the nests occupied by the bolder birds that stayed on their eggs were studied. Two different groups were used: one, consisting of early breeders, gave information about the rôles of the sexes and, later, of the length of the fledging period. Eleven such pairs included birds sufficiently tame to be marked on the forehead with red enamel. This, when well pressed down into the feathers, remained visible throughout the breeding season. Once one member of each pair had been marked, it was easy to see which was on duty. Even if not color marked individual Giant Petrels could also be recognized by the patterns of their irides and by the colors of their beaks. No two birds were alike in all these features.

The second group gave data on the length of the incubation period and was used later to obtain growth curves for the chicks. Once the dates of egg laying had been found and the nest sites pegged, these birds were not disturbed until hatching was imminent. Regular inspections were then begun.

The first eggs seen on 21 August were in solitary nests. Laying of lone pairs continued until about 10 September. Very few eggs were then laid until those of the main body, whose laying extended from about 1–15 October with a peak from 5–11 October.

These early breeders laid before the bulk of the skuas had returned from their winter migration; indeed these Giant Petrels were the first of the island's birds to lay. But soon any eggs left unguarded were immediately lost to patrolling skuas and to Wekas (*Gallirallus australis*). However, if I promptly hid such eggs under the nesting material most birds resumed incubation when they returned, and losses through disturbance were thereby reduced. The bolder Giant Petrels tended to shuffle back off their nests when I came near, or they jerked upwards as if to fly but did not do so. When lifted with a stick so that the egg could be checked, many brayed quietly. Some went through the motions of vomiting but disgorged nothing; others discharged the contents of their stomachs and then either fled or remained. Many apparently tame birds revealed their nervousness by shivering as penguins, albatrosses, and other petrels do in similar circumstances.

Incubation was undertaken by both sexes. Each sat continuously for several days until relieved by the other, a routine that obtains with other petrels; e.g., *Puffinus tenuirostris* (Marshall and Serventy, 1956: 492). A few female Giant Petrels sat for two days after laying, but the males usually undertook the first lengthy shift. Daily checks at the 12 solitary nests studied were not possible; only approximate figures were obtained for the lengths of the incubation shifts. These varied from two to 12 days'

duration, and usually the male had five shifts on the egg and the female four shifts between laying and hatching. Despite the lack of daily inspections it is not thought that any changeovers were missed, and checks at night revealed the same birds sitting as at dusk. A particularly long spell was undertaken by one female, which sat for 25–28 days. On the day before her abandonment I noted that this hitherto tame bird was becoming timid and that her desertion seemed imminent.

During the many visits made to these early nests while incubation was proceeding, only one bird was found at each nest, and no nest reliefs were seen. Nest reliefs were, however, witnessed later at the rookeries. The changeover usually took place without ceremony, the sitting bird raised its wings and jumped off to reveal the egg for a moment. Then its mate walked on and sat down, and the relieved bird flew off. One male sat by its mate for over an hour before taking over and at about 10-minute intervals reached forward toward the female to indulge in mutual display.

Eleven determinations of the incubation period were made. They were 58.5; 61.5; 58.5; 58.5; 60.5; 58.5; 60.5 (each ± 1.5 days); and 61; 58; 59; and 59 days (each ± 1 day). The shortest possible period was 57 days; the longest possible period, 62 days. These are the true incubation periods, for this surface-nesting petrel cannot leave its eggs uncovered as do many burrowing species; this thereby increases the time between laying and hatching. The figures are substantially less than that given by Downes *et al.* (1959: 73) of approximately 70 days at Heard Island but agree with Prévost's (1953a) one record of 60 days for a bird at Terre Adélie. Data for other fulmars are 40–57 days for the Atlantic Fulmar (Fisher, 1952), 43–44 days for the Antarctic Fulmar (Prévost, 1958), and about 45 days for the Cape Petrel (Downes *et al.*, 1959).

THE NESTLING

Birds of either sex were sitting when hatching began, and from one to six days elapsed between the starting of the egg and the birth of the chick. Seven eggs shortly before hatching weighed 210, 220, 230, 240, 250, and 260 g and two just-dry chicks each weighed 220 g.

Lone pairs hatched their eggs between 19 October and 5 November. For the colonial birds this event fell between 3 and 20 December, but a few chicks were not hatched until 1 January. The young were covered by either parent in turn for about 15–24 days (8 records), after which they were not brooded even if a parent was present. During this guard stage the on-duty bird often preened its chick. From time to time adults rose from their nests to beat their wings and to shake their feathers.

The voice of the newly hatched chick was a quiet peep; this changed

to a deep, guttural snorting during the nonguard stage, and later a braying note was added.

Parent-chick feeding behavior was similar to that of other Procellariidae, e.g., to *Puffinus carneipes* (Warham, 1958). The chick used a deep cry as it reached forward to peck at the parent's head, bill, and flanks. The latter swallowed several times and then opened its beak. The chick's cries now got louder, its actions more persistent, and the parent then flattened itself somewhat to the ground, opened its bill widely to allow the chick to insert its own beak across that of the adult bird. Calling stopped as the food was transferred with scissoring movements of the mandibles. The chick then withdrew, both birds swallowed, and the process was then repeated. A series of meals was usually given, the nestling's beak being inside the parent's for about four seconds at each meal. Individual variations were noted; some chicks begged for a long time before their parents responded, yet other adults did so readily and some even initiated feeding by opening their bills before their chicks had started to call.

When the nestlings were old enough to be left unattended, they slept much of the time. On warm days they gaped and panted heavily. In wet or windy weather they hid their heads in the down of their backs and assumed a spherical shape. There were sometimes droplets on the tips of their bills, perhaps the result of salt excretion by the nasal glands. Many chicks added to their nests by reaching out to collect dead grasses and other fragments from the hollows between the nests. During this stage of the breeding cycle the parents were very seldom seen at their nests; this suggests that the adult's feeding visits are brief.

The chicks grew rapidly and at 50 days attained adult weight of about 4.5 kg. Weight variations resemble those of other petrels and of albatrosses, showing a rapid increase to a peak greater than adult weight, followed by a steady decline to fledging. The study chicks flew on attaining weights of 3.6–5.6 kg. There was no evidence that feeding continued until they flew. Rather, there appeared to be a short desertion period.

The first feathers were hidden by down, but at about 40 days of age the wing and tail feathers were both about 2.5 cm in length. At 60 days the primaries were about nine cm and the rectrices six cm in length. By 80 days these were 15 and 11 cm, respectively, and at 100 days they were 25 and 15 cm. Some chicks departed at this stage.

White-phase chicks started life with white down, and those that were to have black spots in their plumage showed these with the unfolding of the first feathers. Some white-phase chicks had legs of a pale grayish-flesh color. But most had pale-blue legs with flesh-colored webs, and

many had gray legs just like those of normal chicks. Pale-footed nestlings were thought to result from matings between two white-phase adults, and because such pairs were scarce, pale-footed chicks were rare. A few normal dark-phase young had particolored webs shaded with dark brown on their outer edges.

Many chicks stayed in their nests even when they seemed able to walk, but others started to wander when about 85 days old; for some time before their departure young birds in the shiny-black juvenal plumage were found several meters from their nests. One of the study chicks would bray when approached and after being weighed would waddle 10 meters back to its nest. This tendency to move became noticeable on calm days in early February when down-free birds ready to leave dotted the coastal moss terraces. These were the young from the solitary nests awaiting the winds they needed for takeoff. Their dependence on strong westerlies meant that spells of calm weather at fledging time stranded the young birds. There was no evidence that any walked down to the shore and swam out to sea as shearwaters often do.

What was believed to be a Giant Petrel's first flight was seen on 11 April. The bird stood on a ridge with its wings out so that a westerly wind with gusts to about 20 knots tended to lift it from its feet. The fledgling beat its wings between gusts but seemed unable to get airborne. Eventually, after several poorly timed attempts, it took off with a short run, rising on flapping wings and gaining height as it moved forward over falling ground. The bird made no attempt to sail on stiffened wings in the manner usual with this species, and it looked rather unstable. Beating its wings steadily it drifted south at about 45° to the breeze until it was over the sea and its migration had probably begun. Others evidently did not get away at their first attempts. Thus the chick from nest 51 was found on the moss about one-half km from its natal rookery. It was free of down and had doubtless reached the moss on its first flight.

Seven determinations of the fledging period were made. They take no account of any stranding due to calms, and, as both hatching and flying dates were not known accurately, the figures are only approximate. They are (in days): 102 ± 4 ; 103 ± 3 ; 106 ± 2 ; 108 ± 4 ; 110 ± 3 ; 113 ± 4 ; and 117.5 ± 1.5 days. By 15 April only occasional stragglers were seen near the rookeries; the rest of the young had gone.

BREEDING SUCCESS

Three colonies were observed in an attempt to determine the ratio between the number of eggs laid and the number of chicks reared to the banding stage. A count of incubating birds was made at each colony on 30 October 1960, when egg laying would have been complete, and another

count of the chicks was made on 12 January 1961. As the rookeries were not visited between these checks, any losses must have been due to natural causes.

At rookery N.15 50 eggs produced 38 chicks = 76% success.

At rookery N.69 104 eggs produced 40 chicks = 39% success.

At rookery N.60 114 eggs produced 75 chicks = 66% success.

The wide variations in these figures, for which I can offer no explanation, suggest that they are not reliable as indicators of the over-all efficiency of breeding on the island during that season.

Most nestings apparently failed during incubation; if the egg hatched the chance of fledging was good. Although skuas were often seen near the rookeries, neither they nor the numerous feral cats are known to have taken properly guarded eggs or chicks. The latter, at the start of the nonguard stage, were quite small but seemed capable of deterring enemies by spitting oil.

During banding, very light chicks, which appeared to be starving to death, were sometimes handled. Others, though of normal weight, had oily, matted down that was of little protection against the weather. These chicks too seemed likely to die.

TWO-EGG CLUTCHES

In the 1960–1961 season, four and possibly five nests (0.14–0.18 per cent) were found with two eggs or two chicks. That these were not the result of two females laying in one nest was suggested by the improbability of a bird leaving its egg without losing it to the skuas, by the obvious territoriality of the breeders (they threaten other Giant Petrels that come near), and by the discovery of a white-phase adult brooding two similar white-phase chicks (Figure 2). The two other chicks believed to belong to one pair were about one-half meter apart. No nest could be seen for the extra bird, and as both were of the same size and wore a similar, rather distinctive, brown-gray down, they were judged to be the offspring of the same female.

Of the nests with two eggs one was not reexamined. The second pair hatched one egg, but the chick was found dead in the nest on 23 December; the unhatched egg was holed and contained a well-developed but dead embryo. At the third nest (Frontspiece) neither of the eggs (66.1×99.3 and 65.1×103.0 mm) hatched; one was slightly developed and the other disappeared between 16 and 22 December. Both these latter pairs continued incubation for over a week after their neighbors had hatched their eggs.



Figure 2. White-phase adult Giant Petrel brooding two white-phase chicks.

Neither of the pairs of birds with two chicks succeeded in rearing both. A second inspection on 6 February 1961 revealed that one chick had disappeared without trace from each nest.

Marshall and Serventy (1956) have described the rapid collapse of the avian testes after ovulation in *Puffinus tenuirostris* and state that this would make it impossible for these petrels to lay a second egg if the first were lost. They add: "In fact, the great size of the one egg, occupying a large part of the abdominal space, and the probable long period between insemination and egg-laying, throws serious doubt on the validity of observations that two-egg clutches sometimes occur in *Fulmarus glacialis* see also Fisher (1952)." Serventy (pers. comm.) suggests that in these two egg layings of *Macronectes* it is more likely that two oöcytes were released from the ovary and both fertilized at one insemination or at inseminations very close together, rather than that twinning occurred in a single oöcyte after its release. It may be noted that

according to Marshall and Serventy (1956), the single egg of *P. tenuirostris* represents about 16 per cent of the female's body weight whereas in the Giant Petrel the egg at about 250 g represents only about 6 per cent of her body weight of 4.3 kg. This makes more understandable the holding of two eggs in the body cavity just before laying.

Two-egg clutches have been reported also in the Atlantic Fulmar. Fisher (1952: 94) records that on the Westmann Islands up to 10 per cent of the nests may contain two eggs and again (p. 461) reports a site where one long and one normal egg were found in 1947 and again in 1948. The latter evidently represented layings of two eggs by the same female, and some of the layings on the Westmanns must surely have been genuine two-egg clutches. However, there seem to be no records of any Atlantic Fulmars that have hatched two eggs, and Gudmundsson, quoted by Fisher, noted that the Westmann birds were incubating only one of their eggs, the other lying cold beside them. This was not the situation with *Macronectes*; the sitting birds covered both eggs, although whether their incubation patches were always large enough properly to accommodate both is unknown. With the two-egg clutches that failed, lack of covering power, particularly by the smaller females, might have been decisive, but the incubation of two eggs is evidently effective sometimes or the chicks in Figure 2 could not have been hatched.

PLUMAGE AND MOLT

Apart from white-phase birds that are white from hatching, three main plumage types were distinguished:

1. Juvenal plumage in which the feathers were a glossy blackish-brown; eye dark brown; bill horn-colored; nails pale green.

2. Body feathers dark brown, lighter around the base of the beak; eye brown or gray; beak and nails pale yellow-green with the nostril horn-colored. No breeding birds were seen in this plumage, which is evidently that of immatures. It is typical of the Giant Petrels that occur off the southern coasts of Australia and New Zealand.

3. Body feathers gray-brown, lighter around the base of the beak and on the cheeks and throat; breast and flanks more or less mottled with pale gray and brown or wholly pale gray; the head either rather dark, freckled gray and brown, or wholly pale gray; eye varying from brown to pale gray; bill greenish to yellow-brown. This was the plumage of the breeding birds, and it was very variable.

That the lone pairs nested consistently six to seven weeks earlier than the majority suggests that the lone pairs belonged to a different age group than the rest. Such early nesters were light, dark or freckle headed, but the colors of the soft parts were more constant. Nearly all were gray eyed or had brown eyes flecked with gray, and their bills were generally pale yellow-brown, reddish towards the tips and with black smudges on the insides of both nails. Colonial breeders were different, for most had pale or freckled heads and very many were dark eyed, although some had gray irides. The greatest difference was in bill color. Most of the colonial

birds had pale, yellow-green bills without black marks on the nails and with horn-colored nasal tubes.

Because of bill and eye color the lone nesting pairs might well be judged to be very old birds. The young *Macronectes* has brown irides, and among breeders every variety between that and the light-gray iris was seen. Many had brown eyes irregularly flecked with gray so that a bird's eyes were seldom identical. Evidently the brown pigment is gradually lost with age, and the high proportion of light-eyed birds among the lone breeders suggests that they were old birds. Again, the greenish bills of the colonial birds were closer to those of the juveniles than to those of the solitary pairs. On the other hand, the plumage changes from blackish through brown to grayish surely represent stages to maturity so that we should expect the later-breeding, light-headed birds to be the older. Incidentally, the suggestion of Falla (1937: 138) that these petrels become light headed through the bleaching action of seal blood was not confirmed. Giant Petrel feathers placed in fresh seal blood were not visibly changed after prolonged immersion.

That the solitary pairs retain the tendency to nest alone and in advance of the others is indicated by male 00208, which bred in 1960–1961 in the same area as that in which it was banded as a solitary breeder in 1957. This recovery may be significant in view of the tendency among sea birds for established pairs to nest earlier than inexperienced ones.

Some counts were made of the white-phase adults in the Giant Petrel population. Of 557 birds counted at rookeries, 44 or 8 per cent were white. In November 1952 F. Soucek and M. Taylor noted that 32 (10 per cent) of 305 adults banded were white, and in December 1959 A. M. Gwynn recorded 10 white birds (9 per cent) among 110. Previously Falla (1937: 145) noted 20 white birds (10 per cent) among 200. Downes *et al.* (1959: 77) state that at Heard Island such birds comprise about one-half of 1 per cent of the population but do not indicate how many they counted. Previous estimates of white-phase birds are, for West Antarctica, 5–12.5 per cent, and for South Georgia and the South Orkney Islands, 2 per cent (Murphy, 1936: 588).

Care of the body surface involved preening and bathing, although preening was seldom seen. The uropygial gland was exposed, the bill oiled, and then worked among the feathers. Similarly, the side of the head was rubbed across the nipple of the gland and then rubbed on the feathers of the back and body.

After feeding on a carcass, Giant Petrels removed seal fat and blood by vigorous and protracted bathing in the sea. The wings were opened and the head ducked under so that water sluiced over the back and tail. The coastal fresh-water lagoons were also popular bathing places, as were the ends of Prion Lake, the southern part of Waterfall Lake, and the eastern beach of Major Lake on the plateau. Parties of petrels were very

common too in early spring on the coastal lakes between Mawson and Aurora points and, at all seasons, on the water of Caroline Cove.

The nests of many birds in early October contained contour feathers, and it seemed that a gradual replacement of the body plumage was taking place. From early October to the end of February birds on the wing showed gaps in the inner flight quills. In October and November this condition seemed to be restricted to nonbreeders, but five breeding birds examined on 22 December 1960 had the three innermost primaries freshly replaced but not full grown. They were new, shiny, and gray in color, and the adjacent secondaries were also new. Biermann and Voous (1950: 36) record birds at sea showing the loss of the innermost primaries as early as 28 December, and two collected on 20 January and 11 February showed a heavy molt of primaries, secondaries, and tail feathers and a heavy body molt. "Consequently, the birds have a generally mixed body plumage consisting of old dull brown feathers and newly acquired fresh dark ones." These conditions would also apply to many Macquarie Island birds on those dates.

A nonbreeding adult caught on 28 February 1961 was in almost completely new plumage—a silvery gray bird with only a few scattered brown feathers on the body. The edges of the new feathers were lighter and gave the bird a scaly appearance. The innermost primaries were short and fresh, and those secondaries adjacent to the axillaries had also been renewed. The tail was molting, and the central feathers were short and growing. At this date many of the petrels flying over the island had gaps toward the tips of their wings. Replacement of the flight feathers appears to proceed from the center of the wing outwards.

FOOD AND FEEDING

The food disgorged by the Giant Petrel chicks contained bird intestines, penguin feet, tongues, and feathers, blubber and seal meat, cephalopod beaks and tentacles, and, more rarely, *Euphausia* and amphipods. The legs of Sooty Shearwaters (*Puffinus griseus*) and prions (*Pachyptila* sp.) were also found in the nests. Downes likewise noted this high proportion of sea birds in food remains from Heard Island. The majority of these victims are certainly not caught on land, and it is strange that large and active species like shearwaters and penguins can be captured, the more so as many of the remains are of adult birds.

During the parturition of the Elephant Seals in September Giant Petrels fed on the placentae and on the many dead pups. At all seasons they fed on the carcasses of seals that died on the beaches, a source of food that was probably of great value during the winter months. At this time too rabbits were eaten. Although Giant Petrels occasionally made shallow

swoops toward rabbits, none was known to have killed a healthy animal: those eaten were believed to have been killed by cats.

Whenever these petrels fed on a carcass a form of "peck order" was quickly established with one or more birds dominating the rest until, with partial satiation, others displaced them. The number of "sealmasters" able to find places to feed at one time depended on the size of the body. Many Giant Petrels appeared to fly regular beats, and when one descended to a source of food others seemed to be attracted by its descent and flew down to investigate for themselves. A freshly killed seal was found within an hour, and within three hours 30 birds were present. Another seal from which no blood was flowing was not attacked for 24 hours, which suggests that the sight of blood is important for prompt recognition of a dead seal. Seals that died at the water's edge posed a problem, for the petrels found difficulty in balancing on the carcass as it rolled in the swell.

Feeding birds disturbed by man generally regurgitated as they fled. Dominican Gulls (*Larus dominicanus*) promptly flocked down to gather up the discarded food.

The petrels destroyed many chicks of the Royal Penguin (*Eudyptes chrysolophus schlegeli*) in early February during descent of the latter to the beaches before going to sea. At Lusitania Bay they also killed the young King Penguins (*Aptenodytes patagonica*) in their winter crèches. Awkward though they are on land, the petrels were agile enough to enter a crèche whose birds opened to admit them.

OIL SPITTING

All fulmars eject proventricular oil, which is used to repel aggressors. At Macquarie Island most young and some adult Giant Petrels could throw oil up to two meters—more if the wind was behind them—but many adults could not do so or disgorged only small quantities of oil. Usually, when approached, a breeding bird merely made retching sounds and jerked its head without disgorging; if caught it would then throw up the stomach contents. Some adults disgorged nothing when handled at their nests. Ejection of oil by flying birds as reported for the Atlantic Fulmar was never seen.

Fisher (1952: 393) quotes an instance in which an Atlantic Fulmar chick squirted oil through a hole in its shell, but none of the many newly hatched *Macronectes* handled at Macquarie Island did this. By the end of the guard stage, however, the chicks could spit effectively, and on entering a colony one was greeted by a barrage of oil from the nearby birds, which revolved on their nests to face the intruder. There was, nevertheless, considerable variation in the chick's ability to spit oil. Thus nestling 91, a

male weighed regularly, never did so, nor did at least one of its parents. But female 92 nearby was a persistent spitter. Oil ejection was most marked early in the nonguard stage and gradually declined with age; after 25 February even 92 stopped spitting when inspected. This "drying-up" process occurs in other oil spitters such as the young *Diomedea exulans*, and it is not simply that regularly weighed chicks become conditioned to handling, for young Giant Petrels caught when ready to fly seldom eject oil even if they have never been handled before. Here again there were exceptions, and a few chicks did remain capable of spitting until they flew. Chick 10, a female, squirted oil on 11 February when about 112 days old, although it had not been fed since about 28 January. Such behavior was quite unusual.

No direct information was gathered on the effectiveness of this device as a defense against the only natural predators now active on the island, the skua and other Giant Petrels. A skua walking among chicks was threatened by several of them, which it ignored, but it was impossible to see whether they actually spat at the bird. No Giant Petrel was seen to attack a chick of its own species, but Falla (pers. comm.) has seen a solitary guarded chick on the Auckland Islands ringed by adult Giant Petrels that were intent on its destruction.

SUMMARY

1. In the 1960–1961 season about 3,000 chicks of *Macronectes giganteus* were reared at Macquarie Island (54° S; 159° E), and the population is estimated at less than 9,000 to over 10,000 breeding birds.

2. No birds banded as chicks have yet been found breeding; maturity is probably not reached for at least five years.

3. There are two classes of breeding birds. A small proportion of pairs nests solitarily about six weeks before the main body. The latter breed in 70 colonies.

4. Some birds, believed to be immature, build nests in the autumn but do not lay eggs at that time.

5. The adult breeders apparently do not migrate, since the colonies are occupied almost daily during the winter.

6. The sites of the larger rookeries seem fairly permanent from year to year, and there is evidence that breeding birds remain faithful to their own colony.

7. Display includes several dramatic threat postures, more restrained courtship behavior, bill stopping during coition, and an aerial display the significance of which is not clear.

8. Both sexes incubate alternately, the males taking the first shift. Total period is 58–61 days.

9. Both sexes feed the chick, which is left unguarded at 15–24 days, reaches adult weight at 50 days, and flies at 102–117 days.

10. About 0.1–0.2 per cent of nests held two eggs or two chicks, probably the product of one female. No pair fledged two chicks.

11. Variations in the plumage and in the colors of the soft parts are described. Evidence is presented that the solitary breeders are very old birds.

12. Chicks are fed largely on sea birds. A form of social hierarchy exists among members of groups at a food source.

13. Oil spitting is well developed in the chick after it is no longer guarded. Some chicks and many adults are unable to spit, and there is a decline in the chick's ability as it feathers.

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