Procellariiforms are seabirds with life histories characterised by a long lifespan, deferred sexual maturity, a single egg clutch and low annual reproductive output (Hamer et al. 2002). Such long-lived species will invest more in longevity than in fecundity, according to life-history theory (Stearns 1992, Weimerskirch 1999). Thus, in poor breeding conditions, procellariiforms are expected to give up their breeding effort to increase their lifetime reproductive success (Ollason & Dunnet 1988, Wooller et al. 1989, Erikstad et al. 1998). For example, it has been shown that several species will abandon their egg when body reserves are reduced to critical levels (Chaurand & Weimerskirch 1994, Tveraa et al. 1997, Weimerskirch 1999).

The Southern Giant Petrel *Macronectes giganteus* is a large procellariiform seabird that breeds on sub-Antarctic islands, on the Antarctic peninsula and at only a few localities on the Antarctic continent (Marchant & Higgins 1990). The species is surface nesting and lays a single egg annually. Completion of the breeding cycle takes about 180 days, which constrains the birds to start breeding early in the summer season. On the Antarctic continent egg laying starts in the second half of October (Mougin 1968, Johnstone et al. 1973), at a time when weather conditions may still be very unfavourable. We report the recovery of three banded adult Southern Giant Petrels on their breeding grounds in the Antarctic that died while incubating their eggs.

Three banded Southern Giant Petrels were found dead on Dewart Island (66°23′S, 110°17′E), one of the three Frazier Islands, approximately 16 km WNW of the Australian Antarctic base Casey. All recovered individuals were found in different areas on the island away from the large colonies, with no nests in close neighbourhood.

One individual was found on 8 February 1994; this bird had been banded as an adult on the same island 16 years earlier (Table 1). A slightly damaged egg was found frozen to the belly

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<tr>
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<tr>
<td>Age, sex, status</td>
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<td>Head length (mm)</td>
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<td>Tarsus length (mm)</td>
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<tr>
<td>Wing length (Imn)</td>
<td>517&lt;sup&gt;d&lt;/sup&gt;</td>
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<td>Body mass (g)</td>
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<sup>a</sup>Measurements were taken according to van Franeker & ter Braak (1993).
<sup>b</sup>Sex derived from skull measurements (see Marchant & Higgins 1990).
<sup>c</sup>Only head of bird had been taken and measured afterwards; head length measured from bare skull.
<sup>d</sup>Both birds showed no moult of primaries.
of the bird. The bird was well preserved and its skin and plumage were intact; no apparent cause of death was visible. Body measurements were not taken in the field, but morphometric measurements afterwards (Table 1) suggest that this bird was a female (Marchant & Higgins 1990).

Two individuals were found on 26 December 1998. No other dead birds were found on the Frazier Islands that day. These two specimens were collected and stored frozen until dissection. Each bird had its egg still properly positioned in the brood- patch, enclosed by belly feathers (Fig. 1).

One individual had been banded as a nestling on Dewart Island almost 21 years earlier (Table 1). Dissection revealed the individual to be a female, with evidence of recent laying of an egg (large ruptured follicle and a strongly enlarged oviduct). The other recovery had been banded as a chick on Ile des Pétrès (66°40′ S, 140°02′ E), Pointe Géologie Archipelago, Adélie Land. It was thus recovered about 1400 km from its natal colony at an age of almost 13 years. This bird was a male, with enlarged testes (c. 10 × 18 mm) indicating death during the early breeding phase.

Both birds found on 26 December 1998 had totally depleted their fat reserves (no subcutaneous or intestinal fat deposits remaining) and had additionally exhausted their protein reserves, as evidenced by emaciated breast muscles. Stomachs contained no fresh food, but hard prey remains such as squid beaks, penguin feathers and seal hair were present in both. Furthermore, the French-banded male had remains of what was probably a large crustacean in its stomach. Internally, both corpses were fairly fresh and showed little signs of decay. Externally, they had suffered some desiccation of the skin, especially on the head and back. The eggs showed cracks and were decaying, but showed no signs of chick development (Fig. 2).

Southern Giant Petrel colonies along the Antarctic coast, such as on the Frazier Islands, represent the most southerly limits of the breeding range of this species. In these peripheral colonies, individuals face additional constraints during the breeding cycle, because the weather and sea-ice conditions are more extreme and fluctuate more strongly than on sub-Antarctic islands where most Southern Giant Petrels breed. This might be the reason why natural mortality of adult Southern Giant Petrels on their breeding grounds is reported only at Pointe Géologie, Adélie Land (Prévost 1953, Mougin 1975) and the Frazier Islands (this study). We suggest that on the Frazier Islands a blizzard had trapped the recovered birds in heavy snow.

Each year during October and November, snow or blizzard conditions regularly occur for one to two days in the area around Casey, but prolonged periods of such conditions are then relatively rare. In 13 seasons (1989–2001) during October and November, we found only five periods of three days with moderate to heavy snowfall or blowing snow, and another five periods longer than three days. The period of snow conditions on 23–30 October 1993 stood out for its long duration and severity. This may have contributed to the mortality of the bird found in February 1994. In spring 1998, however, there were no snow periods longer than two days, and the number of snow days as well as the amount of snow fallen was around average values. Interpretation of correlations between mortality and weather parameters is difficult. For example, timing of extensive snowfall (at beginning or end of the incubation shift, which lasts on average four to six days; Marchant & Higgins 1990), wind conditions at the colonies (amount of snow blown to or away from the nests) and bad weather conditions at sea (where the partner is foraging) might be more important.

The smaller Antarctic surface-nesting fulmarine procellariiforms, such as Southern Fulmars Fulmarus glacialoides and Antarctic Petrels Thalassoica antarctica, regularly allow themselves to be buried under sometimes thick layers of snow during incubation. This appears to have no effect on survival or reproduction because wind and melt usually limit the duration of such snow coverage (Mougin 1968, J.C.S. Creuwels & J.A. van Franeker unpubl. data). Northern Giant Petrels Macronectes halli on Bird Island, South Georgia, breed five to six weeks before Southern Giant Petrels (Hunter 1984), when late snowfalls regularly occur. In several seasons they were seen with their heads poking out of the snow or even completely buried under snow, but in none of these cases have any incubating birds died (A.G. Wood pers. comm.). During blizzards at Pointe Géologie, ice formed temporarily around the heads of Southern Giant Petrels that protruded from the snow cover.

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**Fig. 1.** Corpse of the French-banded Southern Giant Petrel (Paris CF8226) before dissection. The egg is still positioned in the brood patch between the belly feathers. (Photo: J.A. van Franeker)

**Fig. 2.** Damaged and decaying egg of the French-banded Southern Giant Petrel. (Photo: J.A. van Franeker)
(Prévost 1953), but if this affected survival is not known. In the Palmer Archipelago on the Antarctic peninsula, Southern Giant Petrels also experience heavy snowstorm conditions in spring, but with no fatal consequences for the incubating birds having been reported (Parmelee 1992).

A long-lived species such as the Southern Giant Petrel is expected to maximise breeding efforts only in good conditions. The adult annual survival is high (90%–96%; Mougin 1975, Hunter 1984) and even a slight reduction in survival rate would greatly affect their lifetime reproductive output (Erikstad et al. 1998). In poor weather conditions, such as heavy storms and snowfalls, giant petrels are known to leave their nests, which in most cases resulted in breeding failures (Hunter 1984, A.G. Wood pers. comm.). In the Palmer Archipelago, a blizzard on 20–21 November 1975 caused c. 30% breeding failure in Southern Giant Petrels due to abandonment of their nests (Parmelee 1992).

The age of the recovered birds suggests they were not first-year breeders, which makes inexperience unlikely as the cause of their mortality. Furthermore, no evidence was found that the recovered birds stayed on the nest because of impairment by injury, poisoning or disease. For example, in a relatively small (44 active nests) Southern Giant Petrel colony, Prévost (1953) observed five incidents of broken wings during one season, which are fatal injuries for these birds.

Starvation was probably the ultimate cause of death in the two recoveries of the 1998 season, which was also apparent in their extremely low body masses (Table 1). The average body mass for males is around 4.9–5.1 kg and for females around 3.9–4.2 kg (Marchant & Higgins 1990). Females especially need to be in good breeding condition to be able to lay an egg and start incubation, and thus their body mass is expected to be relatively high. The mass loss may be exaggerated by some dehydration during storage, but is unlikely to have caused the total mass loss of the recovered birds.

Desiccation of the skin of all three recoveries suggests that the dry cold air and windy conditions might have quickly ‘freeze dried’ the birds. When examined in The Netherlands, the birds may have suffered from further desiccation because of the long freezer storage. The skin could have further dried out and a few small cracks of the skin at head and back could have occurred. The relatively fresh condition of these two corpses, as well as the corpse found in 1994, suggests that the birds died shortly before recovery. Developmental stages of sexual organs and eggs point to death at a moment soon after egg laying, sometime in late October or early November.

Why the two Southern Giant Petrels continued incubating until reaching a lethal starvation level remains uncertain. Snow and ice cover may possibly have prevented them from leaving their nests. Also, the upper snow layer might have been iced because of increasing temperatures. In such conditions, poor air circulation could have induced some lethargy in the birds incubating under snow. Another snow-buried Southern Giant Petrel was found dead on Pointe Géologie, Adélie Land, after bad weather in the winter of 1963 (Mougin 1968). This bird could not have been incubating, and unfortunately no further details of this recovery are given.

Snow-related mortality accords with the observation that precipitation in the Casey area has strongly increased over the past decades, particularly during the late winter and spring periods (van Franeker et al. 2001). This may bring Antarctic fulmarine petrels in this area, such as Southern Giant Petrels on the Frazier Islands, into situations hitherto not experienced during incubation.

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REFERENCES


