

**BREEDING ECOLOGY OF
ANTARCTIC PETRELS AND SOUTHERN FULMARS
IN COASTAL ANTARCTICA**

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**BREEDING ECOLOGY OF
ANTARCTIC PETRELS AND SOUTHERN FULMARS
IN COASTAL ANTARCTICA**

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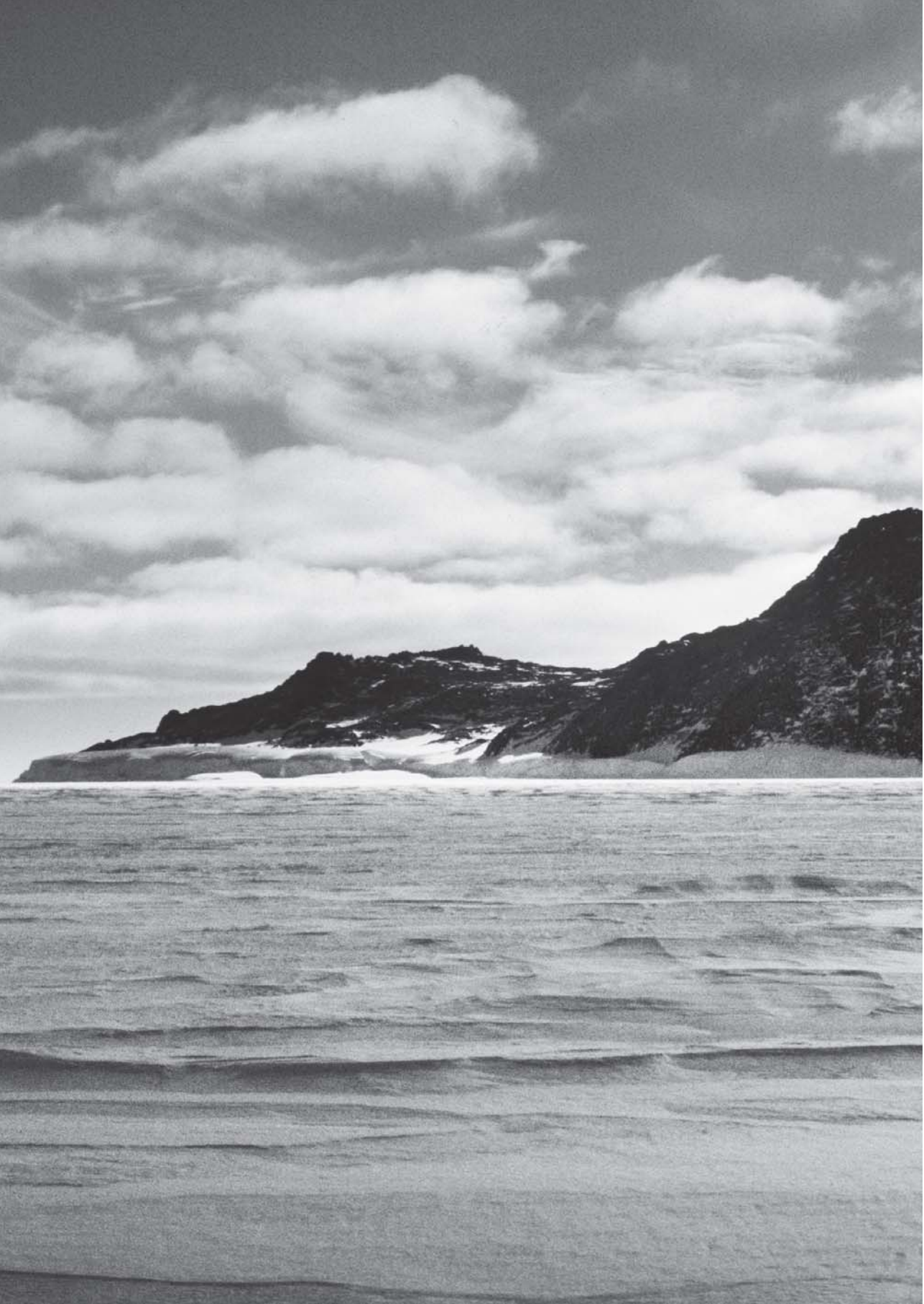
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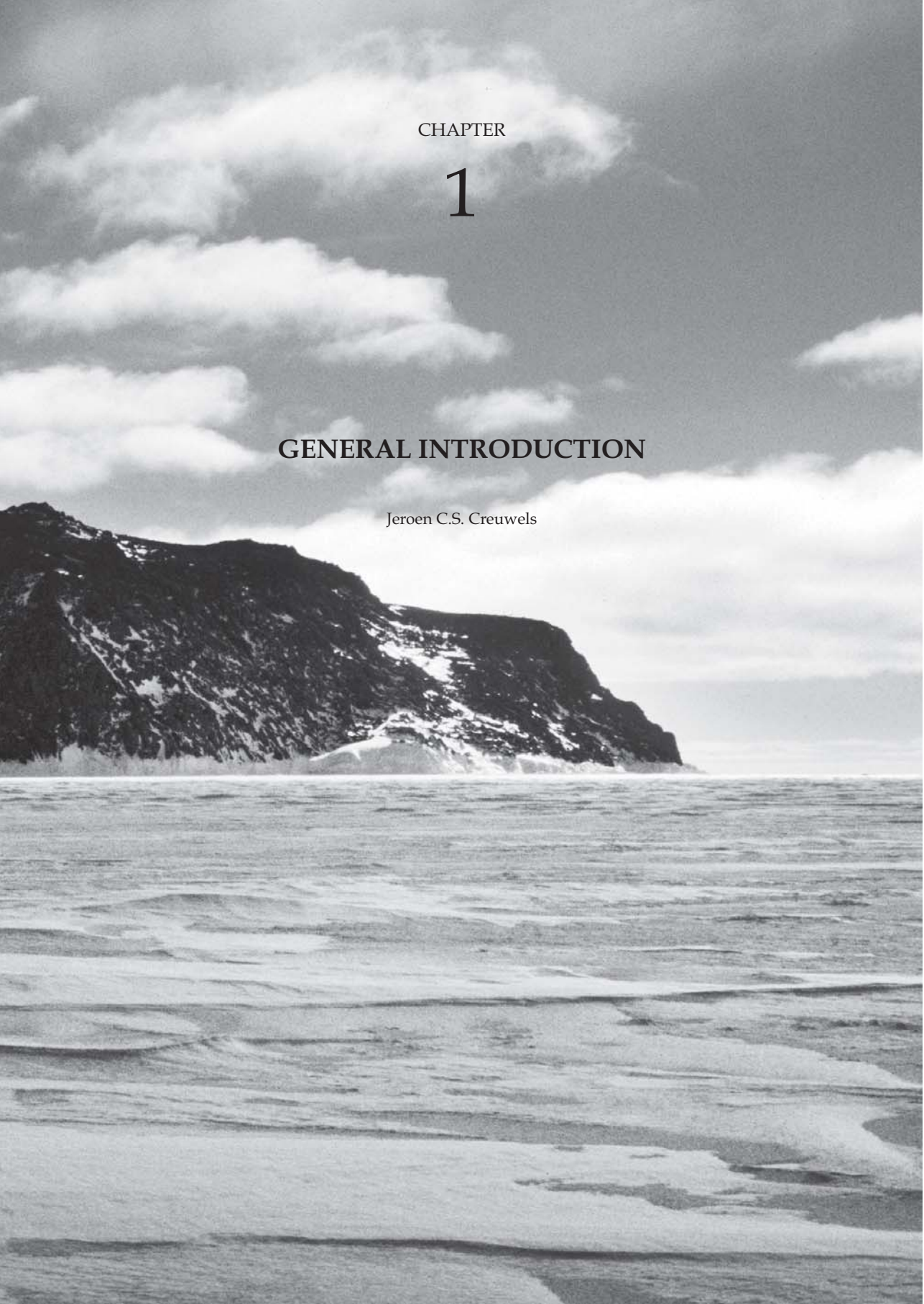


CHAPTER

1

GENERAL INTRODUCTION

Jeroen C.S. Creuwels



ANTARCTICA AND ITS INHABITANTS

The vast ice-covered continent of Antarctica is extremely inhospitable to most plant and animal species. The 2% of its land area that is ice-free is home to a limited number of lichens, mosses, algae and only a few highly specialized invertebrates. The conditions on this driest, coolest and windiest continent are so harsh that even in summer terrestrial life is hardly possible. Thus, almost all Antarctic wildlife is found where the “white desert” meets the surrounding Southern Ocean. In this boundary zone climatic conditions are less severe and food sources are available in the adjacent sea water.

Large parts of the Southern Ocean close to the Antarctic continent are frozen, but the extent of the sea ice fluctuates heavily during the year. In wintertime the ice edges advance northwards and sea-ice cover increases fivefold, effectively doubling the area of Antarctic ice.

The seasonal pack-ice zone around Antarctica sustains a highly productive food web, starting with a rich and abundant phytoplankton community which is grazed by large numbers of zooplankton such as copepods and krill. This zooplankton attracts a variety of species of higher trophic level such as fish, birds, seals, and whales. Birds and seals need a substrate for breeding, which several seal species and the Emperor Penguin *Aptenodytes forsteri* find on the sea-ice itself. Flying seabirds and other penguins, however, need ice-free localities along the continental coast and on small offshore islands to rear their young.

Penguins are typical inhabitants of the sea-ice habitat, but they are outnumbered by flying seabirds (Croxall 1984, Knox 2007). The latter play an important part in the Antarctic ecosystem and account for 20-40% of prey consumption by the seabird community in the Southern Ocean (Van Franeker *et al.* 1997). Among the flying seabirds the Procellariiformes dominate the community. Within these, the fulmarine petrels can be considered as true specialists of the polar region, being the only group of tubenoses with members breeding beyond 80° latitude in both hemispheres (Van Franeker 2001).

FULMARINE PETRELS

The family of petrels (Procellariidae), together with albatrosses (Diomedidae), storm petrels (Hydrobatidae) and diving petrels (Pelecanoididae) form the order of petrels (Procellariiformes). This order of seabirds can be identified by one single morphological feature; all species have horny tubes on their bill covering the nostrils (Warham 1990). Albatrosses have two tubes, but in the other three families the tubes are merged to one. This is why all Procellariiformes are also called tube-nosed seabirds, or in

earlier times Tubinares. All species have a pelagic lifestyle, and consequently spend a large proportion of their lifetime at open sea. All species lay a clutch of only one egg.

The group of fulmarine petrels (Fulmarinae) consists of seven species, of which six breed in Antarctic and sub-Antarctic areas. Although species of this group do not have unique morphological or anatomical features, and vary considerably in body size and plumage, recent genetic research confirmed that they should be considered as a distinct clade within the Procellariidae (Nunn & Stanley 1998, Penhallurick & Wink 2004). The six southern hemisphere fulmarine petrels are: Southern Fulmar (*Fulmarus glacialoides*), Antarctic Petrel (*Thalassoica antarctica*), Cape Petrel (*Daption capensis*), Snow Petrel (*Pagodroma nivea*), Southern Giant Petrel (*Macronectes giganteus*) and Northern Giant Petrel (*Macronectes halli*). It should be noted that the taxonomic status of the latter two is not fully clear, despite their difference in appearance and ecology. Interbreeding does occur between the *Macronectes* spp. and mitochondrial DNA sequencing suggests the status of subspecies (Penhallurick & Wink 2004). The seventh species is the Northern Fulmar (*Fulmarus glacialis*), a sibling species of the Southern Fulmar and the only one living on the northern hemisphere. Probably part of the *Fulmarus glacialoides* population crossed the equator during Pleistocene glaciations evolving into *F. glacialis* (Voous 1949).

Antarctic fulmarine petrel species differ in their pelagic distribution, probably not so much by differences in diet preferences but rather by differences in foraging techniques that are partly determined by physical properties of the habitat. For example, Antarctic and Snow Petrel exploit sea-ice edges by 'pursuit plunging' to catch their prey; they are relatively scarce when ice-edge habitat is absent (Ainley *et al.* 1984). It has been suggested that various seabird communities exist and that the sea-ice edge forms the demarcation between a pack-ice and an open-water community (Fraser & Ainley 1986). This view has been further elaborated, and many communities have been distinguished, differing in species composition, and depending on season, sea-ice conditions or geographic location (Ainley *et al.* 1992, 1993, 1994). It is in any case clear that some species are more attracted to a sea-ice habitat, while others prefer larger stretches of open water. For example, Antarctic Petrels and Snow Petrels are among the most pagophilic species, and also have the most continental breeding distributions. Some colonies are found up to a few 100s of km inland Antarctica (Croxall *et al.* 1995, Van Franeker *et al.* 1999, Goldsworthy & Thomson 2000). On the other hand, Southern Fulmars and Cape Petrels are more observed in open waters and breed mostly in the vicinity of polynyas or other areas where open water is guaranteed.

BACKGROUND OF THIS STUDY: THE CCAMLR ECOSYSTEM MONITORING PROGRAM

The Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) came into force in 1982, as part of the Antarctic Treaty System (<http://www.ccamlr.org>). It was established mainly in response to concerns that an increase in krill catches in the Southern Ocean could have a serious effect on krill populations and therefore on other marine life forms; particularly birds, seals and fish, which mainly depend on krill for food. The aim of the Convention is to conserve marine life of the Southern Ocean. However this does not exclude harvesting carried out in a rational manner. Achievement of this aim is not simple – it requires the collection of large quantities of information and the development of appropriate scientific and analytical techniques. A ‘precautionary’ approach has been implemented to minimize the risk associated with unsustainable practices in uncertain conditions. This approach is complemented by the need to take into account ecological links between species and ‘natural’ as opposed to ‘human-induced’ variability – the ‘ecosystem approach’. Finally, conservation measures adopted by CCAMLR are based on scientific advice, and require enforcement to be effective.

One of the tools adopted by the Commission of the Convention is its monitoring program. This CCAMLR Ecosystem Monitoring Program (CEMP) has been implemented in 1987 in order to collect data on both the harvestable resources and the dependent predator species. The program is especially elaborate and well established for penguin species and Antarctic fur seals on various monitoring sites. Among flying seabird species, the Antarctic Petrel, Cape Petrel and Black-browed Albatross *Diomedea melanophrys* have been designated as indicator species within CEMP. Parameters proposed for CEMP monitoring of seabirds include the size of breeding population, as well as breeding success, survival and recruitment, and chick diet (CCAMLR 2004). As a part of a broader study on the ecology of Antarctic fulmarine petrels, a research program on Ardery Island was established in 1984 by a predecessor of the Netherlands Institute for Marine Resources and Ecosystem Studies (IMARES) in cooperation with and supported by the Australian Antarctic Division. Much of the research program was set up to develop appropriate methods and collect data of direct use to the purposes of CCAMLR in CEMP (Mehlum & Van Franeker 1995, CCAMLR 2004).

For a more complete picture of the Antarctic ecosystem, knowledge is also needed on other key species, starting with basic population estimates and the distribution of their breeding colonies. The earlier Group of Experts on Birds of the Scientific Committee on Antarctic Research (SCAR-GEB; currently merged into the

SCAR Expert Group of Birds and Marine Mammals SCAR-EGBAMM), has taken the task to publish comprehensive reviews on the distribution and abundance of all Antarctic seabirds. For the fulmarine petrels this series started with reviews for Snow Petrels (Croxall *et al.* 1995) and Antarctic Petrels (Van Franeker *et al.* 1999), more recently followed by those for Southern Fulmars (Creuwels *et al.* 2007), both giant petrel species (Patterson *et al.* 2008) and Cape Petrels (Hodum *et al.* in prep).

The CEMP and SCAR settings of the Australian-Dutch fulmarine petrel research on Ardery Island (Van Franeker 2001) form the general background and framework of issues addressed in this thesis.

STUDY SPECIES

This study focussed on the breeding ecology of the two species of Antarctic fulmarine petrels that are most similar in body size, nesting habits, and diet preferences: Antarctic Petrel and Southern Fulmar. Both species breed sympatrically on various locations on the coast of Antarctica and are, in comparison to the other small fulmarines that also breed on Ardery Island, relatively indifferent to human disturbance (Pryor 1968, Cowan 1979). Their high tolerance to research activities in the colony made them suitable study species.

Antarctic Petrel *Thalassoica antarctica*

The Antarctic petrel is a medium-sized petrel with a dark brown and white plumage (Fig. 1). The dark brown parts may fade during the season to very pale brown. Head, neck and back are chocolate brown. Bill is very dark to black. The upperwing is dark brown with a large white bar over the secondary and first primary feathers, which is visible in flight. Underwing and belly are largely white. Sexes are alike, although males are slightly larger. The weight of adult birds fluctuates but is generally around 650-700g (Marchant & Higgins 1990, Hodum 2002).

Antarctic Petrels occur all around Antarctica and have breeding colonies between 65° and 80°S. The majority of the birds breeds in inland Antarctica where they occur in colonies on cliffs or nunataks or other ice-free areas. Antarctic Petrels are generally associated with pack ice year-round: in summer normally south of 62°S and in wintertime they might be seen up to 48°S. They are often seen roosting on, and foraging close to, icebergs and ice floes. After their winter absence, the first adults



Figure 1. Antarctic Petrel of nest T040 with is chick.

arrive in the colony begin October, and are soon followed by many others. Their breeding biology is more synchronous than that of Southern Fulmars. The birds stay in the colony until begin November when all depart for a pre-laying exodus, leaving the colony totally deserted for about three weeks until their return and start of egg laying in late November (Luders 1977, Murray & Luders 1990). First hatchlings appear in the second week of January, and fledging commences in late February, lasting until the first week of March (Van Franeker *et al.* 1999).

Southern Fulmar *Fulmarus glacialoides*

The Southern Fulmar is a medium-sized petrel with a gull-like appearance (Fig. 2). The head is white to light grey with large dark eyes. The relatively large bill is flesh-pink coloured with bluish nostrils and a dark tip. Neck, back and tail are pale grey. Upperwing is blue-grey with white flashes on coverts and inner primaries and with black trailing edge and outerwing. Underparts are predominantly white. Female and male have similar plumage, but males are larger. Adult mass fluctuates over the



Figure 2. Southern Fulmar with its chick.

season, and is generally around 800-900g (Marchant & Higgins 1990, Hodum 2002).

Southern Fulmars have a circumpolar range and are found in Antarctic and sub-Antarctic seas. In summer, they prefer cold waters south of the Antarctic Convergence close to the Antarctic continent, but in winter they have a broader distribution including warmer waters north of this zone up to 40°S. Colonies are located on cliffs and steep slopes, often facing north to catch as much sunlight as possible. The nest is usually not more than a simple scrape on the ground that is sometimes lined with some small rock material or feathers.

Towards the end of winter they return to their colonies, and the first individuals in East Antarctic colonies arrive during the first half of October (Falla 1937, Prévost 1953, Mougin 1967, Pryor 1968, Luders 1977). Like other fulmarines, both parents leave the colony during November and into the first week of December for a pre-laying exodus. Breeding events in the colony are highly synchronous. Egg-laying occurs in December, with most eggs being laid in the second week of December. Hatching commences in the third week of January and chicks fledge by mid-March.

AIMS OF THIS STUDY

This study aimed to describe and to quantify parameters of the breeding biology of Antarctic Petrels in order to develop a more complete and detailed monitoring program for this species. The Antarctic Petrel has been chosen as an indicator species for the condition of the Southern Ocean ecosystem within the CCAMLR monitoring program, although this species could be considered as somewhat peculiar in some aspects. For example, it has the southernmost breeding distribution of any seabird and thus has to fly long distances between the breeding and feeding grounds. Especially in spring, these distances could be large when there is still much sea-ice cover present. This species may therefore have adapted a unique foraging strategy, which could differ from other species.

Therefore, it was decided that a comparison of these parameters with a similar species would be useful to see how representative these parameters are for flying seabirds in Antarctica. In general, fulmarine petrels have a contracted breeding cycle in comparison to other similar-sized procellariiformes, which allow these species to fit their breeding activities within the narrow time window available for breeding at high latitudes (Warham 1990). If such a narrow time window exists, then events especially in the early and late phase of the season are expected to influence breeding success. On Ardery Island four petrel species breed sympatrically. Of these, Antarctic Petrels and Southern Fulmars have the largest body size and longest breeding cycle. These species are also the first, respectively, the last species that start breeding on Ardery Island. This made the Southern Fulmar an interesting study species for a comparison with the Antarctic Petrel.

Another aim of this study was to find an explanation for the decreasing breeding success of Antarctic Petrels on Ardery Island, and to investigate whether this was a general phenomenon in other petrel species in the area. During the first three study seasons on Ardery Island (1984-85, 1986-87 and 1990-91), the number of successful nests of Antarctic Petrels in the Northern Plateau study colony showed a sharp decline (Fig. 3). The reasons for the decline of the number of successful nests of Antarctic Petrels were not evident. The proportion of breeding individuals within the population may have declined, but also egg losses early in the season might have increased. It is known that many breeding failures occur just after egg-laying (Dunnet *et al.* 1963, Mougin 1975). The graph showed that during these three seasons, already in the late egg phase, large differences existed in the number of successful breeding attempts. Chick mortality of Antarctic Petrels appeared to be low in the second half of the chick period (from early February onwards).

Without more detailed information on the beginning of the breeding season

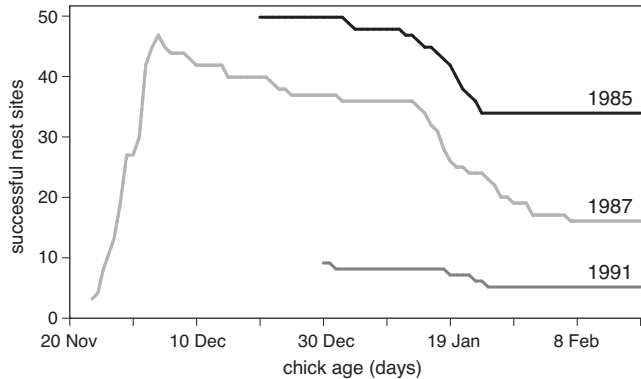


Figure 3. Breeding success of Antarctic Petrel on Ardery Island in the field seasons 1984-85, 1986-87, 1990-91. Number of successful nest sites in the colony increased early in the season by egg laying, and decreased by losses of eggs and younger chicks; in February very little chick mortality occurred in all three seasons.

we could only speculate on the potential causes for the declining breeding success. Poor feeding conditions prior to, or early in the breeding season were considered to be a serious possibility. Because Procellariiformes generally have to fly long distances to find food, the feeding conditions in their foraging grounds are crucial for successful breeding. To investigate how Antarctic Petrels and Southern Fulmars were affected by environmental conditions and food availability, an automatic system was installed in order to record the presence and absence of each individual bird and to monitor its weight and foraging success throughout the breeding cycle (Creuwels *et al.* 2000).

STUDY SITE

Description of Ardery Island

Ardery Island (66°22'S, 110°28'E) is part of the Windmill Islands group in the east of Vincennes Bay, Wilkes Land, Antarctica. The Windmill Islands are a group of rocky islands along the coast of Budd Land, where the Australian Antarctic station Casey is located (Fig. 4). Ardery Island is situated approximately 11 km south of Casey. It is about 1 km long and 0.5 km wide and has an east-west orientation. There are vertical cliffs that are heavily fractured, steep boulder slopes and ravines providing both

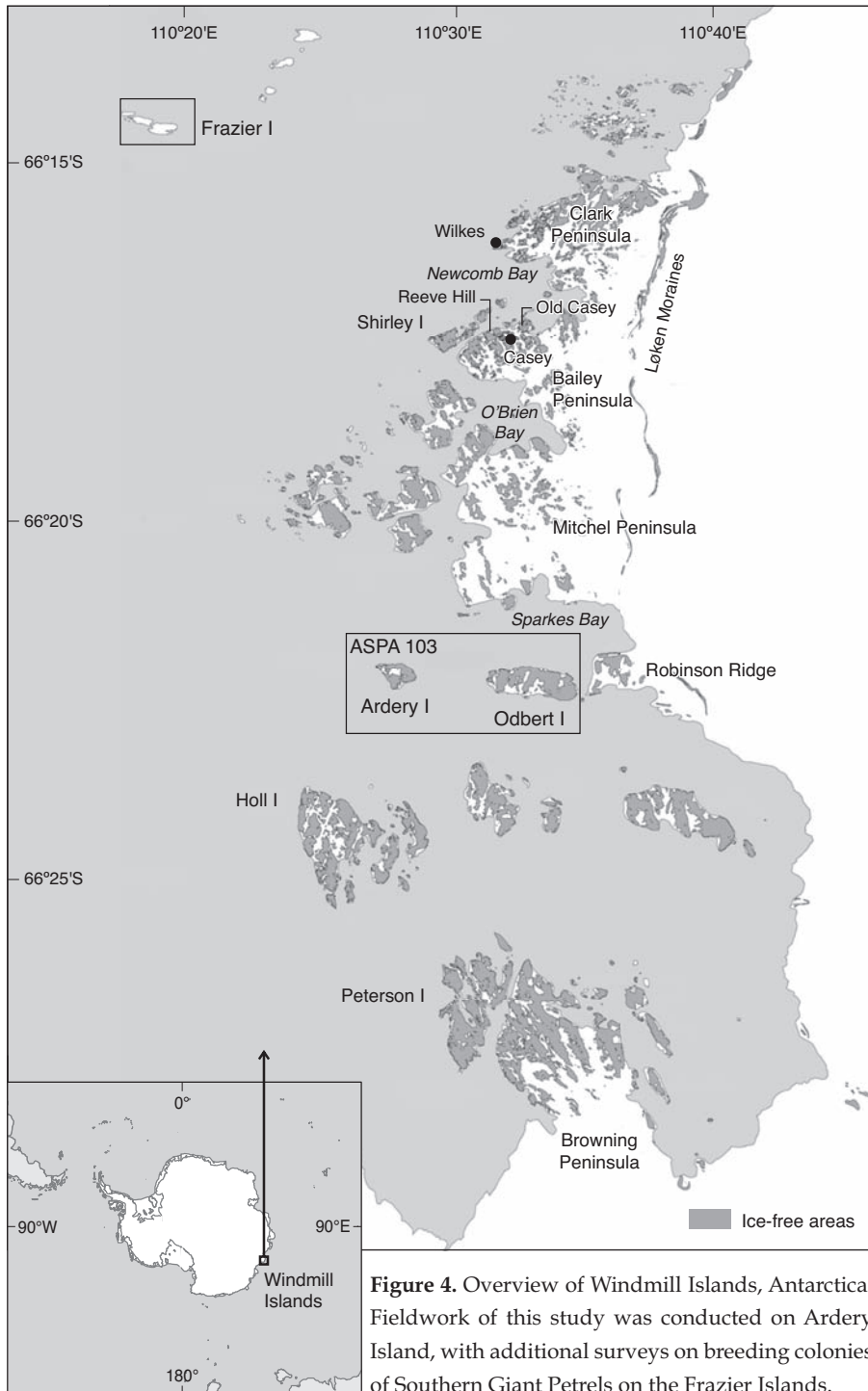


Figure 4. Overview of Windmill Islands, Antarctica. Fieldwork of this study was conducted on Ardery Island, with additional surveys on breeding colonies of Southern Giant Petrels on the Frazier Islands.

narrow exposed ledges and deep burrows which in summer are occupied by nesting seabirds. The highest point is 113 m above mean sea level and the terrain on the island is rugged and dissected by fissures. On the hillsides and plateau region, the exposed rock is ice-smoothed and the valley floors are covered with moraine. During the season there is a variable amount of snow cover on the flat and less steep areas of the island, which varies between and within seasons. The beginnings of the breeding seasons 1996-97 and 1997-98 were characterised by unusual high snow cover, although during December much snow was disappearing. On the plateau there is one main tarn which is frozen in winter and filled with melt water throughout the summer. The field camp of 1996-1999 was located on the plateau close to this tarn.

The climate of the Windmill Islands region is frigid-Antarctic. Meteorological data at Casey station (altitude 32 m) on Bailey Peninsula are collected by the Bureau of Meteorology of the Australian Government. Data for the period 1989-2010 show mean daily maximum temperatures for the warmest and coldest months of 2.2 and -11.1°C, respectively, with extreme temperatures ranging from 9.2 to -38°C. May –August are the coldest months with mean daily maximum temperatures of -10 / -11°C and mean daily minimum temperatures of -18°C.

The climate is dry with a mean annual snowfall of 222 mm per year (rainfall equivalent). Snowfall has been increasing in the last decades and precipitation as rain has now been recorded in the summer. There is an annual average of 96 days with gale-force winds (>62 km per hour or Beaufort scale 8), predominantly easterly in direction, coming from the polar ice cap. Blizzards are frequent especially during winter. In summertime most days are relatively calm, except during periods with katabatic winds, which often start with little warning and can last for several days.

Snowfall is common during the winter, but the extremely strong winds scour the exposed areas. On most hill crests in the area snow gathers in the lee of rock outcrops and in depressions on the ground. On Ardery Island, especially on the western side of the island, snow forms deeper drifts further down the slopes. Some sea ice is present in Vincennes Bay year-round, but only to a limited extent during summer. From late autumn to early spring, waters around Ardery Island are often fully covered with sea-ice. This sea-ice is unstable because each blizzard blows most of the sea-ice out to the west, creating open waters. More stable sea-ice lasts into spring only in Sparkes Bay, between the neighbouring Odbert Island and the continental shore.

Seabird fauna of Ardery Island

On Ardery Island four species of fulmarine petrels breed sympatrically. Southern Fulmars, Antarctic Petrels, Cape Petrels and Snow Petrels breed here in relatively high numbers (Van Franeker *et al.* 1990, Barbraud & Baker 1998). Antarctic Petrels

were found in two colonies on Ardery Island where in total about 275 'apparently occupied nest sites' were counted (Van Franeker *et al.* 1990, Barbraud & Baker 1998, Fig. 5A). The largest colony, on Northern Plateau, contains about 150 sites in the main area with 25 sites scattered in smaller groups around. Antarctic Petrels breed with their nests packed very close together on relatively flat or gently sloping sections of otherwise steep cliffs. They avoid isolated nesting on small ledges and do not mix with Southern Fulmars although boundaries of colonies of both species might adjoin each other. In the Windmill Islands area around Casey station, Antarctic Petrels breed only on Ardery Island, Odber Island and Nelly Island (Frazier Islands) (Van Franeker *et al.* 1999).

It is estimated that there are approximately 3000-3900 'apparently occupied nest sites' of Southern Fulmars on Ardery Island (Van Franeker *et al.* 1990, Barbraud & Baker 1998). The largest colonies are located on the northern cliffs and around the eastern tip of the island (Fig. 5B). Nests were situated on small cliff ledges but also on large nearly flat terraces or shallow slopes, with most birds nesting on open sites on the ground, between loose rocks and sometimes in broad crevices. The breeding localities for Southern Fulmars in the Windmill Islands are restricted to Ardery Island and Odber Island, Nelly Island and Dewart Island (both Frazier Islands) and Holl Island (Chapter 7).

For other species it was estimated that there were around 600 'apparently occupied nest sites' of Cape Petrels and 800-1000 'apparently occupied nest sites' of Snow Petrels (Van Franeker *et al.* 1990, Barbraud & Baker 1998, Fig 5C, D). Ardery Island is the only known area in Antarctica that harbours separate colonies of two different subspecies or distinct size morphs of snow petrels (Cowan 1981, Croxall *et al.* 1995, Van Franeker *et al.* 1990, Van Franeker 2001). The fifth member of the group of the fulmarines regularly observed on the island is the Southern Giant Petrel. It is a regular visitor often seen roosting on flat areas and snow fields near main concentrations of breeding petrels. It breeds on the Frazier Islands approximately 21 km NW of Ardery Island (Fig. 4).

Other bird species breeding on Ardery Island are Wilson's Storm Petrel (*Oceanites oceanicus*) and South Polar Skua (*Catharacta maccormicki*). Wilson's Storm Petrels breed well hidden in deep burrows, especially along the northern coast of the island. These burrows are very hard to locate, thus the estimated 1000 breeding pairs is very approximate. Nests may be betrayed by the appearance and disappearance of provisioning parents or by presence of nearly full-grown chicks in front of their burrows late in the season. South Polar Skuas are breeding in 10-20 territories scattered around the island, often including (parts of) petrel colonies (Fig. 5A-D). The tarn close to our field camp was regularly used for bathing by a group of South Polar Skuas, probably mostly by individuals that were not holding a territory on the island. Small

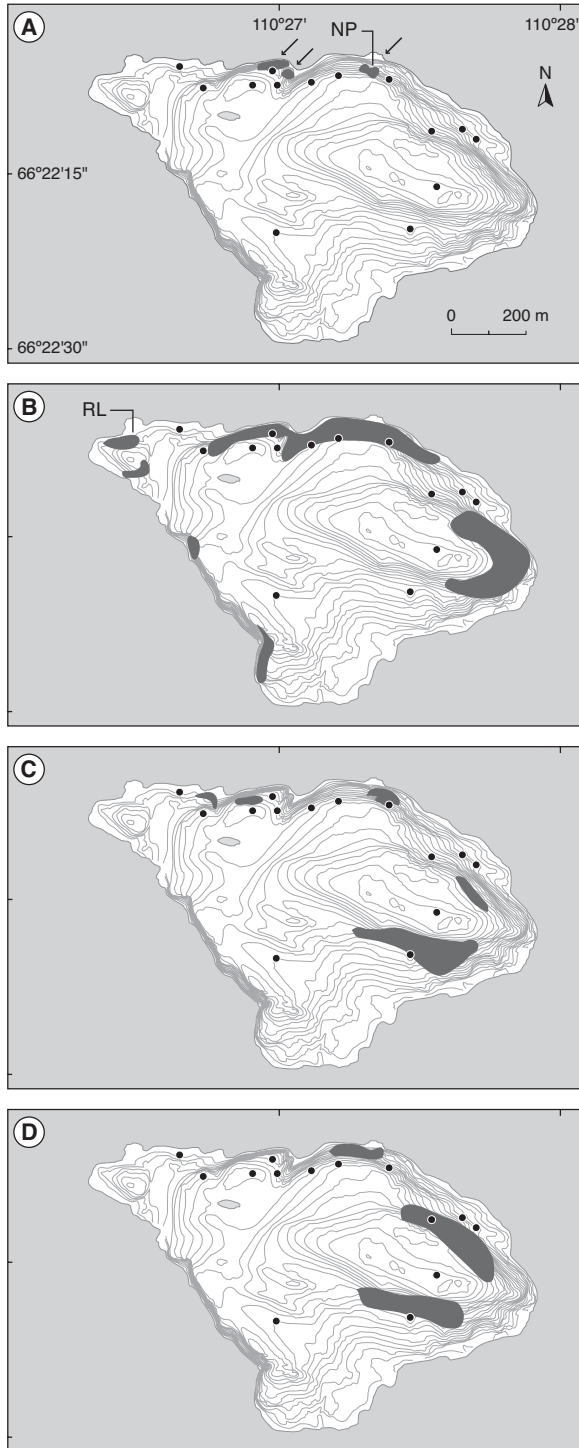


Figure 5. Distribution of the breeding colonies of seabirds on Ardery Island. Location of breeding areas are given for A) Antarctic Petrels, B) Southern Fulmars, C) Cape Petrels and D) Snow Petrels. Black dots in each figure indicate locations of South Polar Skua nests. NP = Northern Plateau study site and RL = Robertson Landing study site

numbers of Adélie penguins *Pygoscelis adeliae* can be found moulting on the island later in the season.

Because of its diverse and abundant avian wildlife, Ardery Island with nearby Odbert Island (66°22'S, 110°33'E) has been designated as Antarctic Specially Protected Area (ASP) No. 103 under the Madrid Protocol. Entrance to these islands is only allowed for scientific purposes and all scientific activities should be in accordance with the management plan for the Area. For example, no helicopter flights are allowed during the sensitive parts of the breeding season. Transport of goods and people during the season occurred mostly by zodiac boats and occasionally, when sea-ice was of sufficient thickness and the weather forecast was good, by skies and sledges.

Study colonies on Ardery Island

In the 1980s, Van Franeker had set up study plots and reference areas for all fulmarine petrels on Ardery Island (Van Franeker 2001). The research on Antarctic Petrels and Southern Fulmars was concentrated in two study areas.

Antarctic Petrels were studied in the Northern Plateau colony. This is situated on a small moderately sloping terrace with boulders halfway the otherwise steep vertical cliffs at the northern side of the island (Fig. 5A). This 'platform' is at a height of 30-40 m above sea level and can be reached by descending along a track over gentle gradients from the east or by abseiling from the plateau. The eastern part of the colony, measuring 20 by 25 m, was designated as the study area, containing approximately 100 potential nest sites. The remaining nest sites of the (western part of the) colony comprised the reference area. Adjacent to the western boundary of the study plot, a Southern Fulmar colony was located. A boulder at the northern border of the colony which gave a good overview of the colony was used as a viewpoint for distant counts.

Southern Fulmars were studied on the Mast Point area on the western tip of the island (Fig. 5B). The Robertson Landing study area comprised the eastern part of this colony and measured about 600 m². The study area is a rock-face which was interspersed with large boulders, and rising to about 30 m above sea level. Nests were irregularly scattered in this area. In total there were 130 potential nest sites. All nests in the colony were individually marked and mapped for future studies. A large boulder situated 20 m north at the lower side of the colony near the landing area for the zodiacs gave a somewhat elevated position and was used as our view point for distant counts.

Ornithological research on Windmill Islands & Budd Coast, Wilkes Land

The area of the Windmill Islands and Budd Coast has a long tradition of ornithological

research, although on a somewhat irregular and intermittent schedule. During the International Geophysical Year (IGY) in 1957-58 Wilkes station was built by the U.S. Navy on the Clark Peninsula (Fig. 4). In late 1950s and early 1960s, the American ornithologists Eklund and Penney of the United States Antarctic Research Program (USARP) studied South Polar Skuas and Adélie penguins. Also during this period, large efforts were made in banding birds in the Windmill Islands, especially of South Polar Skuas, Adélie Penguins and Southern Giant Petrels. This was done partly in collaboration with Australian researchers. Antarctic bird banding programs were becoming increasingly popular, inspired by recent demographic and dispersal studies on individually marked birds which revealed remarkable long-distance migrations, longevity, and site and mate fidelity (Sladen 1965, Sladen *et al.* 1968). Australians took over Wilkes station in 1959 and built two new stations on Bailey Peninsula at the opposite side of Newcomb Bay (see Fig. 4): Repstat, later renamed as Casey (1964-1988) and the new Casey station (since 1988). The current station Casey is located near the Adélie Penguin colony on Shirley Island and the Snow Petrel colony at Reeve Hill. Both colonies are part of research and monitoring programs by researchers and volunteers from the station since the 1960s (Murray & Luders 1990, Woehler *et al.* 1994, Olivier *et al.* 2005).

Ardery Island was already identified as an important area for the present avian fauna, during zoological surveys in the early 1960s (Orton 1963). Ornithological research, however, did not occur on a regular basis on this island, mainly due to its isolated situation. Cape Petrels were banded in 1960, and Southern Fulmars were banded in 1961-63 by American and Australian biologists (Murray *et al.* 1972, Van Franeker & Montague 1987). While banding Southern Fulmars, the only flea species known to occur on the Antarctic continent (*Glaciopsyllus antarcticus*) was discovered on Ardery Island by Orton in 1961 (Smit & Dunnet 1962, Murray *et al.* 1967, Bell *et al.* 1988). Medical officers of overwintering parties went out for surveys and exploratory descriptive research (Orton 1963, 1968, Cowan 1979). Detailed observational research was conducted on the pre-breeding behaviour of Southern Fulmars and Antarctic Petrels in 1972 (Luders 1979). New impetus to ornithological research on Ardery Island occurred in 1984, when a Dutch-Australian study on the breeding and foraging ecology of fulmarine petrels commenced (e.g. Van Franeker *et al.* 1990, Van Franeker 2001). Studies initiated within this project included surveys of organochlorine pollutants (later redirected to Rauer Islands near the Australian Antarctic research station Davis; Van den Brink 1997a, b, Van den Brink *et al.* 1998) and plastic litter (Van Franeker & Bell 1988). In summer 1995-96, French-Australian research was conducted on Ardery Island which focused on the variation in body size of Snow Petrels in relation to their breeding ecology (Barbraud 1999, Barbraud *et al.* 1999).

OUTLINE OF THIS THESIS

In **Chapter 2**, we examine the breeding phenology of Southern Fulmars and Antarctic Petrels. Various aspects of the breeding biology of both study species were already known from a number of studies, but very few studies were able to follow the same individuals at the same location on a daily schedule during the whole breeding season. A high proportion of individually recognizable birds in our study areas enabled us to study the variation in attendance patterns and breeding behaviour between individuals and between species in detail. We especially focussed on the different strategies of these two species in timing of breeding within the short summer time-window, and how this affected reproductive success in both species.

Many studies have shown that the body condition of the chick influences post-fledging survival. Therefore, in **Chapter 3**, we look beyond breeding success, and examine how well chicks were prepared by their parents for a life on their own. Chick provisioning rates are supposed to be highly influenced by environmental conditions and food availability. We investigated how provisioning of the chick influenced chick growth and how flexible chick growth was both between and within species. From other studies it is known that both species differ in the duration of the foraging trips while rearing their offspring. These interspecific differences in provisioning shifts called into question whether the total amount of food supplied to the chick per day (calculated as the feeding frequency times the meal mass) also differed between species. Ultimately, we tried to ascertain whether chicks of both species were leaving the colony at relatively similar masses at fledging.

The study on the breeding and foraging ecology of fulmarine petrels took a slightly different course than we had anticipated. Five years after Van Franeker's last field season, the situation was very different on Ardery Island. In October 1996, when we arrived, it was, first of all, very white. The island was covered under a deep layer of snow, but the first Antarctic Petrels were already returning to their colonies. Thus, in **Chapter 4** we investigate the effects of snow on the breeding success of fulmarine petrels. We concentrate on the Antarctic Petrel because the reduction in breeding success was most prominent in this species. We subsequently discovered an unexpected chain of ecological events that could explain the observed decline in breeding success in the last decades.

Thus after an eventful start of the first season, we realised that predation was an important factor influencing breeding success of Antarctic fulmarine petrels. We therefore examine in **Chapter 5** the breeding population of the main predator: the Southern Giant Petrel. On the Frazier Islands the whole breeding population of Vincennes Bay of this species is located and historical population data could indicate whether the predation pressure by the largest fulmarine petrel had changed over

the years. For this purpose, we needed to consult the grey literature and non-published information sources (field notes, station logs). Many surveys appeared to be at different times of the season and to follow different methodologies. We therefore present in this chapter not only the results of breeding population trends of Southern Giant Petrels on the Frazier Islands, but also a proposal to standardise census methodologies of these birds.

While surveying the breeding colonies of Southern Giant Petrels, these birds surprised us once again and in a completely different way. In **Chapter 6** we describe an unusual phenomenon where individuals of this species apparently died while incubating an egg. Life-history theory predicts that a long-lived species such as the Southern Giant Petrel balances its current breeding efforts against reproductive chances in the future (Roff 1992, Stearns 1992). Thus individuals of these species are generally assumed not to jeopardize their own survival by over-investing in a single reproductive event. We discuss the circumstances in which these birds were found and give an explanation why they, probably involuntarily, had remained on the nest.

Southern Fulmars and Antarctic Petrels are abundant in circumpolar waters, but the pelagic distribution of both species is somewhat segregated; large numbers of one species occur where the other is scarce (Hunt & Veit 1983). On Ardery Island Southern Fulmars and Antarctic Petrels breed together, but there are not many other places where they breed sympatrically. A comprehensive review on the distribution of Antarctic Petrels had been completed earlier (Van Franeker *et al.* 1999), but a review on Southern Fulmars was lacking. Therefore, in **Chapter 7** we review extensive published and unpublished information on the breeding distribution of Southern Fulmars. We adapted the classification of census methodologies of Chapter 5 in order to evaluate the breeding population numbers that we collated from different sources. We also show seasonal fluctuations in distant estimates of the breeding population on Ardery Island and demonstrate how timing and the methodology used could influence the census results.

Finally, in **Chapter 8** I review the differences in the breeding biology and chick provisioning behaviour between the Antarctic Petrel and Southern Fulmar. Despite differences in their strategies, both species achieved a similar reproductive output. Although we were able to relate the trends in breeding success to the changed local weather conditions on Ardery Island in the last decades, we had not foreseen the rather unpredictable chain of events that finally caused these trends. However, this demonstrates how narrow the margins are for fulmarine petrels for breeding successfully in Antarctica.



CHAPTER

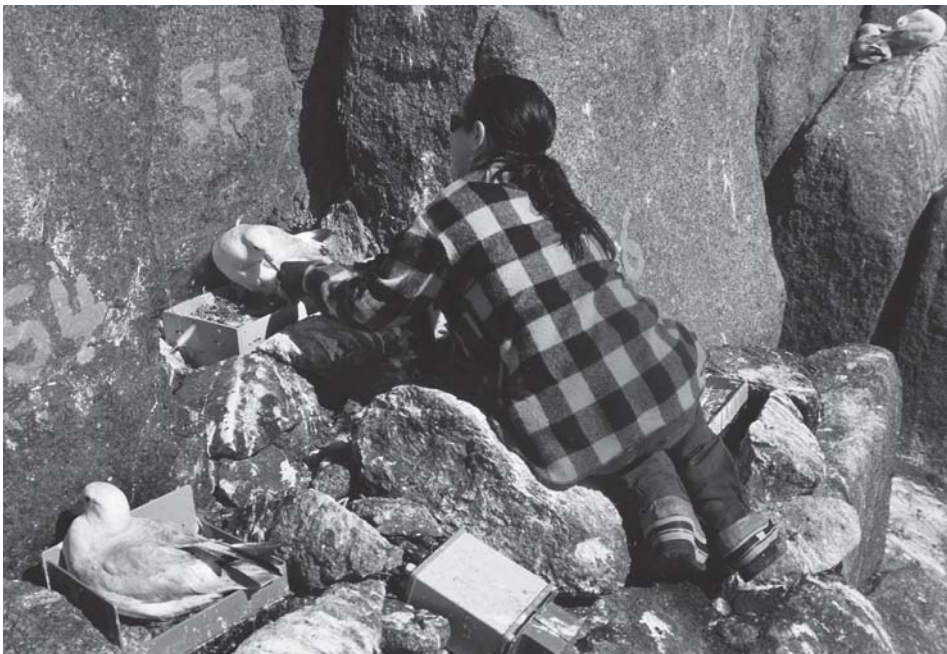
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**BREEDING STRATEGIES OF
ANTARCTIC PETRELS *THALASSOICA ANTARCTICA*
AND
SOUTHERN FULMARS *FULMARUS GLACIALOIDES*
IN THE HIGH ANTARCTIC
AND
IMPLICATIONS FOR REPRODUCTIVE SUCCESS**

Jeroen C.S. Creuwels, Jan A. van Franeker, Susan J. Doust, Anna Beinssen,
Belinda Harding and Oliver Hentschel

ABSTRACT

Breeding strategies of two closely related fulmarine petrels were studied on Ardery Island, on the continental coast of East Antarctica, where short summers are expected to narrow the time-window for reproduction. Both species had a similar breeding period (97 days from laying to fledging) but Antarctic Petrels *Thalassoica antarctica* bred up to 18 days earlier than Southern Fulmars *Fulmarus glacialisoides*. During the pre-laying exodus, all Antarctic Petrels deserted the colony, whereas some Southern Fulmars remained. Antarctic Petrels exhibited stronger synchronization in breeding, made longer foraging trips and spent less time guarding their chicks than Southern Fulmars. Overall breeding success of both species was similar but failures of Antarctic Petrels were concentrated in the early egg-phase and after hatching, when parents ceased guarding. Southern Fulmars lost eggs and chicks later in the breeding cycle and so wasted more parental investment in failed breeding attempts. Different breeding strategies may be imposed by flight characteristics; Southern Fulmars are less capable of crossing large expanses of pack ice and need to delay breeding until the sea ice retreats and breaks up. However, due to the short summer they risk chick failure when weather conditions deteriorate late in the season.



INTRODUCTION

Seabirds at high latitudes face a narrow window of time in which to complete their breeding cycle. Due to seasonal variation in the extent of sea ice, food is only available within range of the breeding colonies for a short period (Ashmole 1971, Croxall 1984, Carey 1988). However, during this short period food is abundant, making possible high chick provisioning rates and rapid chick growth (Volkman & Trivelpiece 1980, Croxall 1984, Warham 1990, Weimerskirch 1990a, Hodum & Weathers 2003). Other factors limiting the time window for breeding are temperature, storm frequency and intensity, and snowfall and snow accumulation. Snow-free surfaces are needed as a substrate for breeding. The short summers offer little opportunity for adjusting the timing of breeding, so adverse conditions at the beginning or end of the breeding season could seriously affect productivity. Late breakup of the sea ice, late spring thaw and accumulation of snow in the colony have all been shown to cause delays in egg laying, lowering breeding efforts or breeding success and even increasing adult mortality (Ainley & Le Ressaiche 1973, Sealy 1975, Chastel *et al.* 1993, Van Franeker *et al.* 2001, Creuwels *et al.* 2004, Gaston *et al.* 2005). Conversely, in late summer, deteriorating food and weather conditions may increase breeding failures (Cooke *et al.* 1995, Quillfeldt 2001).

The timing of breeding is particularly important for the fulmarine petrels, a closely related group of tubenoses specialized in breeding at high latitudes. Fulmarines have contracted incubation and chick-rearing periods that shorten the total nest-cycle by 28% in comparison to other procellariids (Warham 1990, Hodum 2002). The smaller Antarctic fulmarines (Southern Fulmar *Fulmarus glacialisoides*, Antarctic Petrel *Thalassoica antarctica*, Cape Petrel *Daption capense* and Snow Petrel *Pagodroma nivea*) are obligate summer breeders (Warham 1990), requiring only 90-99 days from laying to fledging (Hodum 2002).

Antarctic Petrel and Southern Fulmar are closely related, with comparable body size and similar diet and preferences for nest locations (Warham 1990, Nunn & Stanley 1998, Van Franeker 2001, Hodum 2002, Creuwels & Van Franeker 2003). Despite these similarities, Antarctic Petrels start breeding about two weeks earlier than Southern Fulmars at the same location (Hodum 2002, Creuwels & Van Franeker 2003). Such a difference could have reproductive consequences, given the narrow window for breeding in the high Antarctic. For the the late-laying Southern Fulmar in particular, birds may face problems in completing the breeding cycle in time, resulting in lowered breeding success. In a study on Ardery Island over three consecutive breeding seasons we assessed differences in breeding strategies between Antarctic Petrels and Southern Fulmars and the consequences of those strategies for reproductive success.

METHODS

Study species, area and timing

Antarctic Petrels and Southern Fulmars were studied on Ardery Island (66°22'S 110°30'E), Wilkes Land, Antarctica, 11 km south of the Australian Casey Station (Fig. 1). Approximately 250-275 pairs of Antarctic Petrels and 3000-3900 pairs of Southern Fulmars breed on the island (Van Franeker *et al.* 1990, Barbraud & Baker 1998). Study areas, each containing approximately 100 potential nest-sites, were situated on the northern side of the island. The Antarctic Petrel study area ('Northern Plateau') consisted of a 400 m² section of gentle sloping boulder slope in the otherwise steep cliffs at the northern side of the island, 30-40 m asl. The study area for Southern Fulmars was situated at Robertson Landing, at the northwestern tip of the island and consisted of about 600 m² of steep rockface and large boulders rising to about 30 m asl. Both species lay a single egg, incubated alternately by the two parents. Fieldwork was conducted during three austral summers: 1996/97 (abbreviated to '1996'), 1997/98 ('1997'), and 1998/99 ('1998'). Studies started in early October in 1996 and 1997 and in early November in 1998, and continued at least to late March in all three seasons, thus covering the full breeding season in each year.

Nest observations

In both study areas, all nest sites were marked with painted numbers, and a large proportion of the birds were individually marked with uniquely numbered metal and Darvic rings. Nests were checked daily, except in rare instances when extreme weather hampered colony visits. Before entering the colony, the number of birds present in the study area was counted from a fixed viewpoint overlooking the whole colony. Following the overall count, all nests were approached closely for identification of attending birds and their breeding status, in terms of the presence and condition of an egg or chick. Chicks disappearing at an age of 45 days or older were considered to have fledged successfully. Southern Fulmars and Antarctic Petrels are tolerant of disturbance by humans and are strongly attached to their nest site. Breeding birds and even most non-breeding birds did not leave nests at close human approach or even physical contact, and were carefully lifted by hand or with a short stick to check individual markings or the nest content.

Breeding biology

We divided each breeding period into an incubation period (from egg laying to hatching) and a chick period (from hatching to fledging). The chick period started with the guarding period, which we defined as the period from hatching until the first day the chick was left unattended. The synchrony of breeding events was expressed

in two ways: as standard deviations from the mean date, and as the proportion of occurrences of each event in the breeding cycle happening in a period from 3 days before to 3 days after the mean date for that event (Hatch 1989). Hatching success was estimated as the percentage of all eggs laid that hatched, fledging success was the percentage of chicks hatched that went on to fledge, and overall breeding success was the percentage of eggs laid that produced a fledged chick.

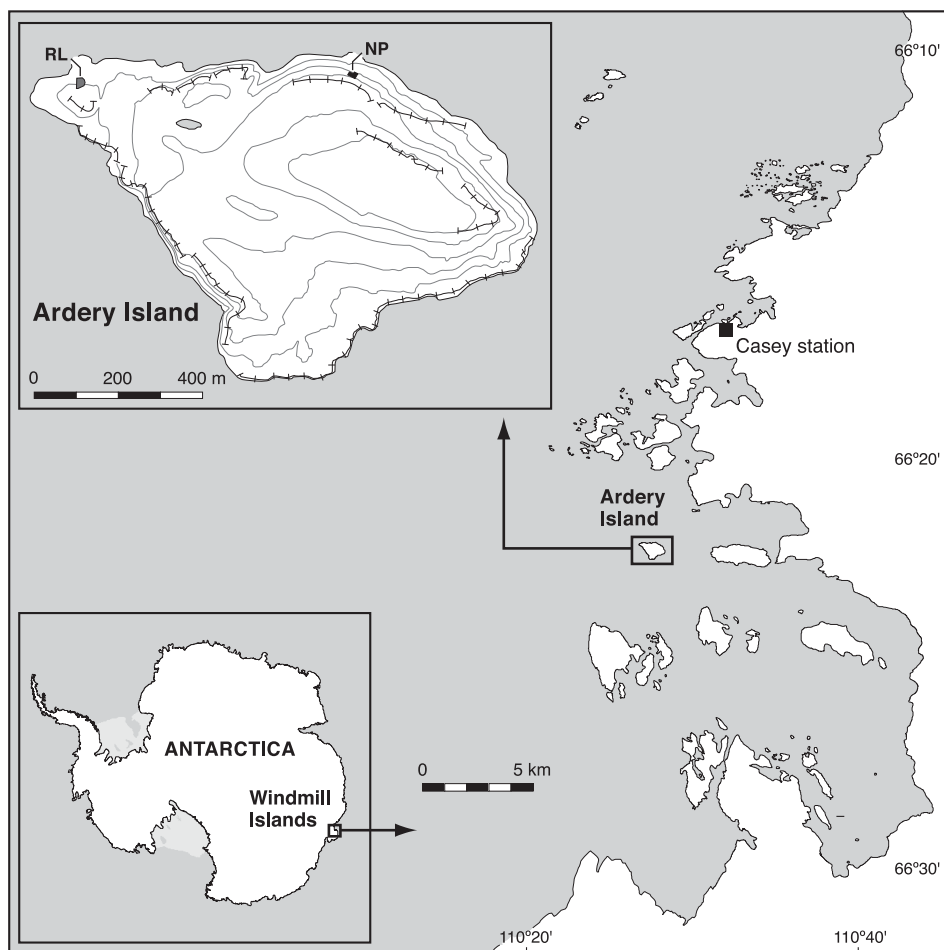


Figure 1. Ardery Island. Windmill Islands, Wilkes Land, Antarctica. On the detailed map of Ardery Island, 20m-height contours are shown, and study colonies are denoted by RL for Robertson Landing (Southern Fulmars), and NP for Northern Plateau (Antarctic Petrels).

Foraging shifts

The first female shift in which the egg was laid was termed 'incubation shift 0'. The next shift, by the male, was shift 1 (not including its possible pre-laying attendance); the following female shift was shift 2, etc. Thus, all incubation shifts with even numbers represented female attendance, uneven numbers male attendance. The incubation shift in which the egg hatched was termed 'guarding shift 0' and both sexes could be present. Thus, guarding shift numbers were unrelated to male or female attendance. In most cases only a single bird attended the nest and the duration of each incubation or guarding shift could be easily determined. Occasionally, when both male and female parents were present and shift lengths were not clear, we allocated half of the shared time to the female shift and half to the male. We determined incubation shifts only from nests that successfully completed the incubation period and guarding shifts only from nests that successfully completed the guarding period. In Southern Fulmars, guarding shifts were very short and only the duration of hatching and the first post-hatching shifts could be reliably calculated. After that, the average duration of guarding shifts became shorter than the observation interval of one day (Weimerskirch 1990a, Van Franeker 2001, Creuwels & Van Franeker unpublished data). The sex of adult birds was determined with a generalised discriminant analysis from measurements of head length, bill depth, tarsus length and bill length (Van Franeker & Ter Braak 1993), supplemented with observations of copulation position and cloacal condition in the egg-laying period.

Statistical analyses

In analysing whole colony counts, 7-day running means for each date were calculated, to account for short-term fluctuations and missing counts. As the numbers of attending birds fluctuated between seasons, we expressed each mean as a percentage of the yearly maximum. These percentages were averaged for the three seasons to show general patterns of seasonal attendance.

Dates of breeding events and breeding periods were not normally distributed, but as the variance between the sub-groups did not differ, small deviations from normality were accepted and standard parametric tests were used (Underwood 1997). We checked the results by repeating the tests without the outliers and by performing non-parametric tests, both giving similar results with similar significance levels. The homogeneity of variances between the groups was tested with a Levene's test. When we tested two groups that had unequal variance, Welch's approximate *t*-test (*t'*) was used with adjusted degrees of freedom (Sokal & Rohlf 1996). When comparing more than two groups, multiple comparisons were performed with Hochberg's GT2 test, due to unequal sample sizes (Sokal & Rohlf 1996). However, when variances between the groups differed significantly, the Games-Howell multiple comparisons test was

used (Sokal & Rohlf 1996).

When comparing incubation and guarding shifts between species, the mean shift length and mean number of shifts per nest were calculated. Data on breeding failures deviated from normality and transformation of the data did not reduce heterogeneity of variance (Underwood 1997), so non-parametric tests were used. Differences between proportions were estimated with log-likelihood ratio tests (G-statistics) and the synchrony of breeding events examined by testing homogeneity of variances (Levene's test). A logistic regression model was used to test the difference in chick attendance between the two species (with factors season, species, day number and all interactions included in the model). Mean values are given with their standard deviation or range, and significance accepted at $\alpha = 0.05$.

RESULTS

Colony attendance

Antarctic Petrels began to arrive at the colony in early October and highest numbers were recorded around mid-October. By the end of October a pre-laying exodus started and for 15-17 days no birds were present in the colony (Fig. 2). After 17 November, Antarctic Petrels quickly reoccupied their nests in the colony. Most Southern Fulmars arrived around mid-October and, although the numbers in the colony fluctuated considerably, highest numbers were recorded in November. The pre-laying exodus was not so apparent in Southern Fulmars, but lower attendance levels in the first week of December indicated that many also left the colony before egg laying.

Numbers of Antarctic Petrels were high from the end of December until mid-January, and dropped rapidly in the second half of January. Antarctic Petrels were seen in the colony only occasionally during February, representing short visits by chick-feeding parents. The last adults were seen on 25 February. Southern Fulmars had a peak in colony attendance at the end of December, after which numbers declined slowly until late March. Adults were seen in the colony until 25 March, after chicks had fledged.

Timing of breeding

Antarctic Petrels laid eggs between 18 November and 6 December. In comparison to 1997 and 1998, egg laying in 1996 was later by about 3 to 4 days (Table 1) due to exceptionally heavy snow cover of the study area in that season. Southern Fulmars laid between 4 December and 23 December, which was on average 13.2 days later than Antarctic Petrels in 1996, and 16.3 days later in both 1997 and 1998. Antarctic Petrel chicks hatched between 5 January and 19 January and Southern Fulmar chicks

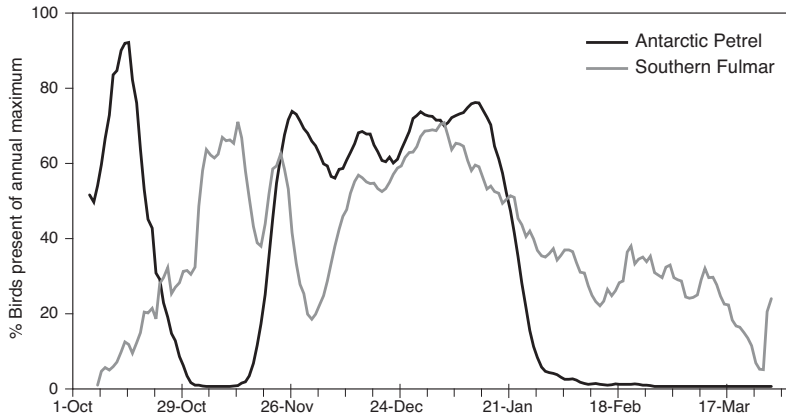


Figure 2. Relative colony attendance. Seven-day running means of the number of counted birds expressed as a percentage of the yearly maximum, and averaged over the three seasons.

Table 1. Timing of breeding events. Mean dates (\pm standard deviations) are given with sample sizes in parentheses. Where there were significant differences between seasons, pairs of seasons sharing a superscript letter did not differ significantly¹.

	mean 1996-98		1996 season		1997 season		1998 season	
Antarctic Petrel								
egg-laying	25 Nov	± 2.9 (136)	28 Nov	± 2.6 (29) ^c	24 Nov	± 2.6 (53) ^a	25 Nov	± 2.2 (54) ^b
hatching	11 Jan	± 2.3 (73)	15 Jan	± 0.0 (2) ^b	10 Jan	± 2.0 (26) ^a	11 Jan	± 2.3 (45) ^a
end guarding	26 Jan	± 2.8 (57)	31 Jan	± 2.1 (2) ^b	28 Jan	± 1.5 (19) ^b	24 Jan	± 2.6 (36) ^a
fledging	01 Mar	± 2.7 (50)	04 Mar	(1)	28 Feb	± 2.0 (18) ^a	02 Mar	± 2.7 (31) ^b
Southern Fulmar								
egg-laying	11 Dec	± 2.9 (220)	11 Dec	± 2.8 (66) ^{ab}	10 Dec	± 2.8 (74) ^a	11 Dec	± 3.1 (80) ^b
hatching	26 Dec	± 2.7 (117)	26 Jan	± 2.3 (22)	26 Jan	± 2.4 (33)	26 Jan	± 2.9 (62)
end guarding	15 Feb	± 6.7 (111)	09 Feb	± 3.1 (20) ^a	19 Feb	± 7.6 (31) ^c	15 Feb	± 5.6 (60) ^b
fledging	17 Mar	± 2.8 (77)	18 Mar	± 1.9 (12)	17 Mar	± 2.3 (27)	16 Mar	± 3.1 (38)

¹ Differences between seasons were tested with Hochberg's GT2 multiple comparisons test, except for fledging of Antarctic Petrels, which was tested with a *t*-test and for end guarding of Southern Fulmars which was tested with Games-Howell due to inequality of variances.

hatched between 20 January and 5 February. Except for Antarctic Petrels in 1996, when only two eggs survived and hatched considerably later, hatch dates did not differ between the years (Table 1). The incubation period of Antarctic Petrels was 1.2 days longer ($t_{188} = 7.79$, $P < 0.001$) than that of Southern Fulmars (Table 2).

Antarctic Petrels guarded their chicks for 9-21 days, on average 5.8 days shorter than Southern Fulmars (Table 2; $t_{160} = 8.12$, $n = 168$, $P < 0.001$). The guarding period of Southern Fulmars was highly variable both within and between seasons, ranging from 14 days to one extreme outlier of 53 days (the full chick period). Antarctic Petrel chicks fledged between 23 February and 7 March and Southern Fulmar chicks between 11 March and 25 March, but fledging dates in both species varied significantly between seasons. On average, the chick period in Antarctic Petrels was 1.4 day shorter ($t_{125} = 4.77$, $P < 0.001$) than in Southern Fulmars. Overall, the total breeding period did not differ between species (96.6 days; $t_{125} = 0.01$, $P = 0.996$).

Table 2. Duration of different phases of the breeding period. Mean durations (\pm standard deviations) are given in days with sample sizes in parentheses. Where there were significant differences between seasons, pairs of seasons sharing a superscript letter did not differ significantly¹.

	mean 1996-98	1996 season	1997 season	1998 season
Antarctic Petrel				
incubation	47.7 \pm 1.0 (73)	47.0 \pm 2.1 (2)	48.0 \pm 0.9 (26)	47.5 \pm 1.1 (45)
guarding	14.3 \pm 2.7 (57)	16.0 \pm 2.1 (2) ^{ab}	16.8 \pm 2.3 (19) ^b	12.9 \pm 1.7 (36) ^a
chick period	48.7 \pm 1.7 (50)	48.5 (1)	48.1 \pm 1.6 (18) ^a	49.1 \pm 1.6 (31) ^b
total breeding	96.6 \pm 1.9 (50)	97.0 (1)	96.3 \pm 1.8 (18)	96.7 \pm 2.0 (31)
Southern Fulmar				
incubation	46.5 \pm 1.1 (117)	46.1 \pm 1.2 (22) ^a	46.8 \pm 1.0 (33) ^b	46.5 \pm 1.0 (62) ^{ab}
guarding	20.1 \pm 6.5 (101)	14.8 \pm 2.9 (20) ^a	23.8 \pm 7.9 (31) ^c	19.9 \pm 5.2 (60) ^b
chick period	50.1 \pm 1.6 (77)	51.1 \pm 1.4 (12) ^b	50.8 \pm 1.5 (27) ^b	49.3 \pm 1.4 (38) ^a
total breeding	96.6 \pm 2.0 (77)	97.2 \pm 1.8 (12) ^b	97.6 \pm 1.6 (27) ^b	95.6 \pm 1.8 (38) ^a

¹ Differences between seasons were tested with a Hochberg's GT2 multiple comparisons test, except for both the chick period and the total breeding period of the Antarctic Petrels, which was tested with a *t*-test and for guarding of Southern Fulmars which was tested with Games-Howell due to inequality of variances.

All breeding events were highly synchronised in both species (Table 3). Over 80% of records of each breeding event occurred within a seven-day period, except for the end of the guarding period in Southern Fulmars (56% in a seven-day period). The end of the guarding period was significantly less synchronised than other breeding events in Southern Fulmars ($G = 31.81$, $P < 0.001$), but not in Antarctic Petrels ($G = 0.13$, $P = 0.989$). Overall, breeding events were more synchronous in Antarctic Petrels than in Southern Fulmars, but only significantly so for egg-laying and for the end of guarding (Table 3). However, when we compared between species within seasons (Levene's test, Table 1), only the synchrony in egg laying in 1998 was significantly different ($F_{1,132} = 5.02$, $P = 0.027$), as well as the end of guarding in 1997 ($F_{1,48} = 13.26$, $P = 0.001$) and in 1998 ($F_{1,94} = 7.39$, $P < 0.008$).

Table 3. Synchrony of events during the breeding cycle. Figures represent percentages of occurrences within the 7 days around and including the median date. Data for 1996-1998 are combined¹ and sample sizes shown in parentheses.

	Antarctic Petrel		Southern Fulmar		species comparison	
egg laying	90.4%	(123/136)	81.0%	(179/221)	$G = 6.10$	$P = 0.013$
hatching	89.0%	(65/73)	82.1%	(96/117)	$G = 1.76$	$P = 0.184$
end guarding	89.3%	(50/56)	55.9%	(62/111)	$G = 21.17$	$P < 0.001$
fledging	90.0%	(45/50)	85.9%	(67/78)	$G = 0.48$	$P = 0.488$

¹Differences between species in each season were not significant (all $P > 0.05$), except for end of guarding in 1997 ($G = 23.18$; $P < 0.001$) and 1998 ($G = 6.83$; $P = 0.009$)

Shifts during incubation and guarding

The first female shift, during which the egg was laid, was very short in Antarctic Petrels (0.4 days, range 0-3, $n = 61$), but somewhat longer in Southern Fulmars (1.6 days, range 0-10, $n = 97$). The longest incubation shift was the second female shift (12.2 ± 1.9 days and 5.8 ± 1.4 days respectively), after which shift lengths gradually decreased (Fig. 3). The mean incubation shift length in Antarctic Petrels (8.6 ± 0.8 days) was almost twice as long as in Southern Fulmars (4.4 ± 0.6 days; $t'_{132} = 25.17$, $P < 0.001$). Consequently, the mean number of shifts between laying and hatching in Antarctic Petrels (5.4 ± 0.7) was only half that in Southern Fulmars (10.5 ± 1.8 ; $t'_{106} = 33.43$, $P < 0.001$).

After hatching, shift lengths dropped considerably in both species (Fig. 4). In Antarctic Petrels, hatching shifts (4.3 ± 1.6 days) were almost twice as long as the first

guarding shifts (2.2 ± 0.8 days; paired- $t_{47} = 9.03$, $P < 0.001$). Antarctic Petrels guarded their chicks for 7.7 shifts (range 4 - 13) and shifts lasted on average for 1.8 ± 1.0 days, but lengths decreased towards the end of the guarding period. In Southern Fulmars, hatching shifts (2.8 ± 1.6 days) were also almost twice as long as the first guarding shifts (1.5 ± 0.8 days; paired- $t_{72} = 6.14$, $P < 0.001$).

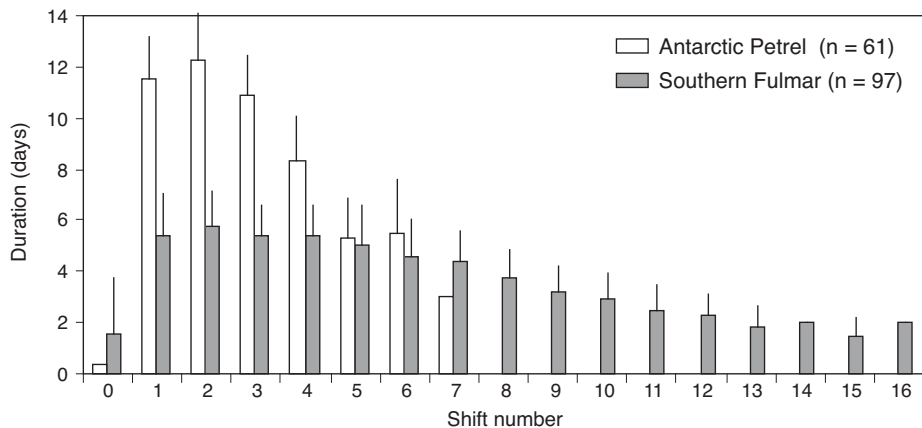


Figure 3. Incubation shifts. Means \pm standard deviations are given for the duration of shifts from egg laying (shift number 0) until the last shift before hatching. Odd numbers are male shifts; even numbers are female shifts. Hatching occurred on average at shift number 4-5 for Antarctic Petrels, and at shift number 9-10 for Southern Fulmars. Data of three seasons were combined and the initial sample sizes are given in parentheses.

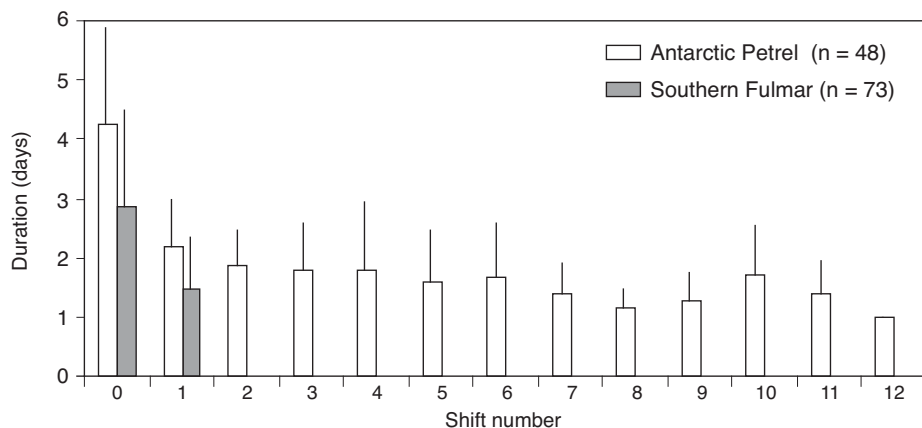


Figure 4. Guarding shifts. Means \pm standard deviations of the duration of hatching shifts (shift number 0) and guarding shifts are given. Shift numbers were irrespective of sex, and for Southern Fulmars only the first guarding shift could be reliably estimated. Data of three seasons were combined and the initial sample sizes are given in parentheses.

Breeding success

Averaged over three seasons, hatching, fledging and overall breeding success were very similar between species (Table 4; log-likelihood ratio tests, all $P > 0.7$). When looking within individual seasons, species did not differ in breeding success except in 1996 for hatching success ($G = 8.59$, $P = 0.003$) and overall breeding success ($G = 4.45$, $P = 0.035$). Hatching success and overall breeding success was lowest for both species in 1996, and highest in 1998 (Table 4). Due to exceptional snow conditions early in the 1996 season, fewer Antarctic Petrels attempted to breed (46.3% less than in other years), and only 3.4% of the eggs resulted in a fledged chick. In Southern Fulmars, the number of breeding attempts as well as the hatching success was also reduced in 1996, but less so than in Antarctic Petrels. Heavy snow conditions late in the 1998 season (1-7 March 1999) severely affected the Southern Fulmar chick survival. Initially, Southern Fulmars had a very high reproductive output in 1998 with 96.8% of all chicks still alive at the beginning of March. After 8 March 1999, 19 out of 22 chick failures occurred (45.2% of all breeding failures of that year).

Table 4. Guarding shifts. Means \pm standard deviations of the duration of hatching shifts (shift number 0) and guarding shifts are given. Shift numbers were irrespective of sex, and for Southern Fulmars only the first guarding shift could be reliably estimated. Data of three seasons were combined and the initial sample sizes are given in parentheses.

	mean 1996-98	1996 season ¹	1997 season ¹	1998 season ¹	Difference
Antarctic Petrel					
hatching success	53.3%(73/137)	6.9% (2/29)	48.1%(26/54)	83.3%(45/54)	$G = 51.33 P < 0.001$
fledging success	68.5%(50/73)	50.0%(1/2)	69.2%(18/26)	68.9%(31/45)	$G = 0.30$ ns
overall breeding success	36.5%(50/137)	3.4% (1/29)	33.3%(18/54)	57.4%(31/54)	$G = 28.69 P < 0.001$
Southern Fulmar					
hatching success	52.5%(117/223)	32.8%(22/67)	44.0%(33/75)	76.5%(62/81)	$G = 32.64 P < 0.001$
fledging success	66.7%(78/117)	54.5%(12/22)	81.8%(27/33)	62.9%(39/62)	$G = 5.56$ ns
overall breeding success	35.0%(78/223)	17.9%(12/67)	36.0%(27/75)	48.1%(39/81)	$G = 14.54 P < 0.001$

¹Differences between species in each season were not significant (all $P > 0.2$), except in 1996 for both hatching ($G = 8.59$, $P = 0.003$) and overall breeding success ($G = 4.46$, $P = 0.035$)

Although overall breeding success was on average similar, the timing of breeding failures differed between the two species. In the egg-laying period, a more pronounced failure rate occurred in Antarctic Petrels than in Southern Fulmars (Fig. 5). Antarctic Petrels laid in a period of 12-16 days, during which 41 out of 136 (30.1%) eggs failed. Southern Fulmars layed during a period of 14-17 days, in which time 39

out of 220 (17.7%) eggs failed. Antarctic Petrels therefore suffered a higher rate of egg loss (median 6.0 days after laying, $n = 63$) than Southern Fulmars (median 14.0 days, $n = 102$; Mann-Whitney, $Z = 3.54$, $P < 0.001$). Even if extreme 1996 egg failures were removed from the dataset, Antarctic Petrels showed higher rates of egg loss (Mann-Whitney, $Z = 2.32$, $P = 0.021$). Averaged over three seasons, 40 out of 136 (29.4%) of all breeding attempts by Antarctic Petrels had failed by 4 December, when the first Southern Fulmar laid its egg. Conversely, after 7 March (when the last Antarctic Petrel chick had fledged), 22 out of 220 (10.0%) of all Southern Fulmar breeding efforts failed.

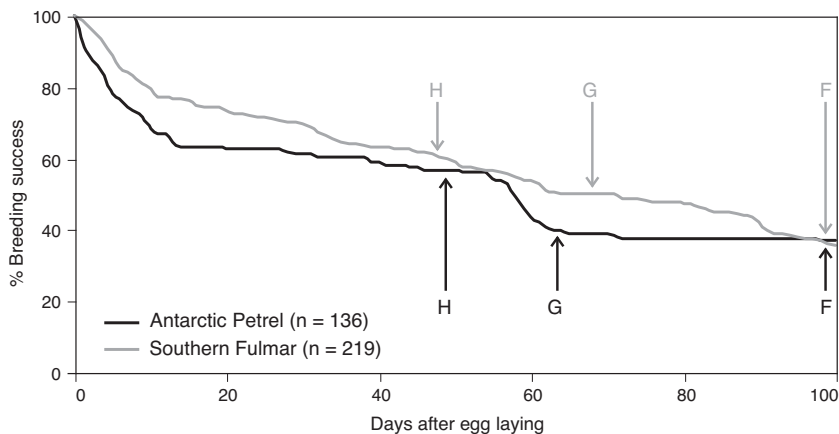


Figure 5. General trends in breeding success. Each nest started at the day the egg was laid (day 0). Data of three seasons were combined and totals are given in parentheses. Mean dates of main breeding events are indicated with arrows, black arrows for Antarctic Petrels, and grey arrows for Southern Fulmars (H = hatching, G = end of guarding period, and F = fledging).

Chick guarding and chick survival

In Antarctic Petrels, a second peak in breeding failures occurred around 60 days after egg laying (Fig. 5). In total, 26.7% of all breeding failures and 82.6% of all chick failures occurred towards the end of the guarding period, between 55–65 days after laying (7–17 days after hatching). Loss of Antarctic Petrel chicks was rapid and 68.2% of all failed chicks had not been observed as being unattended (Fig. 6). In this species, the relationship between guarding and chick survival could not be tested, because few chicks died between the end of the guarding period and fledging. In Southern Fulmars, guarding periods for fledged and failed chicks were not significantly different.

As a consequence, Antarctic Petrel chicks failed earlier (median 12.0 days

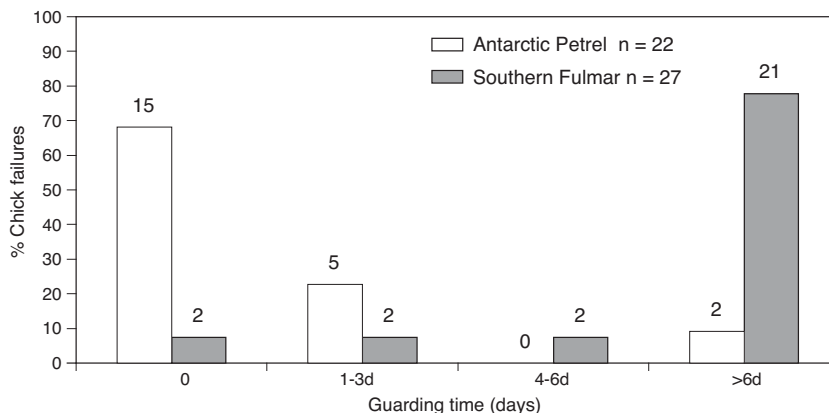


Figure 6. Chick failure in relation to guarding. All chick failures, categorized in the number of days a chick had been unattended. Data of all seasons are combined, and sample sizes of chick failures are indicated above the bars.

after hatching, $n = 23$) than Southern Fulmars (median 38.0 days, $n = 39$; Mann-Whitney, $Z = -4.25$, $P < 0.001$). The average age of Southern Fulmar chicks at failure was heavily influenced by a high mortality late in the 1998 season linked to heavy snowfall at the end of that season. Excluding this season, chick failure of Southern Fulmars occurred halfway through the chick period (median 24.0 days, $n = 16$), which was still significantly later than in Antarctic Petrels (Mann-Whitney, $Z = -2.45$, $P = 0.013$).

After the guarding period, parents of both species reduced attendance of their chicks towards the end of the breeding season (Fig. 7), but more rapidly so in Antarctic Petrels than in Southern Fulmars (Wald- $\chi^2 = 120.6$, $P < 0.001$; logistic regression model with season, species, day number and all interactions included).

Investments in failed breeding attempts

In all three seasons, Antarctic Petrels invested considerably fewer days in failed breeding attempts than did Southern Fulmars (Fig. 8). On average, Antarctic Petrels invested 6 days in failed incubation and 12 days in failed chick rearing, compared with 14 days and 38 days, respectively, in Southern Fulmars. Across all three seasons, the median number of days invested in failed attempts was 10.5 days ($n = 86$) for Antarctic Petrel and 32.0 days ($n = 141$) for Southern Fulmar (Mann-Whitney, $Z = -3.19$, $P < 0.001$).

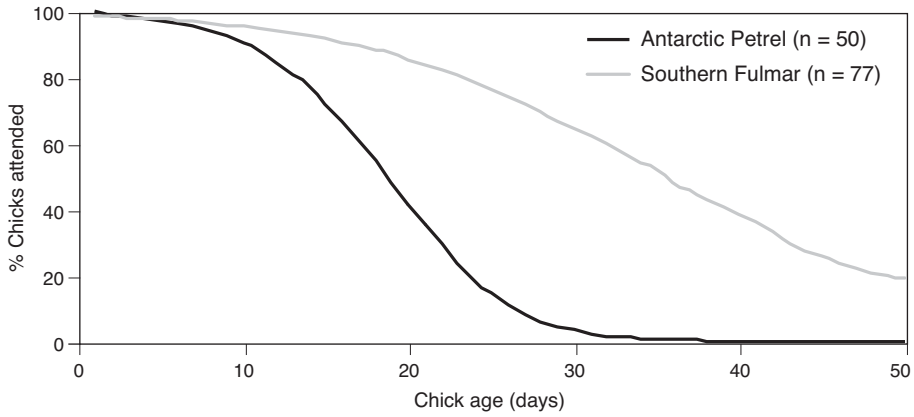


Figure 7. Chick attendance. Predictions, averaged over three seasons, are plotted from the logistic regression model (see text for details) on percentage of attended chicks. Sample sizes of total number of chicks are indicated in parentheses.

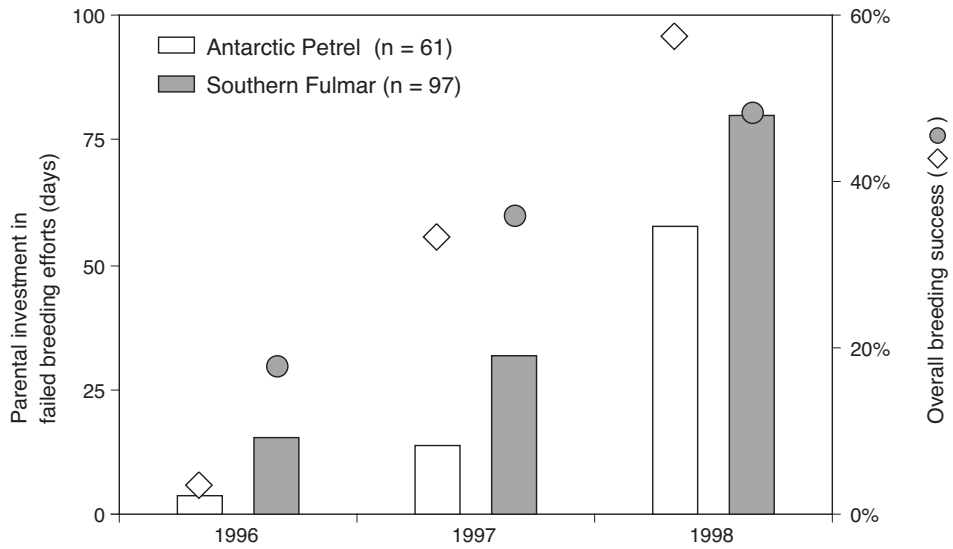


Figure 8. Investments in failed breeding attempts. Parental investment is expressed as the average number of days until nest failure, in different years with variable overall breeding success.

DISCUSSION

Breeding strategies and breeding success

On average over three seasons on Ardery Island, the total breeding period was not different between the two species. However, Antarctic Petrels started laying up to 2.5 weeks earlier than Southern Fulmars, a difference apparent in all stages of the breeding cycle, from spring arrival to fledging. Antarctic Petrels have a longer incubation period and shorter chick period than Southern Fulmars. The Southern Fulmar may have a slightly longer breeding period, but in our data this is masked by the 1998 season when Southern Fulmar chicks fledged 1.6 days earlier. Heavy snow fall in March caused considerable mortality and probably early fledging of the surviving but starving Southern Fulmar chicks.

Apart from the difference in the timing of breeding, our results show that Antarctic Petrels and Southern Fulmars differed in a number of important aspects of the breeding biology and subsequent reproductive success. The synchrony of the breeding events was higher in Antarctic Petrels than in Southern Fulmars. The pre-laying exodus was complete in Antarctic Petrels, with no birds in the colony for 2.5 weeks, whereas that of Southern Fulmars was only partial. Shifts of nest-attendance and foraging trip absence of Antarctic Petrels were twice as long as those of Southern Fulmars throughout the breeding period, and Antarctic Petrels guarded their chick for less time and showed lower post-guard attendance than Southern Fulmars. Breeding success showed some annual differences between species, but increased in both species over three seasons and was on average similar. Finally, breeding failures differed temporally between the species. Antarctic Petrels had high losses in the early egg phase and towards the end of guarding, whereas failures of Southern Fulmars were more evenly spaced. As a consequence, Southern Fulmars wasted more parental investment in failed breeding attempts.

The dates of egg laying, hatching and fledging and associated duration of incubation and chick-rearing on Ardery Island differed little from those recorded elsewhere (Prévost 1958, 1964, Mougin 1967, Lorentsen & Røv 1995, Tveraa *et al.* 1998, Hodum 2002, Varpe & Tveraa 2005). Reported durations of guarding the chicks are variable but are consistent in shorter guard periods in the Antarctic Petrel (Hodum 2002). Differences in breeding strategy between the two species therefore appear consistent over a range of locations and years.

Annual variations and the time-window for breeding

The overall breeding success varied between the three seasons. Initial egg losses decreased (and hatching success increased) because the extent of initial snow cover in the colony decreased in successive years. The thick layer of snow early in 1996, and

to a lesser extent early in 1997, facilitated access for Southern Giant Petrels *Macronectes giganteus*, which predated adults birds after 'crash-landing' into soft snow on otherwise inaccessible cliffs (Van Franeker *et al.* 2001). South Polar Skuas *Catharacta maccormicki* took advantage of the disturbance by quickly taking deserted eggs. The thick snow cover at the start of the 1996 season caused almost complete failure of the early breeding Antarctic Petrels.

Conversely, high Southern Fulmar chick mortality occurred late in the 1998 season because of heavy snowfall in the first week of March. Some parents could not feed their buried chicks for two weeks, some chicks froze to death and chick predation was also higher (because of access to colonies for Southern Giant Petrels) than in other seasons. Antarctic Petrel chicks were not affected, because they had already fledged or were about to fledge.

The strong effects of snowfall early in the 1996 season and late in the 1998 season support the existence of a climatically reduced time-window in which Antarctic fulmarine petrels must complete their breeding cycle. Antarctic Petrels encountered the limits to early breeding, Southern Fulmars the limits to late breeding. However, even when the two more extreme events were omitted from analyses, the consequences of early or late breeding were still apparent in the data.

Implications of breeding strategies

Breeding requires a considerable energetic investment the by parent bird, potentially affecting its future survival and reproduction (Drent & Daan 1980). Thus, even with similar reproductive success, it should be beneficial to adopt a breeding strategy that reduces wasted efforts on failed breeding attempts. In that sense, in the situation of Ardery Island, the early breeding of Antarctic Petrels seems to be the better strategy. Southern Fulmars probably cannot start breeding earlier because of morphological limitations to their mode of flying. Antarctic Petrels perform more flapping flight than Southern Fulmars (Watson 1975, Marchant & Higgins 1990), which is needed when flying over ice-covered areas (Griffiths 1983, Ainley *et al.* 1993). Southern Fulmars have a different wing morphology, which is more adapted to oceanic soaring and less suitable for prolonged flapping (Spear & Ainley 1998, Dijkstra 2003).

The adaptation of Antarctic Petrels to flapping flight enables them to exploit breeding locations far inland, as well as covering large distances over closed sea ice. When Antarctic Petrels on Ardery Island start laying eggs, the edge of the pack ice is on average 435 km away, compared with 315 km when Southern Fulmars start laying (distances calculated from monthly sea ice data of 1978-2002; Australian Antarctic Data Centre). The lower efficiency of Southern Fulmars in flying over dense sea ice

forces them to delay the start of breeding until the ice edge recedes and the pack-ice is breaking up.

In Antarctic Petrels, the pronounced pre-laying exodus and long shift durations at the start of incubation are necessary implications of the early breeding strategy when their foraging locations along the northern rim of the pack ice are distant (Van Franeker 1996). It is not clear why Antarctic Petrels persist in a pattern of longer shifts later in the season, when potential foraging locations are closer by. In the chick-rearing period, the continued long shifts and short guarding seem a disadvantage leading to relatively high chick losses.

Sympatric breeding of Antarctic Petrels and Southern Fulmars is limited to a few locations along the continental coast of East Antarctica. About 65% of the Antarctic Petrel population breeds at inland colonies and the continental coast represents the northern limit of their breeding range (Van Franeker *et al.* 1999). In contrast, Southern Fulmars predominantly breed on islands of the Scotia Arc and the Antarctic Peninsula, with less than 3% of the breeding population occurring sympatrically with Antarctic Petrels in the coastal zone of East Antarctica (Creuwels *et al.* 2007). Southern Fulmars breeding in coastal Antarctica are probably at the southern limit of their potential breeding range. Breeding locations further south would demand a strategy that they cannot adopt because of morphological limitations. The consequences of that limitation are visible in the Ardery Island location in spite of an apparently 'normal' level of breeding success.

ACKNOWLEDGEMENTS

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Timing of moult in the annual cycle

The timing of the moult is an aspect of the annual cycle that deserves special attention when studying species that breed in a highly seasonal environment with short summers. Like many other bird species, most procellariiformes have little temporal overlap in breeding and moult periods, due to the high energetic costs of both episodes (Stresemann & Stresemann 1966). Feather synthesis is highly energy demanding and the moult of the wing feathers might reduce flight capacity or manoeuvrability (Warham 1996). We investigated how the Southern Fulmars and Antarctic Petrels fitted their wing moult in their annual cycle, given the different timing of their breeding events.

We routinely measured the moult of the wing feathers in individuals that were banded during the season. Fulmarine petrels annually moult their primaries in a relatively simultaneous and regular manner, starting with the most innermost primary and ending with the most outermost primary. Moult scores of ten large primary remiges (the minute eleventh was not considered) were determined according to standard methods (Ginn & Melville 1983, Lowe 1989) in which feather growth was estimated on a scale of 0 (old feather) to 5 (new feather). To reduce the handling time and because wing moult is rather synchronous in fulmarine procellariiforms, only one wing was examined (Hunter 1984, Barbraud & Chastel 1998). Moulting scores were then multiplied by two, resulting in a Primary Moulting Score (PMS) of 100 when a bird has been fully moulted.

We banded birds in and outside the study areas on Ardery Island during 1996-99 and data on breeding status (active breeding, failed breeders, or unknown) were recorded when available. Individuals with a breeding failure less than 2 days ago were counted as successful breeding. We present only data of birds after 1 January, because none of examined individuals before this date were moulting. Data of three seasons were combined, because sample sizes in each year were small and no seasonal effects were found.

From Fig. 1 it is clear that Southern Fulmars start moulting earlier than Antarctic Petrels, especially if we take the differences in timing of breeding into account. For successfully breeding birds, wing moult in Southern Fulmars on average starts 41 days after egg laying, whereas in Antarctic Petrels this is after 71 days. Wing moult

in successfully breeding individuals was observed in 76.2% of the Southern Fulmars and 22.6% of the Antarctic Petrels that were examined after 1 January. In both species, the group 'Unknown' probably consisted of many non-breeding or early-failed individuals, which were able to start their primary moult about 2-3 weeks earlier. Failed breeders have a moulting pattern which falls somewhat in between the two other breeding status categories, but this sample size was small. The first completely moulted Southern Fulmars were observed in the second week of March. In Antarctic Petrels, the colony attendance declines rapidly in the second half of January (see Chapter 2), which explains the low numbers and the occurrence of only successful breeders in February.

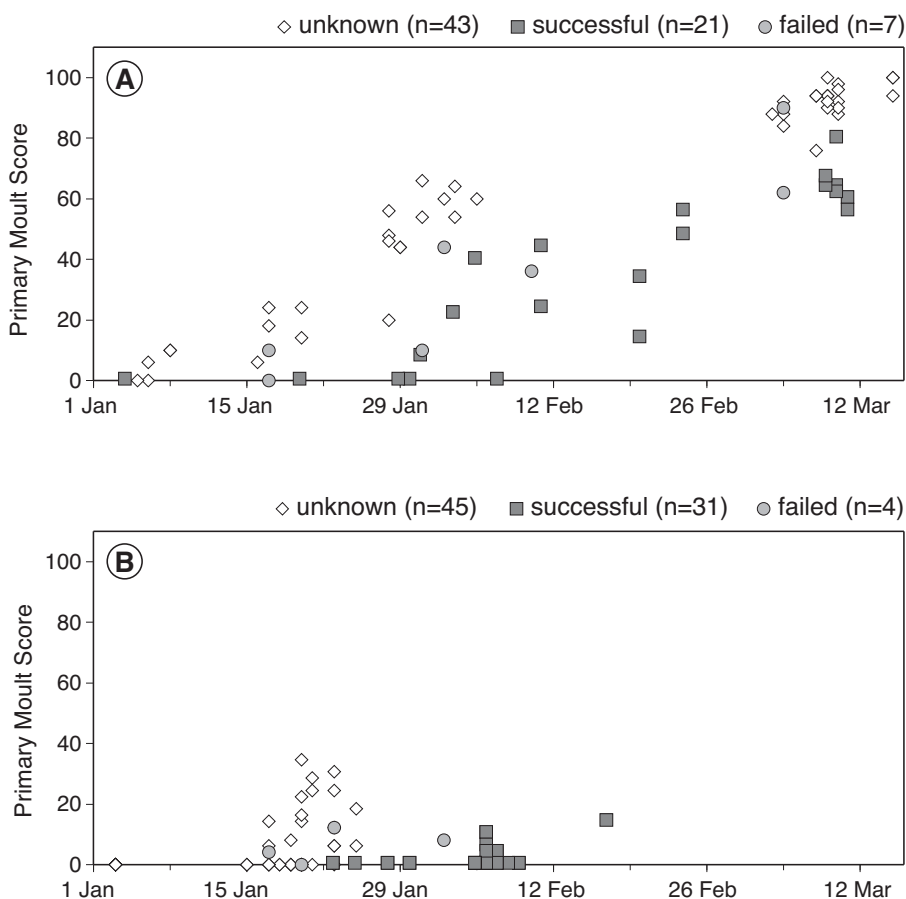


Figure 1. Primary Moulting Score of Southern Fulmars (a) and Antarctic Petrels (b). Data of three years are combined and only individuals that were examined after 1 January are shown.

The rate of primary moult did not differ between the various groups with a different breeding status, probably due to small sample sizes in some categories ($F_{5,110} = 0.58$, $P = 0.713$). Southern Fulmars, however, moulted their primaries earlier than Antarctic Petrels (2-way ANCOVA; $F_{1,117} = 84.04$, $P < 0.001$).

It was suggested that by shifting the breeding period to the earlier part of the season Antarctic fulmarine petrels would allow time for completion of the wing moult on the breeding grounds (Beck 1970). This appeared not to be true for Antarctic Petrels. Successfully breeding Antarctic Petrels were postponing their moult until very late or even after the chick period, like Snow and Cape Petrels (Beck 1969). Antarctic Petrels might need their flight feathers for their long provisioning flights to compensate their high wing loading. Antarctic Petrels deliver relatively heavier meals to their chicks than Southern Fulmars (see Chapter 3). In order to arrive in time at their favourite habitat for moulting they might have to compress their time in the colony and to desert their chicks about a week before fledging (Chapter 3). Ainley *et al.* (2006) observed in February-March almost flightless Antarctic Petrels which had lost most of their wing and or tail feathers together with Snow Petrels in a similar condition roosting on ice floes.

Southern Fulmars start their moult already during early chick period, but we did not find that all individuals were already moulting their primaries in early January like in another colony on the coast of East Antarctica (Barbraud & Chastel 1998). Due to the late fledging date and longer moult periods (larger feathers) Southern Fulmars probably cannot avoid a temporal overlap of these two costly periods of the annual cycle, which is only possible when energy and nutrients are sufficiently available. We do not have data on individual moulting schedules, but based on a longitudinal dataset (Fig. 1) we would estimate that Southern Fulmars need about 75 days to complete wing moult. Despite reforming sea-ice in March, successfully breeding Southern Fulmars are still seen in the colony after their chicks have fledged. Thus the fact that Southern Fulmars have higher colony attendance and remain much longer at their colonies may thus not only be related to the high chick requirements that they have to satisfy, but could be also a consequence of their moulting strategy.



CHAPTER

3

CHICK PROVISIONING AND CHICK GROWTH OF FULMARINE PETRELS IN THE ANTARCTIC

Jeroen C.S. Creuwels, Georg H. Engelhard and Jan A. van Franeker

ABSTRACT

Seabirds at high latitudes breed in environments with short, but highly productive, summers. Not many species can utilize these narrow windows of time to complete the full breeding cycle, but fulmarine petrels (Procellariiformes, Procellariidae) appear particularly well adapted because of a relatively short period in which they raise their chick. We developed an automatic weighing system with artificial nests to study food provisioning and chick growth. During three seasons (1997-1999), we collected data on chick provisioning of Southern Fulmars (*Fulmarus glacialisoides*) and Antarctic Petrels (*Thalassoica antarctica*) on Ardery Island (66°S 110°E) near the Australian Antarctic station Casey. Although Southern Fulmars started breeding about 2.5 weeks later than Antarctic Petrels, both were similar in total duration of the breeding period (97 days) and in the diet they provide to their chicks. Southern Fulmars delivered meals to their chicks about every 14 hours, almost twice as frequent as Antarctic Petrels. Meal sizes varied between the seasons and species, and averaged from 111g to 152g. On average, Southern Fulmars delivered 240-265 gram per day to their chick, whereas Antarctic petrels delivered 122-140 gram per day. Southern Fulmars were delivering in a more pronounced bimodal distribution pattern and provisioned their chicks more during daylight than Antarctic Petrels. Antarctic Petrels did not compensate their lower chick-feeding rate through larger meals, but their prolonged foraging trips probably enable them to process more of the food into stomach oil and thus produce meals with a higher energy density. Furthermore, Southern Fulmar chicks need more energy for thermoregulation and are thus less efficient in converting food into body mass. By using a "double Gompertz growth model" we were able to investigate both chick growth until peak mass and mass recession until fledging. We investigated the differences in growth between species and how the provisioning and growth parameters were correlated. The average peak mass of chicks was 140% of the mean adult mass in Southern Fulmars and 136% in Antarctic Petrels. At fledging, Southern Fulmar chicks were on average 101.5% and Antarctic Petrels chicks 91.7% of the mean adult mass. In Southern Fulmars, the provisioning rate was positively correlated with growth rate, peak mass and fledging mass, but in the Antarctic Petrel these correlations were not significant, probably due to low samples size. The differences in chick provisioning fit in the overall strategies of two related seabird species that have to adapt to conditions at opposite extremes of their main habitats.

INTRODUCTION

Seabirds provisioning their chicks are typical examples of central-place foragers. Procellariiform seabirds (albatrosses, petrels) are extreme examples with foraging trips that may cover more than 15,000 km during one trip or last up to 29 days (Hyrenbach *et al.* 2002, Weimerskirch & Cherel 1998, Klomp & Schultz 2000). It has long been assumed that the scattered and unpredictable availability of marine resources was responsible for a low chick provisioning rate and hence for the slow chick growth of pelagic seabirds (Ashmole 1971). Consequently, the accumulation of large amounts of adipose tissue in procellariiform chicks was explained as an insurance against periods with poor feeding conditions in which parents had low foraging success (Lack 1968). Currently, however, the relationship between chick development and the marine environment is thought to be more complex. Prolonged periods without parental provisioning are rarely encountered and the deposition of fat reserves greatly exceeds what is needed to withstand normal fasting periods (Ricklefs *et al.* 1980a, Granadeiro *et al.* 2000). Furthermore, food-rich areas prove to be rather predictable at meso- and larger scales (>100 km) due to oceanic features such as shelf edges, upwelling zones and sea-ice edges (Weimerskirch 2007). When provisioning chicks, most seabird species seem to commute in directed flights. When arriving at the feeding grounds they slow down and start searching in restricted areas for patchy food sources (Weimerskirch 1998a).

Parents of long-lived species such as seabirds must balance their current reproductive efforts against their own survival and future reproductive output (Drent & Daan 1980, Stearns 1992). Thus the parental body condition seems the key factor in provisioning strategies (Weimerskirch 1998b, 1999). The trade-off of allocating limited food resources to either the chick or the adult is especially visible during the early chick period when at least one parent is guarding the young and the energetic demands of the parents could be high (Ricklefs 1990). This is probably why many procellariiform species adopted a dual foraging strategy, where parents alternate or mix short foraging trips with long trips (Chaurand & Weimerskirch 1994, Weimerskirch *et al.* 1994, Baduini & Hyrenbach, 2003). Short foraging trips are used by parents to increase the feeding rate of the chick at the expense of their own body condition, whereas they may use long trips to recuperate and restore their own reserves.

The rate at which a chick is provisioned depends on the frequency and the quantity of the delivered meals. Pelagic seabirds foraging on distant food resources are supposed to try to maximize the efficiency of their provisioning efforts by reducing the commuting costs. For example, adults could forage closer to the colony or try to minimize the number of foraging trips and carry larger loads if this is not impairing

their flying capacity and causing extra flying costs. In various procellariiform studies, it has been shown that the feeding frequency rather than the meal size determines the overall chick provisioning rate (Ricklefs *et al.* 1985, Obst & Nagy 1993, Hamer & Hill 1997, Hamer & Thompson 1997, Huin *et al.* 2000, Hedd *et al.* 2002, Pinaud *et al.* 2005). Experimental studies in which the parents were handicapped generally resulted in reduced chick growth (Mauck & Grubb 1995, Weimerskirch *et al.* 2000a) which suggests that the food load can usually not be increased. The intra-specific variation in chick growth is generally found to be much smaller than the intra-specific variation in the chick-provisioning rate (Gray *et al.* 2005a), possibly because of internal constraints such as nutrient limitations or development of the gut-capacity (Ricklefs *et al.* 1998).

Peak weight and maximum growth rate of a chick are often taken as a proxy for the entire individual growth trajectory, but it is not sure if these parameters reflect best the future survival chances. Procellariiform chicks show a typical growth curve in which some species could attain masses up to 200% of the parent weight, followed by a period in which weight recession occurs towards fledging (Mauck & Ricklefs 2005). Most procellariiform chicks would have difficulty to take off at times when they have attained their peak weight, even with full-grown flight muscles and wings. In swifts, where chicks have a similar growth pattern, it has been shown that chicks try to achieve optimal wing loadings at fledging (Wright *et al.* 2006). Thus, after reaching peak weight chicks need to lose weight and most of the weight loss in procellariiform chicks is probably determined by water loss, and not by metabolizing fat (Phillips & Hamer 1999). Chicks first develop relatively heavy organs for processing food, blood circulation and thermoregulation, while later in the chick period, and especially after peak mass, more resources are allocated to developing fat reserves, pectoral muscles and flight feathers. Chicks mass is declining towards fledging because maturing organs lose water, some organs shrink in size, and parents are provisioning less food to their offspring (Ricklefs *et al.* 1980b, Phillips & Hamer 1999, Phillips & Hamer 2000b, Reid *et al.* 2000, Gray & Hamer 2001, Mauck & Ricklefs 2005). Various explanations have been proposed why procellariiform chicks need to become so fat. The original explanation by Lack (1968) that chicks need a buffer for prolonged food interruptions could not be supported by evidence from field studies. With the observed fat reserves, developing chicks could withstand extremely long fasting periods, which have hardly been detected in the field (e.g. Ricklefs *et al.* 1985, Bolton 1995, Hamer *et al.* 1997). Therefore, other hypotheses for obesity have been proposed, such as fat reserves being an insurance against stochastic variability in chick provisioning (Ricklefs & Schew 1994), or sufficient levels of some scarce nutrients could only be achieved when very large meals are delivered (Ricklefs 1979), or giving parents the opportunity to leave their chicks earlier (Brooke 1990) or giving chicks higher survival

chances after fledging (Phillips & Hamer 1999). Generally, it has been shown that procellariiform chicks with higher fledging weights survive better (Perrins *et al.* 1973, Sagar & Horning 1998).

Within the order Procellariiformes, chicks of fulmarine petrels differ from other species in having nestling periods that are half the length as expected on basis of their size (Croxall & Gaston 1988, Warham 1990, Hodum 2002). This fast chick growth has been explained as an adaptation to their predominantly polar and sub-polar distribution where summer seasons are short. Chicks need to grow as fast as physiologically possible in order to allow fledging prior to the onset of bad weather and reforming sea ice late in the season. Antarctic waters potentially allow fast chick growth because they are highly productive in summer, providing abundant prey sources such as fish and krill (El-Sayed 1994, Knox 2007, Flores 2009).

We examined chick provisioning and chick growth in two closely related Antarctic fulmarine species: the Southern Fulmar (*Fulmarus glacialisoides*) and the Antarctic Petrel (*Thalassoica antarctica*). On Ardery Island, where we conducted this study, the chicks of both species receive a similar diet (Fig. 1, Van Franeker 2001). Further, both species are having a similar duration of their breeding periods (both species: 97 days from laying to fledging) and a similar breeding success (Creuwels *et al.* 2008). However, they differ in the timing of breeding with Antarctic Petrels breeding up to 16 days earlier than Southern Fulmars, in chick provisioning rate and in body mass (Norman & Ward 1992, Van Franeker 2001, Creuwels *et al.* 2008). On Ardery Island, Southern Fulmars were weighing on average 800g and Antarctic Petrels 678g (Creuwels, unpublished). Fulmarine petrels have a survival rate of 96% and individuals may live up to 50 years or more (Warham 1996, Grosbois & Thompson 2005). Both species are common seabirds in the Southern Ocean with estimated numbers of at least 1 million breeding pairs (Van Franeker *et al.* 1999, Creuwels *et al.* 2007). Their distribution is circumpolar in Antarctic and sub-Antarctic seas, with Southern Fulmars dispersing northerly to warmer waters up to 40°S in wintertime and with Antarctic Petrels being more strictly confined to the vicinity of the sea-ice zone year-round.

In this paper, we investigated whether the different timing of breeding affects chick growth of both species and how different provisioning rates affect the growth trajectories of the chicks. We used a growth model that was not only able to predict chick growth up to peak mass, but also accounted for the weight recession period. During three summer seasons, we used an automatic weighing system to record the size of the meals and the feeding frequency of Southern Fulmars and Antarctic Petrels. This is the first study using an automatic weighing system in fulmarine petrels. First, we aimed at quantifying exactly the chick provisioning rate in both species and at collecting data on chick growth over the whole nestling period. We were especially

interested how Southern Fulmar chicks were able to finish their development in time to fledge successfully, e.g. by faster growth or by adjusting their peak or fledging mass. Towards the end of the season, however, not only the weather conditions deteriorate for the chicks, but also for the foraging parents that face adverse conditions because day lengths are getting shorter and sea-ice is starting to reform. Next, we investigated whether the different timing of breeding in both species is influencing the timing of meal deliveries, both during the day and during the whole season. Further, we investigated whether the various provisioning parameters are correlated with growth, both before peak mass of the chick and during the weight recession period after peak mass and whether these correlations were different between the species. Finally, we attempt to explain why provisioning rates of both species differ and if this can be related to interspecific differences in chick growth or breeding phenology.

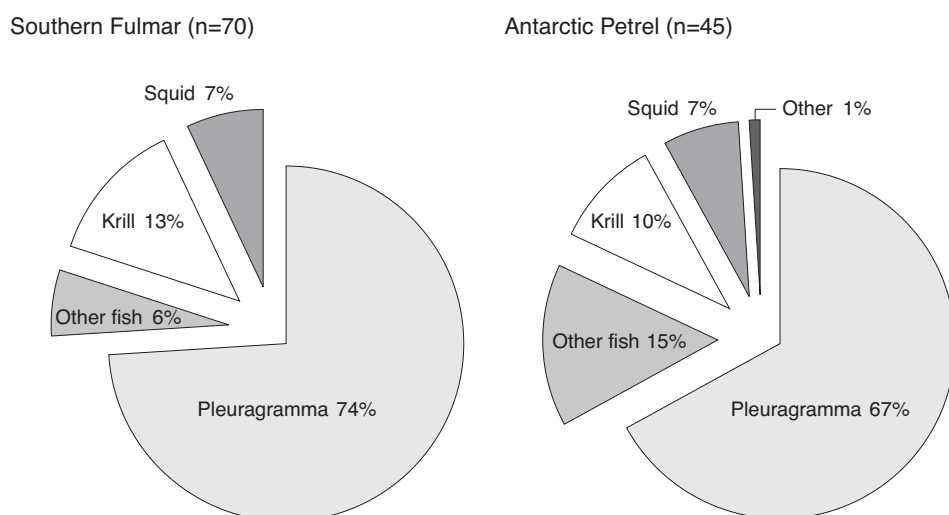


Figure 1. Chick diet on Ardery Island. Percentages denote reconstructed mass proportions of different prey groups in meals delivered to the chicks. On average, meals of both species consist for 80% or more of fish (mainly *Pleuragramma antarcticum*, Antarctic silverfish). Data were obtained by stomach-flushing adults that reared chicks during Jan-Mar 1987 and 1991. For details see Van Franeker (2001).

METHODS

We studied Southern Fulmars and Antarctic Petrels on Ardery Island (66°22'S 110°30'E), Vincennes Bay, Wilkes Land, Antarctica, 11 km South of the Australian

station Casey. We present data from fieldwork during three austral summers, mainly during the chick periods: January - March 1997, 1998 and 1999. For each species, a study colony was established in breeding colonies at separate locations at the north coast of the island during the 1980s (Van Franeker *et al.* 1990, Creuwels *et al.* 2008). The Southern Fulmar study colony consisted of about 130 potential nest sites, but each season only 50-60% of the sites were active (i.e. containing an egg). The Antarctic Petrel study colony consisted of 100 potential nest sites, of which in 1996-97 30% were active and in the latter two seasons 54% contained an egg.

On the island, adults and chicks of four fulmarine petrel species have been ringed for monitoring studies. Individuals were marked in three different ways to allow individual recognition, using: 1) a metal band provided by the Australian Bird and Bat Banding Scheme (ABBBS), 2) a colourband with an engraved number, which enabled visual monitoring at a distance, and 3) an electronic tag (TIRIS transponder) implanted subcutaneously along the tibia. The transponder has a unique identifier that can be detected by a handheld reader or by an automated detection system. In the Southern Fulmar colony the proportion of breeding birds with a transponder (and a colourband) was 61% in 1997, 70% in 1998 and 83% in 1999. In the Antarctic Petrel study colony 52% of the breeding birds in 1997 was electronically tagged and in the later two years 80% of the breeding population. When the birds were ringed, they were usually also measured and weighed.

Monitoring of nests

In both study colonies, all nest sites were individually marked and checked in a daily routine, although occasionally the colonies could not be visited because of extreme weather conditions. All nests were approached closely to identify the attending bird(s) and to inspect the content (egg or chick present). If necessary, birds were gently lifted for this purpose by hand or with a small stick. Almost all birds were tolerant to this disturbance level without signs of stress or nest desertion. On average, Southern Fulmar chicks hatched on 26 January and fledged on 17 March and Antarctic Petrel chicks hatched on 10 January and fledged on 1 March. Continuous chick guarding ended on average for Southern Fulmars on 15 February and for Antarctic Petrels on 26 January (Creuwels *et al.* 2008). As fledging date we used the first date that the chick had left the island as assessed after extensive searches of the area because chick increasingly wandered off their nest sites towards fledging.

Automatic weighing- and identification nest-system

An automatic weighing- and identification nest-system (AWIN) has been developed for the purpose of this study. Artificial nest units were placed on the original nest sites in the colony and were easily accepted by the site-holding birds. These units contained

an automatic transponder reading system and an electronic weighing platform. Data on the weight of each nest and the presence of a transponder were recorded every 5-7 minutes (more details on AWIN can be found in Creuwels *et al.* 2000).

During the chick periods of 1997, 1998 and 1999, there were respectively 20, 26 and 17 nest units active in the Southern Fulmar colony, and 17, 17, and 16 in the Antarctic Petrel colony. Towards the end of the last two seasons, heavy snowfall made the nest data unreliable. When analyzing the first season we included data until 18 March 1997 but for 1998 we had to restrict data usage until 9 March and for 1999 until 28 February. Only incidentally, nest were installed or relocated during breeding. Especially in 1997, when the breeding success was extremely low, 4 chicks on original nest sites were placed on artificial nests. Chicks were generally accepting these nests except for one chick that did not fully accept the nest but nevertheless fledged successfully. In Fig. 2, an example is given of a typical output of an artificial nest during the chick period. To test whether chicks of artificial and control nests might differ in survival, we used a likelihood-ratio test (G-test) (Sokal & Rohlf, 1995).

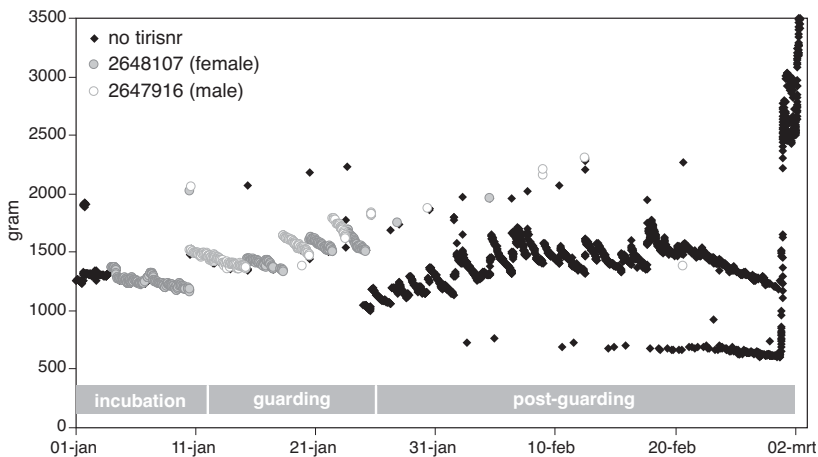


Figure 2. Output of an artificial nest at Antarctic Petrel nest T012 during the chick season in 1999. The tare weight (weight of the nest without parents and egg or chick) fluctuated somewhat around 600 gram. Both parents received a transponder, but the chick did not. Thus when no transponder number was detected this could be because there was no parent present or the system was not able to read the number. The chick hatched on 12 Jan and fledged on 2 Mar. The last meal was given on 22 Feb and none of the parents was seen after this date. Because snow accumulated quickly on 28 Feb (note rapid increase in absolute weight of the nest) we have no reliable data after that date.

Chick provisioning *Data collection*

The automatic nest system (AWIN) allowed us to collect information on meal sizes

delivered to the chick. A sudden weight increment of the chick is equal to the meal mass. Such 'jumps' in weight are only detectable when the chick is sitting on the nest, whereas the parent feeding it is standing besides it. Thus, we were not able to collect data on meal size during the first few weeks after hatching, when parents continuously guard the chicks on the nest.

After this guarding period, the chick was left alone for increasing lengths of time, and late in the season parents were often visiting the colonies only for short periods, just to provision the chicks. A sudden mass increment ($>25\text{g}$) between two weighings was considered a meal. Note that there is always a time lag between consecutive data points (from 5 minutes to several hours) and that chicks, owing to metabolism, lose weight at a rate of 10.13g/hour for Southern Fulmar and 5.37g/hour for Antarctic Petrel chicks (Creuwels, unpublished data). We accounted for this weight loss when estimating each meal size.

Throughout the whole period we were able to collect data on the feeding frequency, as the nest system did allow us to detect when parents alternated their presence at the nest. Even when the parent had no transponder, or the transponder could not be detected, different adults could usually be distinguished by their different body masses. Arrival of a new adult was taken as the moment of meal delivery, unless nest data clearly showed that no meal was given at that time. Visual observations confirmed that in most cases a meal was delivered right after the parent arrived. For examining whether meal deliveries occurred equally over the day and were related to ambient light conditions we used a chi-square test on the distribution of the delivery times. For light conditions we distinguished between daylight, civil twilight, nautical twilight and dark hours. Civil twilight commences in the morning when the center of sun is 6° below the horizon and ends at sunrise; it begins in the evening at sunset and ends when the sun is 6° below the horizon. Nautical twilight is when the sun is between 6° and 12° below the horizon. Reported time is Casey local time (GMT + 8 hours).

Analysis of chick provisioning

In order to reduce the large variation and overcome some gaps in the data, we aggregated data on chick provisioning and meal sizes into 5-day periods. For statistical analysis of differences in meal sizes, fasting intervals and provisioning rates we used linear mixed-effects models (fitted using Restricted Maximum Likelihood). This allowed us to account for multiple measurements that were available for individual chicks, by treating these as random effects in the model. Exploratory analysis showed that provisioning parameters changed with the age of the growing chick (increase followed by decrease or vice versa). To test for non-linear relationships between chick age and provisioning parameters, we included both chick age and quadratic

chick age in the model. Fasting intervals showed a skewed distribution and hence were square-root transformed. Model selection was based on the Akaike Information Criterion (Crawley 2007).

Chick growth *Data collection*

The group of weighed chicks included chicks from natural nest sites that were only manually weighed and chicks from artificial nests that were both manually and automatically weighed. For recording chick growth, we used data collected by manually weighing chicks, which were, if possible, supplemented with data taken by the automatic weighing system. The motivation for using manual weighings was that although the artificial nest system provided high-quality data on the size and frequency of the meals (which imply sudden weight changes), the system might have been less suitable for recording the growth of the chick itself owing to the slow and gradual nature of the weight change. In particular, snow, sand and stones could accumulate on the nest units, but could also disappear again. In either way these factors would influence the tare weight and confound the weight measurements. During nest calibrations and at other moments when a chick was temporarily off the nest, its weight was accurately recorded. However, when parents were present on the nest (most evidently during the phase that chicks were continuously guarded), data on the weight of the chick alone could not be recorded, which prevented investigating chick growth early in the season. Therefore, we took regular manual weight measurements of chicks using small Pesola spring scales. On average, we weighed Southern Fulmar and Antarctic Petrel study chicks every 2 days. For some newborn chicks where no weight measure was taken within 2 days of hatching, we used the projected weight of the egg at hatching as initial weight (each egg was weighed 4-5 times during incubation). In 1997, we did not measure egg weights during the incubation and therefore we used the average value of these eggs in later seasons (82g). All chick weight data for 1998 and most for 1999 were collected by manually weighing chicks; most weight data for 1997 and some weight data for 1999 were extracted from the artificial nest system dataset.

Estimating chick growth using the double Gompertz curve

Exploratory analysis of the growth data for chicks of both petrel species revealed that it could be described most appropriately by the 'double Gompertz growth curve' (Huin & Prince 2000). Therefore, growth curves of chicks were fitted applying equation (5) of Huin & Prince (2000), which is a combination of a 'classic' Gompertz curve representing the chick growth phase, and a negative Gompertz curve representing the weight loss phase that typically follows. The double Gompertz equation is as

follows:

$$W(t) = A \exp[-\exp(-k_1(t-t_1)) - \exp(k_2(t-t_2))]$$

where $W(t)$ is weight at time t after hatching, k_1 is a growth constant during the weight gain phase of the chick, and k_2 is a weight loss constant during the weight loss phase. As pointed out by Huin & Prince (2000), the parameters t_1 and t_2 are akin to, but not equivalent to the times of growth inflexion; and A is a weight scaling factor for the asymptote, but not equivalent to the asymptotic weight of the chick.

We used non-linear mixed effects models in the R package to estimate double Gompertz growth curves for Southern Fulmar and Antarctic Petrel chicks. Model selection was done by a comparison of the Akaike Information Criterion (AIC) between models. Only chicks with at least 5 weight measurements were included in curve fitting. All individual chicks were weighed repeatedly, hence random effects for each chick were accounted for when estimating the parameters A , k_1 , t_1 and t_2 . No random effects on k_2 could be included, owing to scarcer data for the weight loss phase. To avoid overparameterisation, not all five growth parameters could be estimated and a common k_2 of 0.0572 was estimated for both species combined (model comparisons suggested no species difference in k_2).

To facilitate biological interpretation of the double Gompertz curves, five 'classical' growth parameters were calculated for each chick, once the 'best' double Gompertz model was selected based on the AIC. These included (1) the age t_{\max} at which the maximum weight is achieved, calculated using equation 6 of Huin & Prince (2000); (2) the maximum weight W_{\max} reached by the chick, calculated by solving the double Gompertz equation for the time t_{\max} ; (3) the growth rate, defined as the mass gained divided by the time between 10% and 90% of t_{\max} ; (4) the fledging mass, calculated by solving the double Gompertz equation for the time of fledging; and (5) the mass loss rate, defined as the mass lost divided by the time between age at peak mass and age at fledging. In addition, (6) the age at fledging was known from direct visual observations of chick presence on Ardery Island. We used conventional analysis of variance to test for species and seasonal differences in growth parameters (Huin & Prince 2000).

The chick-provisioning rate is the total amount of food ingested by the chick per day, hence the sum of all meals of that day. When investigating the influence of chick provisioning rate on chick growth, we used the provisioning rate prior to reaching peak mass, thus the average rate over the 30 days following hatching, for correlations with t_{\max} , W_{\max} and chick growth rate. For correlations with fledging age and fledging mass, we used the chick provisioning rate over the whole chick period, which included provisioning after the chick had reached peak mass.

RESULTS

Fledging success on artificial and control nests

We found no evidence that the artificial (AWIN) nests were affecting the birds negatively in terms of a lower breeding success. In total, 5 out of 6 Southern Fulmar chicks were successfully raised on artificial nests in 1997, 7 out of 8 chicks in 1998 and 11 out of 13 chicks in 1999. The fledging success, i.e. the proportion of fledging chicks out of all chicks that hatched, was on average higher on the AWIN nests than on the control nests studied, although the difference was not significant (Table 1). In the Antarctic Petrel colony no chick fledged from any artificial nest in 1997 (and only one chick in the whole colony). In 1998, 4 out of 6 Antarctic Petrel chicks on AWIN nests fledged, and in 1999 9 out of 11 chicks. Again, no differences in fledging success could be shown between Antarctic Petrels on artificial and control nests (Table 1).

Table 1. Comparison of fledging success between artificial (AWIN) and control nests. Percentages of successful nests are given with sample sizes between parentheses (chicks fledged/chicks hatched). G-test was used to examine for differences in fledging success between artificial and control nests.

year	species	number	control nests		AWIN nests		Difference	
1997	Southern Fulmar	21*	43.8%	(7/16)	80.0%	(4/5)	G=2.130	P=0.144
1998	Southern Fulmar	33	80.0%	(20/25)	87.5%	(7/8)	G=0.245	P=0.621
1999	Southern Fulmar	62	57.1%	(28/49)	84.6%	(11/13)	G=2.972	P=0.085
1997	Antarctic Petrel	2	50.0%	(1/2)		(0/0)		
1998	Antarctic Petrel	26	70.0%	(14/20)	66.7%	(4/6)	G=0.024	P=0.877
1999	Antarctic Petrel	45	64.7%	(22/34)	81.8%	(9/11)	G=1.219	P=0.270

*One surviving chick has been excluded from analysis, because artificial nest of this chick was installed after the guarding period had ended

Timing of meal deliveries

Both species showed a bimodal pattern of meal deliveries over the course of the day, with a clear peak in the morning between 5:00 and 8:00 and a second smaller peak between 16:00 and 20:00 hours in Southern Fulmars (Fig. 3A) and between 18:00 and 23:00 in Antarctic Petrels (Fig. 3B). The peaks in the meal delivery distributions were more obvious in Southern Fulmars than in Antarctic Petrels, which tended to distribute their feedings more equally over the course of the day. Considerably more meals were delivered during the peak in the morning (5:00 – 9:00) than during the evening peak (for Southern Fulmars 16:00 – 20:00 and for Antarctic Petrels

19:00 - 23:00), which was highly significant in both species (Southern Fulmars $\chi^2 = 133.3$, d.f. = 1, $P < 0.0001$ and for Antarctic Petrels $\chi^2 = 22.5$, d.f. = 1, $P < 0.0001$). Southern Fulmars showed significant differences in distributions of meal deliveries between years ($\chi^2 = 137.7$, d.f. = 42, $P < 0.0001$). There was no evidence of such a difference between years in Antarctic Petrels ($\chi^2 = 28.1$, d.f. = 23, $P = 0.211$).

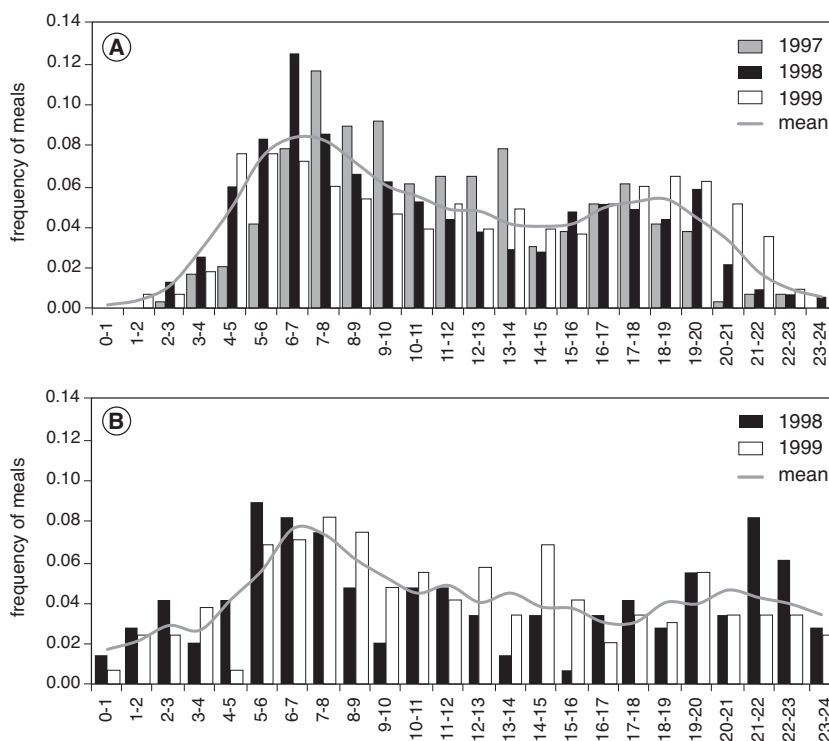


Figure 3. Distribution of occurrences of meal deliveries of A) Southern Fulmars and B) Antarctic Petrels over each hour of the day. Bars show the frequencies by season, and the line indicates the running grand mean over all seasons.

Virtually no meals were delivered to chicks during darkness, only one by Southern Fulmars just past nautical twilight (0.1% of all deliveries) and none by Antarctic Petrels. Proportionally, Southern Fulmars delivered food more during daylight hours (91.3% of deliveries; Fig. 4A) than Antarctic Petrels (84.2%; Fig. 4B) reflecting the more equal distribution of chick feedings over the daily cycle in the latter species (Fig. 3).

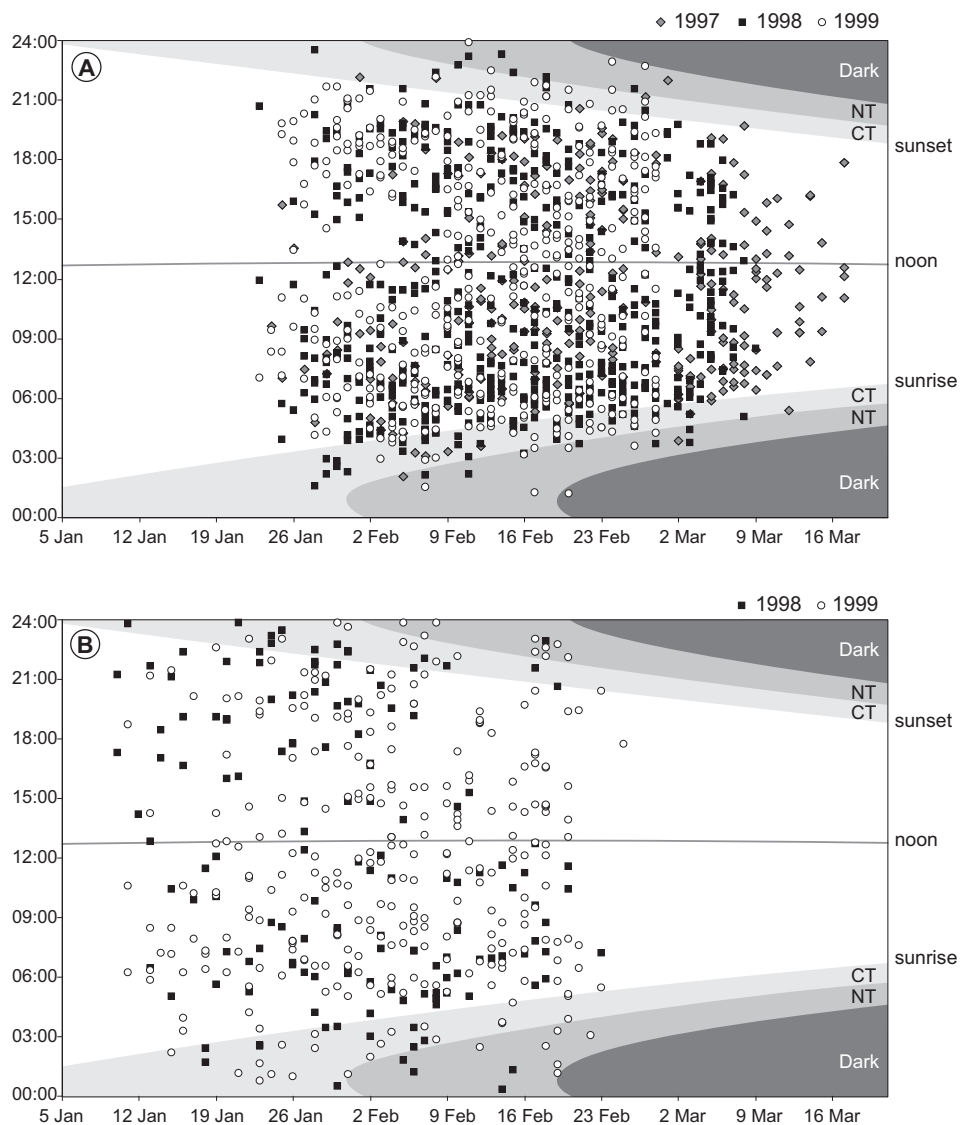


Figure 4. Timing of food delivery of A) Southern Fulmars and B) Antarctic Petrels over the course of the breeding period. Symbols indicate meal deliveries by season. Differences in background shading indicate periods of daylight, civil twilight (CT), nautical twilight (NT) and darkness (DARK). The slightly curved line at midday indicates the timing of solar noon.

There was intra-annual variation in meal deliveries, mirroring seasonal changes in daylight patterns. When considering only meal deliveries in the morning, Southern Fulmars tended to deliver their meals later as the season progressed, on average delaying these by approximately 2 minutes each day (linear regression, $P < 0.001$). No such delay was detected in Antarctic Petrels ($P = 0.8$). In the evening, Southern Fulmars on average advanced their deliveries by approximately 4 minutes per day as the season progressed ($P < 0.001$) and Antarctic petrels did so by 3 minutes per day ($P = 0.02$).

Chick provisioning

In 1997, Southern Fulmars delivered on average meals of 154 ± 55 g (mean \pm SD; $n = 237$), of 127 ± 45 g ($n = 281$) in 1998, and of 123 ± 44 g ($n = 184$) in 1999 (Fig. 5A). In 1997, meals were significantly larger than in 1998 (linear mixed model, accounting for individual effect: $P = 0.012$) and in 1999 ($P = 0.020$), but there was no difference between 1998 and 1999 ($P = 0.9$). Antarctic Petrels on average delivered meals of 111 ± 44 g ($n = 83$) in 1998 and of 152 ± 47 g in 1999 ($n = 238$) (Fig. 5B), a difference that was significant (linear mixed model: $P = 0.004$). Overall, Southern Fulmars delivered smaller meals (135 ± 50 g, representing 16.9% of the mean adult body mass) than Antarctic Petrels (142 ± 49 g representing 20.9% of the adult body mass).

We tested for species and seasonal differences in meal sizes. Meals of Southern Fulmars during 1998 and 1999 and meals of Antarctic Petrels in 1998 were of similar size (averaging 127g; linear mixed model, both factors species and season $P > 0.2$), but meals delivered by Antarctic Petrels in 1999 were significantly larger (on average 38g more, interaction species*season $P = 0.012$). Although meal sizes were highly variable, there was evidence that on average there was an increase in meal sizes until about the middle of the chick period followed by a decrease until the time of fledging. Average meal sizes delivered to Southern Fulmar chicks for the three seasons combined tended to be highest 25-35 days post-hatching (quadratic regression of chick age on meal size, effect of age: $P < 0.0005$; effect of age²: $P < 0.0005$). In Antarctic Petrel chicks, average meal sizes were highest 25-35 days post-hatching (quadratic regression, effect of age: $P < 0.005$; effect of age²: $P < 0.005$).

On average, chicks of Southern Fulmars received approximately 1-2 meals per day, with a feeding frequency that was highest between 25 and 35 days post-hatching (Fig. 5C). There was very little difference in feeding frequency between years. Consequently, the median fasting intervals of chicks were virtually identical during the three study seasons (median 14.4 hours in each season; $n = 275$ in 1997, $n = 542$ in 1998 and $n = 383$ in 1999; see Table 2), with no evidence of a year effect on fasting interval (linear mixed model on square-root transformed interval length, effect of season: $P > 0.5$). There was a significant quadratic relationship between chick

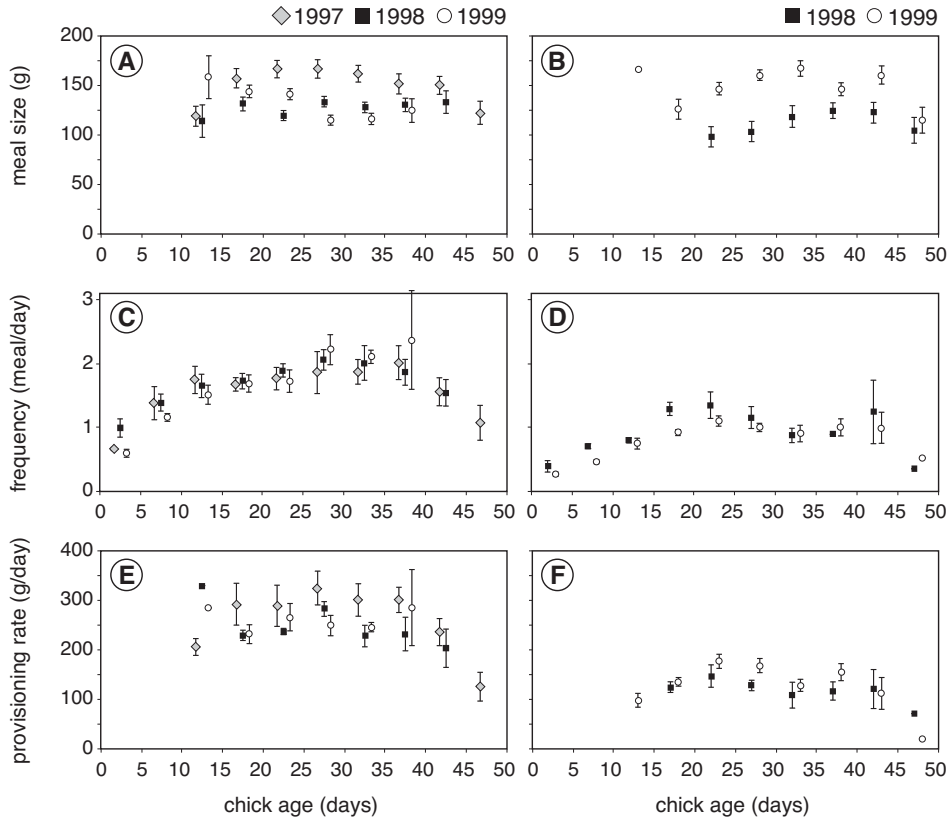


Figure 5. Changes in meal mass (A, B), feeding frequency (C, D), and provisioning rate (E, F) over the course of the chick period in Southern Fulmars (left panels) and Antarctic Petrels (right panels). Symbols show the means (with SE) during ten 5-day periods after hatching, shown separately for each study season. No data on meal sizes and provisioning rate could be collected during the first 10-15 days of the chicks when they were still brooded and guarded.

age and the duration of fasting intervals (effect of age: $P < 0.0001$; effect of age²: $P < 0.0001$).

Chicks of Antarctic Petrels were fed less frequently and received approximately 0.5-1.5 meals per day, and also in this species the feeding frequency was highest between 15 and 25 days post-hatching (Fig. 5D). Average fasting intervals of Antarctic Petrels were almost twice as long as those in Southern Fulmars, with medians of 25.2 hours in 1998 ($n = 146$) and of 26.4 hours in 1999 ($n = 295$; Table 2), a difference statistically highly significant (linear mixed model on square-root transformed interval length, effect of species: $P < 0.0001$). As in Southern Fulmars,

there was no significant season effect on interval length (linear mixed model on square-root transformed interval length, effect of season: $P = 0.26$). Likewise, there was a significant quadratic relationship between chick age and the duration of fasting intervals (effect of age: $P < 0.0001$; effect of age²: $P < 0.0001$).

The artificial nest system provided also data on the last recorded meal delivery, and thus estimates for the fasting period until fledging. In 1997, Southern Fulmar chicks fasted on average 2.6 days (SD = 0.8, $n = 5$) and for the other season there were no data available. Antarctic petrels fasted on average 6.5 days (SD = 2.6, $n = 4$) in 1998 and 8.9 days (SD = 2.9, $n = 9$) in 1999.

Table 2. Overview of the fasting intervals in hours. Data show the grand means (\pm SD) of 5-day averages per individual chick. The number of chicks is given between parentheses.

	Southern Fulmar			Antarctic Petrel	
	1997	1998	1999	1998	1999
0-5d	36.2 \pm 1.9 (2)	27.7 \pm 9.9 (9)	42.9 \pm 12.7 (7)	77.2 \pm 50.3 (4)	99.1 \pm 34.6 (9)
5-10d	18.5 \pm 5.5 (3)	18.4 \pm 4.7 (9)	21.1 \pm 3.3 (7)	34.1 \pm 3.3 (4)	53.7 \pm 11.1 (9)
10-15d	14.4 \pm 3.5 (4)	15.7 \pm 4.0 (9)	16.8 \pm 4.2 (7)	30.3 \pm 3.2 (4)	35.6 \pm 12.7 (9)
15-20d	14.5 \pm 2.1 (5)	14.4 \pm 2.9 (9)	14.7 \pm 2.8 (7)	18.9 \pm 2.6 (4)	26.6 \pm 4.1 (9)
20-25d	14.1 \pm 2.6 (5)	12.9 \pm 2.1 (8)	14.9 \pm 4.5 (7)	19.0 \pm 5.5 (4)	23.0 \pm 6.4 (9)
25-30d	14.8 \pm 6.3 (5)	12.2 \pm 3.0 (8)	11.6 \pm 3.3 (7)	22.1 \pm 6.0 (4)	24.8 \pm 5.1 (9)
30-35d	13.6 \pm 4.4 (5)	13.6 \pm 5.5 (8)	11.5 \pm 1.3 (6)	28.4 \pm 7.3 (3)	29.4 \pm 8.2 (9)
35-40d	12.5 \pm 3.3 (4)	13.9 \pm 3.9 (8)	14.2 \pm 8.8 (4)	26.8 \pm 0.1 (2)	27.1 \pm 9.8 (8)
40-45d	17.1 \pm 6.9 (5)	16.4 \pm 4.4 (4)		22.9 \pm 13.0 (2)	31.1 \pm 14.6 (6)
45-50d	28.1 \pm 15.7 (4)			67.7 (1)	45.3 (1)
50-55d	16.5 \pm 15.3 (2)				
average	17.1 \pm 8.5(44)	16.3 \pm 6.7(72)	18.8 \pm 11.5(52)	33.1 \pm 25.1(32)	39.5 \pm 27.3(78)

The similar meal sizes but clear differences in feeding frequencies between the two species resulted in marked differences in provisioning rates. On average, Southern Fulmars delivered nearly twice as much food per day to the chick (mean \pm SD: 265 \pm 96 g/day in 1997, 240 \pm 59 g/day in 1998 and 256 \pm 61 g/day in 1999) when compared to Antarctic Petrels (122 \pm 33 g/day in 1998 and 140 \pm 52 g/day in 1999), a species difference that was highly significant (linear mixed model, $P < 0.0001$). In both species, the provisioning rate increased until approximately 25-30 days post-hatching, then decreased again, so that there was a significant quadratic relationship between chick age and provisioning rate (effect of age: $P < 0.001$; effect of age²: $P < 0.0005$).

In Southern Fulmars, the provisioning rates were significantly higher in 1997 than in 1998 (linear mixed model of season effect, 1997 vs. 1998, $P < 0.05$) but

at intermediate levels in 1999 (1999 vs. 1997, $P = 0.11$; 1999 vs. 1998, $P = 0.71$). In Antarctic Petrels there was some evidence that the provisioning rate was higher in 1999 than in 1998 (by on average 18g per day). Although the effect of season per se was statistically significant ($P = 0.11$), a linear mixed model that included season as a factor performed significantly better based on the Akaike and Bayesian Information Criteria (AIC = 789.10, BIC = 802.76) than a similar model that excluded season (AIC = 796.75, BIC = 808.20).

Chick growth

Chick growth in both species followed the typical procellariiform pattern, well described by a double Gompertz curve (Fig. 6): initially fast growth until reaching a plateau at around 30-35 days, followed by a period of weight loss until fledging. A range of non-linear mixed effects models with a double Gompertz model incorporated was examined describing growth for both species combined; amongst these, the 'best' model (based on AIC) included species differences in the following coefficients of the model: k_1 ($P = 0.0145$), t_1 ($P < 0.0001$) and t_2 ($P < 0.0001$), but indicated no species difference in A ($P > 0.7$ if species effect on A added to final model) or in k_2 ($P = 0.18$ if species effect on k_2 added).

The calculated parameters chick growth rate, age at peak mass, peak mass, mass loss rate, age at fledging, and weight at fledging for each year and species are shown in Table 3. Southern Fulmar chicks grew faster (by 4.65 g/day, $P < 0.0001$) and reached higher peak masses (199g heavier, $P < 0.0001$) at a later age (1.74 days later, $P < 0.0005$) than Antarctic Petrels. The mean peak masses constituted up to 140% of the mean adult mass in Southern Fulmars and 136% of the mean adult mass in Antarctic Petrels. After reaching peak mass, chicks of both species lost weight at approximately equal rates (about 20–21g/day, $P = 0.68$). Southern Fulmar chicks fledged at a later age (by 2.0 days, $P < 0.0001$) and at a higher mass (190g heavier, $P < 0.0001$) than Antarctic Petrel chicks. At fledging, Southern Fulmar chicks were on average 101.5% and Antarctic Petrels chicks 91.7% of the mean adult mass.

In our sample of Southern Fulmar chicks, we found no evidence of any year effects on either the growth rate ($P > 0.3$), age at peak mass ($P > 0.1$), peak mass ($P > 0.28$), mass loss rate ($P > 0.3$) or fledging mass ($P > 0.5$). However, the chicks fledged at a significantly younger age in 1999 than in 1997 (by 1.5 days, $P = 0.029$) and in 1998 (by 1.3 days, $P = 0.0068$), although there was no difference in fledging age between 1997 and 1998 ($P > 0.7$).

In contrast, in 1999 Antarctic Petrel chicks fledged at significantly later age than in 1998 (by 1.65 days, $P = 0.0068$). Also for this species, no significant year effects on any of the other growth parameters were found (peak mass, $P = 0.2$; mass loss rate, $P = 0.1$; fledging mass, $P > 0.9$), although there was weak evidence of a somewhat

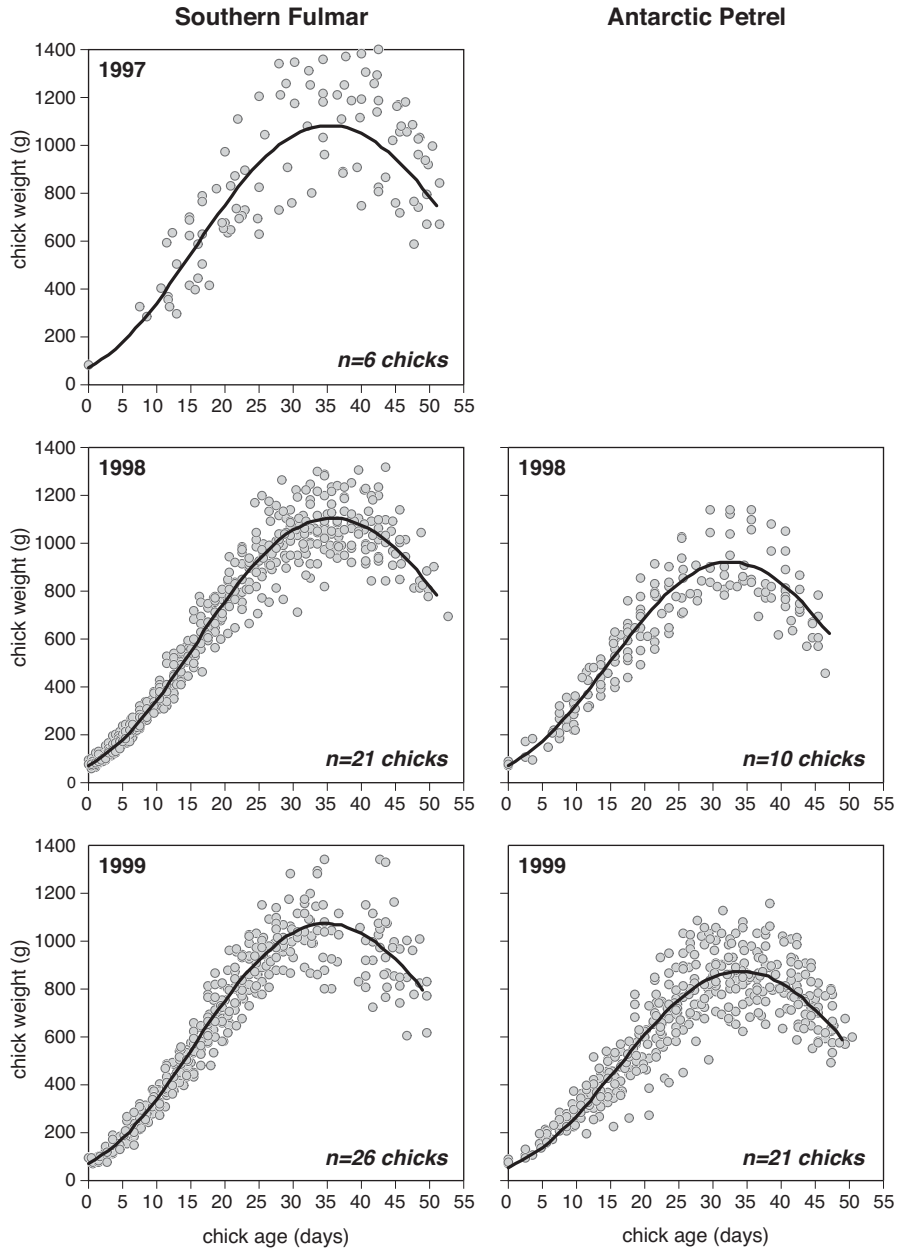


Figure 6. Chick growth in Southern Fulmar (A-C) and Antarctic Petrels (D-E). For each season all weight measurements and numbers of measured chicks are given. The lines represent the mean double Gompertz growth curves through all data points for that season.

Table 3. Parameters describing the growth of successful Southern Fulmar and Antarctic Petrel chicks on Ardery Island. Annual means, standard errors and the numbers of sampled chicks are shown. Average adult mass is 800g for Southern Fulmars and 678g for Antarctic Petrels.

	Growth rate (g/d)	Peak age (d)	Peak mass (g)	Loss rate (g/d)	Fledging age (d)	Fledging mass (g)
Southern Fulmar						
1997	32.8 ± 2.4 (6)	35.3 ± 0.9 (6)	1085.4 ± 84.4 (6)	21.3 ± 1.7 (5)	51.2 ± 0.6 (5)	800.0 ± 83.6 (5)
1998	34.4 ± 0.7 (21)	35.7 ± 0.3 (21)	1144.5 ± 21.9 (21)	21.5 ± 0.8 (19)	51.0 ± 0.3 (19)	803.6 ± 21.7 (19)
1999	34.1 ± 0.6 (22)	34.9 ± 0.4 (22)	1112.8 ± 21.8 (22)	20.3 ± 0.7 (13)	49.7 ± 0.3 (13)	829.5 ± 42.8 (13)
Combined	33.9 ± 0.5 (53)	35.3 ± 0.2 (53)	1119.1 ± 15.8 (53)	21.1 ± 0.5 (37)	50.6 ± 0.2 (37)	812.2 ± 21.1 (37)
Antarctic Petrel						
1998	31.0 ± 1.1 (10)	32.4 ± 0.6 (10)	959.0 ± 37.4 (10)	21.9 ± 1.1 (10)	47.5 ± 0.3 (10)	624.7 ± 41.9 (10)
1999	28.4 ± 0.7 (21)	34.1 ± 0.6 (21)	901.4 ± 22.9 (21)	19.7 ± 0.7 (20)	49.2 ± 0.4 (20)	620.4 ± 17.0 (20)
Combined	29.3 ± 0.6 (31)	33.6 ± 0.4 (31)	920.0 ± 19.9 (31)	20.4 ± 0.6 (30)	48.6 ± 0.3 (30)	621.8 ± 17.6 (30)

slower growth rate ($P = 0.051$) in 1999 than in 1998, associated with a peak age reached somewhat later ($P = 0.075$).

Chick growth in relation to provisioning rate

Data on provisioning rate as well as growth were available for a total of 21 Southern Fulmar chicks. Chick growth rate was significantly correlated with the provisioning rate (Pearson's correlation; $r = 0.713$, $P = 0.0009$; Fig. 7A), and so was the peak mass of chicks ($r = 0.678$, $P = 0.0020$; Fig. 7E). The age at peak mass was not correlated with provisioning rate ($r = 0.126$, $P = 0.618$; Fig. 7C). Linear regression showed that an increase in provisioning rate of 100g/day corresponded with an increase in growth rate of 7.7g/day and, consequently, a higher peak mass with chicks being 272g heavier.

The provisioning rate for the whole chick period was not correlated to the mass loss rate ($r = 0.244$, $P = 0.400$), neither to the age at fledging ($r = -0.228$, $P = 0.433$; Fig. 7G). There was, however, a correlation with the fledging mass ($r = 0.557$, $P = 0.048$; Fig. 7I): an increase in provisioning rate of 100 g/day corresponded with a 212g heavier fledging mass.

In Antarctic Petrels, none of the above correlations between provisioning rate and chick growth was found to be significant, but the small sample size ($n = 13$) of chicks with both provisioning and growth data should be considered. The provisioning rate was not correlated with growth rate ($r = 0.281$, $P = 0.353$), peak age ($r = 0.112$, $P = 0.717$), or peak mass ($r = 0.473$, $P = 0.102$; Fig. 7B,D,F). Nor was the provisioning rate during the 50 days following hatching correlated with mass loss rate ($r = -0.232$, $P = 0.446$), fledging age ($r = 0.339$, $P = 0.257$), or fledging mass ($r = 0.263$, $P = 0.385$; Fig. 7H,J) of Antarctic Petrels.

There was a significant difference in the efficiency of mass transfer from food delivered each day to the mass gained by the chick between the two species (Fig. 8). Southern Fulmar chicks, on average, gained 0.127 ± 0.003 g ($n = 18$) for every g of food delivered, whereas Antarctic petrel chicks gained 0.198 ± 0.008 g ($n = 13$) for every g of food delivered (linear model, $t = 9.373$, $P < 0.00001$). Thus, mass transfer efficiency in Antarctic Petrels was almost 1.56 times higher than in Southern Fulmars. Within either species, we detected no significant difference between years in mass transfer efficiency (linear model, effect of season in Southern Fulmars: $t = 1.086$, $P = 0.294$; in Antarctic Petrels: $t = -1.414$, $P = 0.185$).

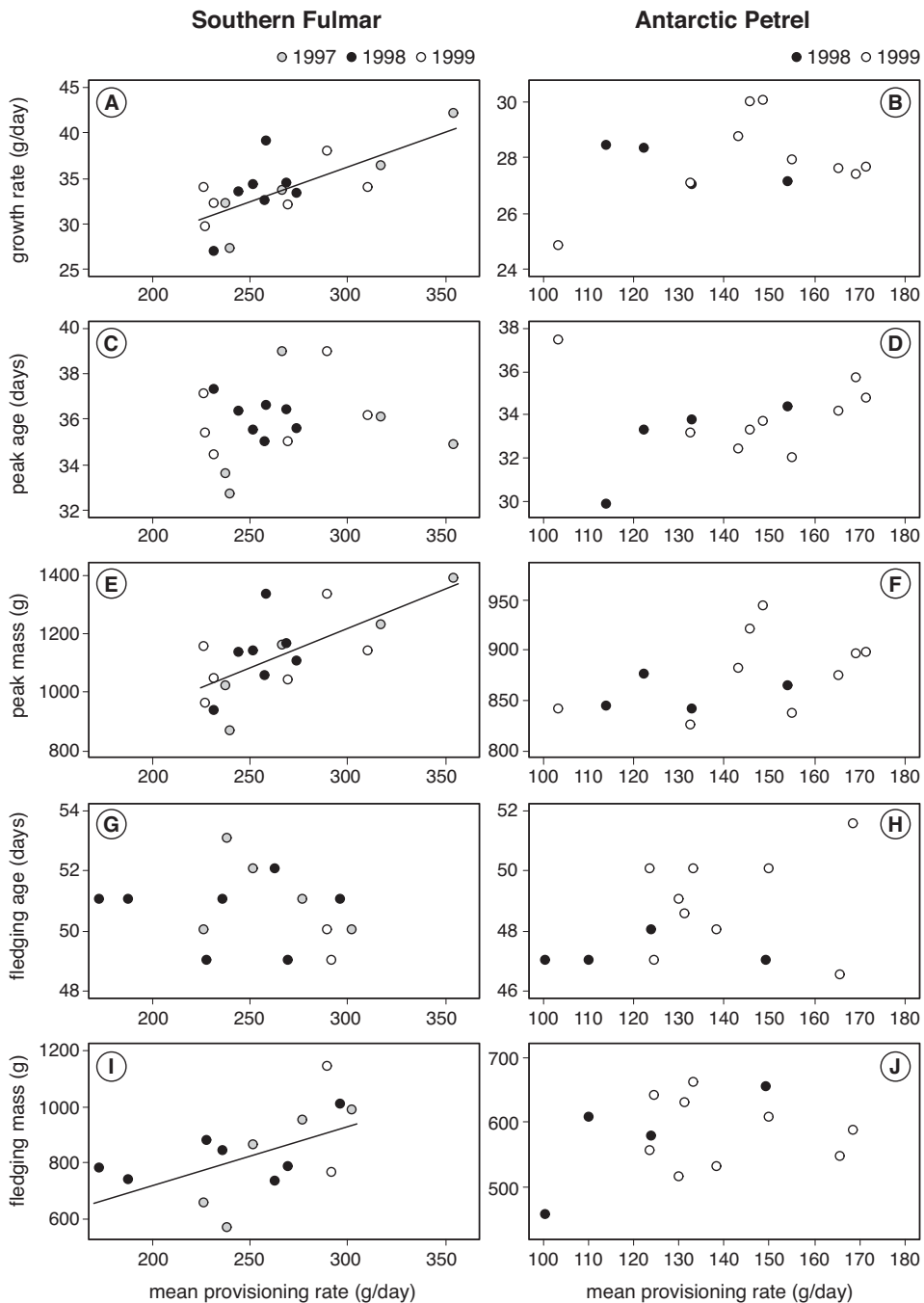


Figure 7. Relationships between average chick provisioning rate and chick growth rate (A, B), age at peak mass (C, D), peak mass (E, F), fledging age (G, H) and fledging mass (I, J), for Southern Fulmars (left panels) and Antarctic Petrels (right panels). Significant regression lines are shown and symbols are coded by season (see legend). In A-F, provisioning rate is averaged over the 30 days after hatching and prior to age at peak mass; in G-J, provisioning rate represents the 50 days after hatching including the mass loss period.

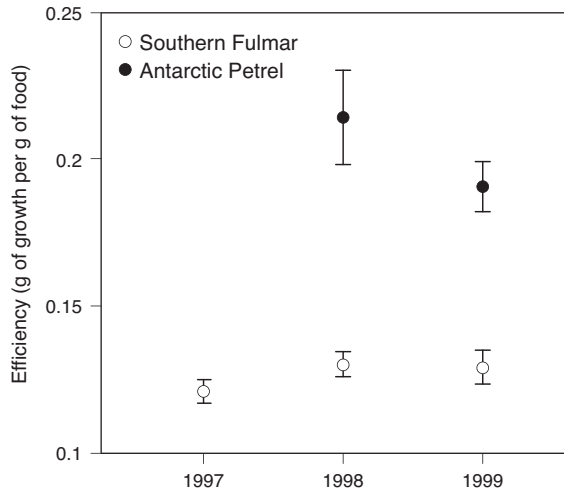


Figure 8. Efficiency of mass transfer expressed as gram of chick growth per day for each gram of food delivered per day. Means \pm 1 standard error are shown for both species and for the study seasons separately.

DISCUSSION

Chick provisioning

The artificial nest system we used on Ardery Island gave a useful insight in the provisioning ecology of two Antarctic fulmarine petrel species and did not have a negative effect on the survival of their chicks. The generally higher survival rates of chicks on artificial nests maybe were related to a non-random position of the artificial nests in the colony. Because we had only a limited number of nest units available, we tended to select sites in the colony with a high chance of eggs being laid and chicks being raised. During the first season 4 nest units were relocated and installed on sites with a chick, which explains the large, but not significant difference between chicks from control nests and artificial nests. In the last season, however, there was a nearly significant difference, but in this season artificial nests were not relocated.

The most obvious difference in chick provisioning between the studied species was the feeding frequency and thus the total mass of food that parents were bringing to their young. Southern Fulmars chicks received almost twice as many meals, and almost twice as much food per day, as Antarctic Petrel chicks. The total chick provisioning rates we found in this study appeared to be much higher than other studies. For example, at Svarthamaren, an Antarctic Petrel colony situated more than 200 kilometers inland, mean meal size (146g) was similar, but the estimated provisioning rate of 90g/day seemed much lower than on Ardery Island (Lorentsen 1996, Fig. 5 in this study). However, this low value can be explained by differences in calculating the provisioning rate. When we ignore the intra-seasonal variation, and use mean values for meal size and feeding frequency (Table 2), we arrive at very similar estimates for Antarctic Petrels at Ardery Island: 80g/day in 1998 and 92g/day in 1999.

Within each season, both meal sizes and fasting intervals varied much, which may indicate that both species are rather flexible in their foraging strategy. Such flexibility is not expected if there is a high need of optimizing the flight loads. For example, closely related Northern Fulmars foraging in areas with high food availability are - instead of maximizing their meal sizes (on average 13% of their adult body mass) -, adjusting their feeding rates to increase chick provisioning, even when food abundance is temporarily lower (Phillips & Hamer *et al.* 1997, Hamer & Thompson 1997, Phillips & Hamer 2000a, Gray *et al.* 2005b). In this species, chick provisioning rates were lower (at peak delivery around 160g/day) than those for Southern Fulmars, but the northern sibling species is slightly smaller in size and chicks take at least 5 days longer to fledge (Mougin 1967, Phillips & Hamer 2000a, Gray *et al.* 2005b).

Between years, mean meal sizes varied considerably, but the observed

differences were different in each species. The larger meal sizes in 1997 for Southern Fulmars could be related to exceptional conditions in the colony in the beginning of that season. Breeding success was extremely low due to high snow cover in the colony and high egg predation by South Polar Skuas *Catharacta maccormicki* (Van Franeker *et al.* 2001). It is possible that the parents of the surviving chicks in the colony were breeding pairs holding good locations in the colony and having a good condition and therefore able to provide larger meals to their offspring. Because the feeding rates of Southern Fulmars were not different between the three seasons, the larger meal sizes in 1997 probably indicated that they were more successful in finding food in this year. For Antarctic Petrels, the smaller meal sizes in 1998 in comparison to 1999 were partly compensated by higher feeding rates, causing only a small difference in the overall provisioning rate between the seasons.

Southern Fulmars brought relatively lighter meals (17% of mean adult body mass) in comparison to Antarctic Petrels (21%), but these results are well within the range of other procellariiformes of similar size (Phillips & Hamer 2000a). The difference between Southern Fulmars and Antarctic Petrels could not be explained by differences in food composition, because the diets of chicks of both species are similar at Ardery Island (Van Franeker 2001). Furthermore, we have no indications that differences in morphology or flight capabilities were causing different chick provisioning rates. For specimens we collected on Ardery Island the wing loading appeared to be similar between both species (Dijkstra 2003).

Unfortunately, we were not able to analyze the provisioning patterns at the individual level of the parents, because our system was not always able to read the transponder at each parental visit. Especially in the post-guarding period, when parents usually stayed near their nests for short periods, we were often unable to read the transponder of the parent delivering a meal. We found a unimodal distribution in fasting intervals which is normal for medium-sized petrels with relatively high feeding frequencies (Baduini & Hyrenbach 2003).

Diurnal patterns in meal delivery

Meal delivery occurred mostly during the day, although Southern Fulmars were more strict daylight provisioners than Antarctic Petrels, which delivered their meals more equally distributed over the day. The dark hours, when the sun was more than 12 degrees below the horizon, started in the second half of February when Antarctic Petrel delivered their last meals, and were avoided by Southern Fulmars by timing their meals later in the morning and earlier in the afternoon as the season progressed. In this study we show that chicks of both species were mostly fed during the morning,

to a lesser extent during afternoon/evening and rarely overnight. Similar diurnal patterns in provisioning have been observed in Shy Albatrosses *Thalassarche cauta* (Hedd *et al.* 2002) and in Northern Fulmars (Hamer & Thompson 1997, Philips & Hamer 2000a). For high Arctic Northern Fulmars, Weimerskirch *et al.* (2001) observed also peaks in delivery in the morning and evening for males, but, interestingly, not for females.

Both species have a peak in meal delivery during the morning and a somewhat lower peak during the evening (Fig. 3). The more pronounced bimodal foraging pattern in Southern Fulmars could be related to their higher feeding frequency, which was averaging to up to 1.5 - 2 meals per day for chicks older than 10 days, whereas Antarctic Petrels delivered about 1 meal per day. Possibly due to the shorter foraging trips Southern Fulmars have less variation in the return times and less variability in fasting intervals (coefficients of variation ranging from 41% to 61%, Table 2) than Antarctic Petrels with CVs of 69-75%. The longer and more variable foraging trips of Antarctic Petrels may explain their more equal distribution of meal deliveries over the day. Furthermore, Southern Fulmar parents might be more constrained during the day because they attend their chicks for longer, even after the post-guarding period (Creuwels *et al.* 2008).

In the literature, there is still considerable debate to what extent procellariiform birds forage during the night. Actual observations on nocturnal foraging are scarce. For example, Harper (1987) found that 13 petrel species (out of 20) were feeding at night, of which 5 species exclusively so. Fulmarine petrels were predominantly feeding during the day, but unfortunately the observations of Harper (1987) did not include Southern Fulmars or Antarctic Petrels. In the Ross Sea, peaks of foraging by flying seabirds which did include Southern Fulmars or Antarctic Petrels (but observations were not specified per species) were seen between 6-11 hours in the morning and 18-23 in the evening (Ainley *et al.* 1984). This periodicity of feeding activities occurred despite long day lengths and relatively equal light conditions because of an almost always overcast weather type. Southern Fulmar chicks on Ardery Island were regularly observed being unattended at night, which may suggest a preference for nocturnal feeding of the adults (Van Franeker 2001, Creuwels pers. obs.). Because Southern Fulmars probably have feeding grounds closer to the breeding grounds, they might be able to perform additional feeding activities before the dark hours and return to feed their chicks.

It is not fully clear whether both species avoid nocturnal food deliveries to their chicks in the colony because it is more dangerous to land in the colony at darkness, or that they would like to profit from vertical migration of prey species which are getting closer to the surface at night. It is possible that birds that arrive back to the colonies during darkness wait at sea until more light is available to land in the

colony. Procellariiformes are well adapted to flying of long stretches over sea, but they do have problems when returning to their nests on the cliffs. All medium and larger-sized species have high wing loadings and high flight speeds and thus have difficulty with landing. When returning to the colonies, Southern Fulmars and Antarctic Petrels regularly flew repeatedly with high speed just over their own nest site apparently for fine-tuning and assessing their stalling and their landing procedures. Despite these exploration flights adults, especially of Southern Fulmars, were still regularly crash-landing somewhere in the colony and making somersaults, not always close to their own nest sites.

Growth parameters

The high chick provisioning rates as we found in this study demonstrate that the chicks were supplied with sufficient food to enable rapid chick growth, which also has been suggested for both species at other locations (Weimerskirch 1990a,b, Hodum & Weathers 2003). Chicks of Antarctic fulmarine petrels show exceptionally rapid chick growth and various studies showed that growth constants as calculated in logistic growth models were among the highest values within the order of the Procellariiformes (Warham 1990, Starck & Ricklefs 1998, Hodum 1999). In this study, we used a different measure and followed Huin & Prince (2000) to estimate linear chick growth. On Ardery Island, chicks grew 34g/day in Southern Fulmars and 30g/day in Antarctic Petrels, and these values were somewhat lower than values of both species at Rauer Islands (43g/day respectively 34g/day, Hodum 1999). Hodum (1999) pointed out that these growth rates deviate enormously (two times or more than predicted) from the regression of growth rate against adult mass in 27 species of procellariiformes (Croxall & Gaston 1988). Antarctic Petrels at Svarthamaren, however, showed a much slower linear chick growth of 19.3g/day which could be related to the harsh weather conditions far inland on the Antarctic continent. Here, chicks attained lower peak masses and probably take longer to fledge at this locality: 35-37 days old chicks were still showing positive growth and weighing on average 100-200g less than chicks of similar age in colonies along the Antarctic coast (Lorentsen 1996, Hodum 1999, this study)

On Ardery Island, Southern Fulmar chicks fledged when they were 2 days older than Antarctic Petrel chicks and this age difference was less than on the Rauer Islands (4 days), mainly because of the compressed chick periods of Southern Fulmars on Ardery Island, especially in 1999 (Hodum 2002, Creuwels *et al.* 2008, this study). Why the chick periods were reduced during the last season is not fully clear. Chicks that survived in this season, hatched on average 1.4 days earlier, but there was no relationship between hatching date and the length of the chick period in the three seasons. Until 1 March 1999, chick survival was extremely high until the heavy

snowfall buried many chicks under a deep layer of snow, and deprived them of being fed for 1-2 weeks. Normally parents are able to dig their chick out of snow within a few days and able to continue to feed them. The build-up of snow in March 1999 was extreme at certain places. Some adults were digging a lot around their nest but still could not find their chick back. More successful parents made a snow cave to be able to feed their chicks, but this happened in this season often after many days. Early hatched chicks might have been able to build up more body reserves to withstand the starvation. The surviving chicks lost weight at a lower rate and fledged heavier in the 1999 season (Table 3) than in other years.

In contrast, the fledging period of Antarctic petrels was longer in 1999 than in 1998. Again various explanations are plausible. First, chick growth might be slower, because in 1999 there were more successful breeding pairs, possibly including pairs with little breeding experience or 'low-quality' individuals. This could be the reason why peak mass was reduced and reached later in this season (Table 3). The weight recession period was equal to that in 1998 and did not contribute to a longer chick period. Second, the deteriorated weather conditions late in the season may have influenced individual chicks to delay their fledging. On average, chicks fledge around 1 March, but they fledged significantly later in 1999 because the first snow showers had just started at this time (Creuwels *et al.* 2008).

Southern Fulmars were fledging relatively heavier (102% of adult mass) than Antarctic Petrels (92% of adult mass), although the weight loss rate after peak mass (20-21g/day) as well as the mass recession period (15 days) was similar between the species. When considering differences in maximum weight, Southern Fulmar chicks lost weight at a rate of 1.9% and Antarctic Petrels at a rate of 2.2% of the peak mass per day. This relatively higher weight loss could partly be explained by the lower provisioning rate of Antarctic Petrels late in the season and the fact that they leave their chicks at an earlier stage in the breeding season. Antarctic Petrels appeared to desert their chicks at about 8 days before fledging, whereas Southern Fulmars deserted their offspring on average probably 2-3 day before the chicks finally flew off. On the Rauer Islands, Southern Fulmar chicks fledged on average with a weight of 91-97% of adult mass, and Antarctic Petrels at 84-89% of adult mass (Hodum 1999).

Since the publication of the "Double Gompertz curve" by Huin & Prince (2000) the equation has still been hardly used, despite the possibility of modeling chick weight loss after peak mass. Furthermore, it does not require to truncate the growth data at an arbitrary chick age or to define assumptions on the asymptotic weight of the chick. Browsing the literature on procellariiform chick growth we found only studies by Silva *et al.* (2007) and Copello & Quintana (2009), but unfortunately they did not mention how well the curves fitted the data. Terauds & Gales (2006) mentioned that they were not able to use this model to describe albatross chick

growth due to poor fit of the growth trajectories. The model has five parameters, and as a drawback it requires relatively many data per individual chick growth curve. In our study, however, which focused on species differences, we incorporated this model in non-linear mixed models, which enabled us to analyze chick growth even of nests with relatively few data points.

Provisioning influencing chick growth

As a general rule, one could expect that chicks that receive more food grow faster, as shown in Antarctic Petrels (Lorentsen 1996). However, in this study we found such a significant relationship only for Southern Fulmars, but not in Antarctic Petrels (Fig. 7). The four nests in 1998 showed even a somewhat negative trend between growth and provisioning, for which we have no explanation. Other studies examining the relationship between growth and provisioning of individual chicks showed no effect (Weimerskirch *et al.* 2000b, Hedd *et al.* 2002), although Huin *et al.* (2000) were able to show a positive effect.

Consequently, we found that the provisioning rate was affecting both peak mass and fledging mass in Southern Fulmars, but not in Antarctic Petrels. In both species there were no correlations of provisioning with age at peak mass or age at fledging. This was not surprising because the timing of the breeding events is highly synchronous in Antarctic fulmarine petrels. Due to the strong correlation between actual date and chick age there was little variation in age at peak mass or age at fledging, as reflected in the low standard errors in Table 3, which may reduce the possibility to detect correlations. When testing the fledging parameters for correlations with provisioning during the first 30 days, we found similar correlations as presented.

For the general absence of significant correlations between provisioning and weight and growth parameters in Antarctic Petrels, we refer to the low sample size. The relationship between provisioning and growth is affected by a suite of parameters, including meteorological conditions, individual qualities of the parents, availability and quality of the food resources. Furthermore, internal factors of the chick, such as development of gut and other organs and tissues, thermoregulatory capabilities and structural size would be expected to influence the observed individual growth trajectories (Ricklefs *et al.* 1998).

Efficiency of food conversion

This study showed that Southern Fulmars were provisioning their chicks with 82-96% more food mass than Antarctic Petrels, which is a difference of about 100g food per day. This is much more than we can explain by their difference in their body size alone: Southern Fulmars adults appeared to be about 18% heavier and their chicks

at their peak mass about 22% heavier than Antarctic Petrels. During the period of positive chick growth, one gram of food delivered per day resulted in 0.13g chick mass added per day in Southern Fulmar and 0.20g per day in Antarctic Petrel. Such a difference could be the result from a higher efficiency in food conversion in Antarctic Petrel chicks or from higher quality of the food supplied by the adult Antarctic Petrels.

Concerning the aspect of efficiency of converting food to body mass, Hodum (1999), Weathers *et al.* (2000) and Hodum & Weathers (2003) showed that Southern Fulmar chicks are less well insulated, have a higher metabolic rate and spend more energy on thermoregulation. Based on their calculations, Southern Fulmar chicks need, per gram of their fledging mass, 17% more energy than chicks of the Antarctic Petrels. Thus, Southern Fulmars simply do need more food.

Also the possible effect of parents delivering food of different quality to their chicks should be considered. The chick provisioning rate does not take into account differences in prey species and digestibility and caloric value of the food. Earlier we concluded that prey composition of meals delivered to their chicks is similar (Fig. 1). However, although we have no quantitative data, Southern Fulmars brought much fresher meals containing lower quantities of stomach oil to their chicks (Norman & Ward 1992, Van Franeker 2001). All procellariiformes with the exception of diving petrels (Pelecanoididae) have the capacity to form energy-rich stomach oil which is derived from their food and which reduces commuting costs considerably (Warham 1990, Roby *et al.* 1997, Obst & Nagy 1993). Processing of the food and producing stomach oil needs time and various studies show more digested food and higher content of stomach after long trips, e.g. in species with a dual foraging strategy (Chaurand & Weimerskirch 1994, Weimerskirch & Cherel 1998, Cherel *et al.* 2002). In this study we compared species with a similar diet, but with clearly different provisioning strategies. The average chick feeding rate of Southern Fulmars was twice that of Antarctic Petrels, thus one could expect differences in the amount of processed food and hence, the energy density of the delivered meals. Antarctic Petrels of Ardery Island make longer foraging trips than Southern Fulmars, because detailed differences in prey composition point to more pelagic foraging areas in this species (Van Franeker 2001). Although we have no direct measurements of the energy contents of chick meals, we hypothesize that Antarctic Petrels enhance the quality of the food by increasing the proportion of stomach oil and lowering the water content.

Concluding remarks

Coastal Antarctica, where we conducted this study, is the southern limit of the breeding distribution of Southern Fulmars (Creuwels *et al.* 2007) and the northern limit of Antarctic Petrel breeding distribution (Van Franeker *et al.* 1999). Most Antarctic

Petrel colonies are situated inland where they breed in harsh conditions at longer distances from the feeding grounds, which could be the reason why inland chicks were growing slower (Lorentsen 1996) than along the coast of Antarctica (Hodum 1999, this study). For Southern Fulmars however, it is the other way around, and they typically breed under warmer conditions, probably closer to the sea and possibly have easier access to food resources (Creuwels *et al.* 2007, 2008). On Ardery Island, Southern Fulmars may have to maximize their feeding rate in order to provide their chicks with sufficient energy to withstand the colder conditions.

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CHAPTER

4

UNEXPECTED EFFECTS OF CLIMATE CHANGE ON THE PREDATION OF ANTARCTIC PETRELS

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ABSTRACT

Antarctic Petrels *Thalassoica antarctica* on Ardery Island, Antarctica (66°S, 110°E), experienced major reductions in breeding success and breeder survival over four study seasons from 1984/85 to 1996/97. In 1996 the reason was revealed. A large snowdrift covered part of the study colony on the cliffs. Southern Giant Petrels *Macronectes giganteus*, normally lacking access to this area, exploited the snow for soft 'crash-landings'. After landing they waited for the disturbed birds to resettle on their nests and then used surprise to seize and kill a victim. Predation continued into the egg period, and only stopped after the snowdrift had melted. Giant petrels showed no interest in the eggs but, during the panic caused by their activities, South Polar Skuas *Catharacta maccormicki* took the deserted eggs. Antarctic Petrel mortality due to predation within the 1996/97 season amounted to 15.4% of experienced breeders, and breeding success was reduced to virtually zero. Weather data from the nearby Casey Station over the 1980-1996 period showed that a significant increase in precipitation has occurred, in combination with shifts in speed and direction of winds. We conclude that the decreases in breeding success and survival in earlier seasons were also related to increased snowfall and predation. Although similar predation behaviour by giant petrels has not been reported before, we think that it is long established and explains why nesting of the smaller fulmarine petrels is limited to steeper cliffs or sheltered sites. The complexity of the response seems unlikely to be predicted by our present understanding of how climate change affects ecosystems.

INTRODUCTION

The Antarctic Petrel (*Thalassoica antarctica* Gmelin) is a characteristic seabird of the high Antarctic. Its population is of the order of 10 to 20 million birds, which forage year-round in and near the marginal ice zones of the Southern Ocean. Breeding colonies are found only along the continental coast of the Antarctic or even further south (Van Franeker 1996, Van Franeker *et al.* 1999). Like the Snow Petrel (*Pagodroma nivea* Forster) (Croxall *et al.* 1995), it is found nesting on barren mountain peaks (nunataks) protruding from the Antarctic icecap, at a distance of hundreds of kilometres from the nearest open ocean waters in even mid-summer. As a representative species of the high Antarctic environment, the Antarctic Petrel has been selected as one of the target organisms in the CCAMLR Ecosystem Monitoring Program CEMP (CCAMLR 1997).

A Dutch-Australian study of petrels was started in 1984/85 on Ardery Island near the Australian Casey Station (Fig.1). Investigations were continued in the 1987/

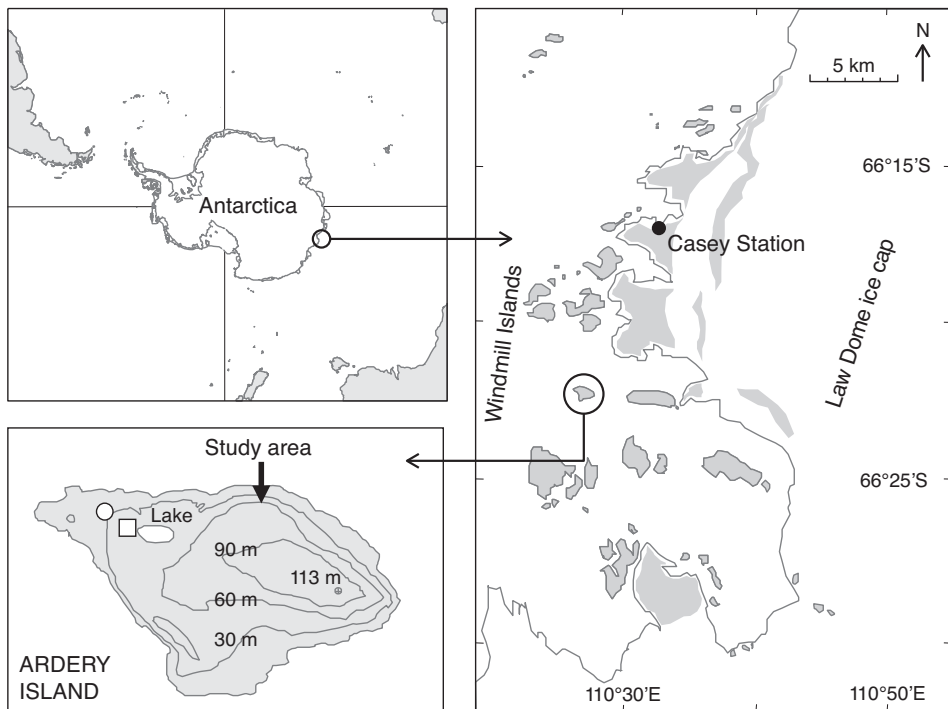


Figure 1. Ardery Island study location. Antarctic Petrels were studied on the 'Northern Plateau', a less steep section halfway down the steep northern cliffs of Ardery Island (arrow). The location of the summer field hut in 1984 and 1986 (circle) was covered by snow in 1990 and huts were placed on a new position (square).

87 and 1990/91 breeding seasons. The breeding success of Antarctic Petrels over these three study seasons showed consecutive sharp decreases. Each time, the major reduction in breeding success was already evident in the egg phase at the start of our observations.

The cause of the declining success was obscure. Timing of the breeding offered no explanation. Differences in starting dates were small and did not correlate with changes in breeding success. The composition of food, and growth of chicks indicated no shortage of food or major changes in prey species. Lacking explanations from the breeding season itself, we hypothesized that a decreasing number of birds attempted to breed, possibly because deteriorating winter foraging conditions lowered the body condition of the birds to below threshold levels required for breeding.

Therefore, in 1996/97 a new phase of the Ardery Island project began, focusing on body condition of individual birds and starting fieldwork as early as possible in the pre-breeding phase. In this season it soon became clear that less subtle factors than pre-breeding condition were affecting the breeding success of Antarctic Petrels on Ardery Island. This paper reports on our observations in 1996/1997, looking back at the situation in previous years.

METHODS

Antarctic Petrels were studied on Ardery Island during the breeding seasons of 1984/85, 1986/87, 1990/91 and 1996/97. Ardery Island (66°S, 110°E) is one of the Windmill Islands, situated in Vincennes Bay, off the eastern coast of Law Dome, Wilkes Land, Antarctica (Fig. 1). The island is just over one kilometre long, 113 m high and has many steep cliffs. The Australian base 'Casey' lies about 11 km to the north. Law Dome is fully glaciated, and only a few coastal outcrops and the small islands become free of snow and ice during summer.

The population of Antarctic Petrels on Ardery Island was relatively small with approximately 275 breeding pairs (Van Franeker *et al.* 1990). This estimate was based on the number of Apparently Occupied Sites (AOS; Walsh *et al.* 1995) counted from viewpoints outside the colonies during the egg period of mid-December 1984. The main colony of at least 175 AOS is located at the cliffs on the northern side of the island. We named this nesting area the 'Northern Plateau' which is somewhat misleading because it concerns a relatively small, less steep section halfway down the otherwise very steep cliffs. It has a rough surface of rock boulders and small terraces where Antarctic Petrels nest closely together. They are surrounded by colonies of Southern Fulmar *Fulmarus glacialoides* (Smith) and Cape Petrels *Daption capense* (L.) and dispersed hole-nesting Snow Petrels and Wilson's Storm-petrels *Oceanites*

oceanicus (Kühl).

Two pairs of South Polar Skuas *Stercorarius maccormicki* (Saunders) patrol the Northern Plateau colonies. The island has a population of about 15 breeding pairs of skua with variable numbers of non-breeders around. They breed on the higher flat part of the island above the cliffs. As no penguins breed on Ardery, the skuas strongly depend on the petrels for food, and fiercely defend feeding territories against other breeders and non-residents (Van Franeker *et al.* 1990; Baker & Barbraud 2001).

Southern Giant Petrels *Macronectes giganteus* (Gmelin) can be seen anywhere in the Casey region, but the only breeding population of ± 150 to 200 pairs in the area is on the Frazier Islands, c. 20 km to the northwest (Murray & Luders 1990, Woehler *et al.* 1990, personal observation).

In 1984 we established a study area for Antarctic Petrels in the lower eastern quarter of the Northern Plateau colony, measuring roughly 20 by 25 m. Straightforward figures for the number of sites or birds in such an area are not easy to give. Frequent counts were made from a fixed viewpoint outside the nesting area. From subsequent detailed nest-checks, the proportion of birds missed in distant counts was estimated at 10% to 20%. Instantaneous counts of individuals (maximum ever 95 birds) or the number of 'Apparently Occupied Sites' (usually 30-40 AOS; maximum ever counted 48) are repeatable measures, but do not properly reflect size of the bird population in the study area. Gradually we have identified close to a 100 sites regularly attended by two or more birds. Colony counts do not reveal this because not all birds attend the colony at the same time, in spite of what seems a high level of synchronization. Banding records indicate that at least 180 different adults are associated with our study area. Bird counts are given as mean \pm sd. Sites in the study area have been marked with painted numbers.

Within the study area, we banded a large part of the adults and all chicks with stainless steel bands from the Australian Bird and Bat Banding Scheme (ABBBS). Additionally, in 1984/85, 90 adult birds were given a combination of three Darvic colourbands for easy individual recognition. From observations during the season of banding, these birds were separated in a 'breeding' category (pairs with egg or chick, or birds frequently resighted on the same site with the same partner throughout the 84/85 season; $n = 75$) and a 'non-breeding' category (not or infrequently resighted after banding, and if resighted, on different sites and/or with different partners; $n = 15$). We thus included well-established site owners with stable partner bonds in the breeder definition because observations started in the egg phase when many pairs had already failed. This initial categorization proved consistent in later years: almost all birds initially labeled as breeders were observed breeding again in later years (64 individuals out of 75), whereas of the 15 initial non-breeders only one is known to have once attempted to breed later (in 1996/97).

A new cohort of 71 adult birds was individually marked with colourbands during the October-December period of 1996. The breeder or non-breeding distinction could not be made for reasons explained in results.

Adult attendance, breeding biology and success were monitored by regular nest-checks. Daily checks were made in 1986/87 and 1996/97 from egg laying until fledging. In 1984/85 and 1990/91 observations started later and were less frequent. At each visit, the breeding success was determined as the number of successful sites in the study area. A successful site is defined as 'with incubated egg or a live chick'. It needs to be emphasized that such a figure is not a measure for the number of eggs produced. Many egg losses may occur during the early laying period. Since egg laying and failure may occur in between two subsequent checks, an accurate figure for the number of breeding attempts is hard to obtain.

Annual adult survival rates between subsequent study seasons were calculated directly from resighted numbers of colourbanded birds. No correction methods for 'missed' but surviving birds were used, as in our study no bird missing in one season returned in a later one. Survival within the 1996/97 breeding season was estimated from directly observed mortality (corpses found) among colourbanded birds.

To be able to control for observer effects, the colony area outside our study plot was left undisturbed as much as possible. No observations were made in this reference area in 1984/85, except for the initial estimate of the number of AOS. In 1986/87 again the area was not entered, and the number of chicks fledging was estimated by counts from outside of the colony. As of 1990/91 the undisturbed area was entered once in each season for chick banding (around mid February).

Changes in population breeding success in the study area were tested by GLM regression using binomial distribution (GENSTAT: Payne *et al.* 1993: p 418), fitting 'year' on response variates 'egg on 31 December' or 'chick fledged'. Chi-square tests were used to compare frequencies in e.g. comparisons to the reference area and in resighting data for survival analysis.

Weather data on snowfall, temperature and wind over the period from January 1980 to December 1996 were obtained from the Australian Bureau of Meteorology. We analysed snowfall patterns from data for 'monthly total precipitation', recognizing the potential for some uncertainty under conditions of 'blowing snow'. We used the mean maximum temperature. Wind speeds and directions were analysed from annual frequency tables containing the number of records per 10 km h⁻¹ wind speed category for each of 16 wind directions. Frequencies were recalculated to percentages of the annual total of observations. Trends in weather data were explored by simple regression analysis (GENSTAT: Payne *et al.* 1993). Anemometers and thermometers at Casey changed location in 1989, but simultaneous records at both locations during

the whole of 1989 revealed no significant differences in any of the measurements (Chi-square tests on frequencies of wind speeds $P = 0.996$; wind directions $P = 0.18$; and t -test on all temperatures $P = 0.80$).

RESULTS

In 1996, observations began on 5 October when the first Antarctic Petrels started to arrive (8 birds over the whole Northern Plateau). A large snowdrift, one to two metres thick, blanketed a considerable proportion of the study area. This snowdrift had never been observed before, but previous observations had not started before 23 November in 1986 and mid-December in other years. The number of pre-breeding attendants in the study area increased from 14 on 8 October, to a maximum of 86 birds simultaneously present on 15 October. Numbers decreased after 20 October, and the colony was virtually deserted by early November (Fig. 2).

During the mid-October attendance period, extensive snow-digging, courtship display and copulations took place. Some pairs were digging out impressive snow caves, but few of those with nest sites in the snowdrift managed to clear the snow down to the rock below. The behaviour of Antarctic Petrels in this period was more nervous than in earlier years. Birds that previously were easily inspected for colourbands appeared shy when more closely approached.

Southern Giant Petrel predation

The reason behind the nervousness of Antarctic Petrels became apparent when on 14 October we observed a giant petrel hovering over the colony. It caused panic among the Antarctic Petrels, with many flying off. No similar event had been observed in any of the previous seasons.

However, in 1996, after the first bird on 14 October, the next day another giant petrel crash-landed in the snowdrift. Its body left a deep impression in the snow, indicating that 'normal' landing in this cliff area was difficult, with a high risk of injury if no snow had been present. All Antarctic Petrels in the vicinity had taken off, but the giant petrel sat quietly, and after a few minutes birds gradually started to resettle on their nest sites. Some of these could not see the giant petrel because they were inside snow caves or behind rocks. At this stage, the giant petrel took a sudden run to one site, and grabbed the Antarctic Petrel. The victim was killed by biting in the head and neck and shaking. After the kill, breast and belly area were plucked and ripped open. The carcass was cleaned in about half an hour.

Similar events were witnessed several times during October. Giant petrels occasionally attempted to chase Antarctic Petrels during the panic directly after

landing, but only the surprise attack strategy was successful. Remarkably, Antarctic Petrels always fled during attacks and never responded by spitting of stomach oil, a successful defense strategy in the fulmarine petrels (Warham 1990). From diet sampling we know that they do accumulate stomach oils like the other species. On rare occasions we observed that chicks are well able to use oil spitting and vomiting in defence and fear. Why this defensive behaviour is so rarely shown by the Antarctic Petrel is unclear.

A considerable number of different giant petrels, recognized by their plumage, were involved in the attacks on Northern Plateau. When wind conditions were suitable for soaring along the cliffs, several giant petrels were checking out the colony each day. However, they did not always land, and not all visits resulted in successful kills. Nevertheless, by October 25, when pre-breeding attendance dwindled (Fig. 2), ten fresh corpses of Antarctic Petrel victims had been found in and around the study area. This is no doubt a minimum figure as corpses in the reference colony may have been missed and others may have been blown away in strong winds or were removed by skuas.

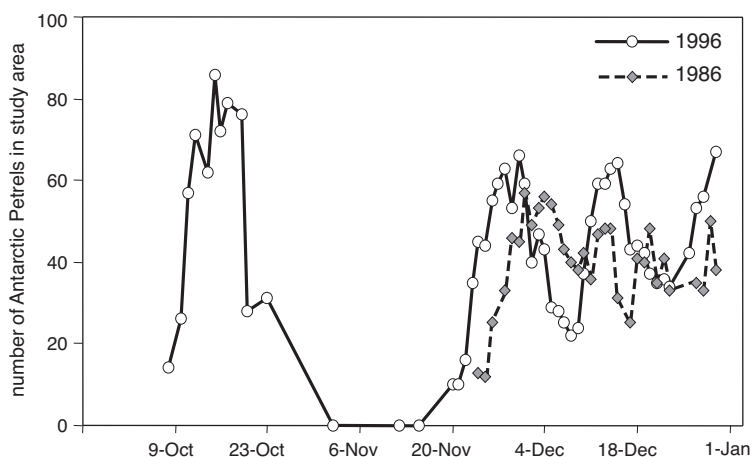


Figure 2. Attendance patterns of Antarctic Petrels in the Northern Plateau study area. Attendance is shown by daily counts of the number of individual birds in the study area during the 1986 and 1996 breeding seasons. Counts were made from the fixed viewpoint outside the colony, before entering for detailed nest checks.

Breeding success

From late October to 20 November 1996, the Antarctic Petrel colony was completely deserted (Fig. 2), all birds being away on the 'pre-laying-exodus' (Warham 1996). First eggs in the study area were laid on 24 November (Fig. 3). In spite of some melt, the

snowdrift covering part of the nesting area was still largely intact. Some eggs were laid on 'snow-nests'. Usually, such eggs melt into the snow and subsequently freeze.

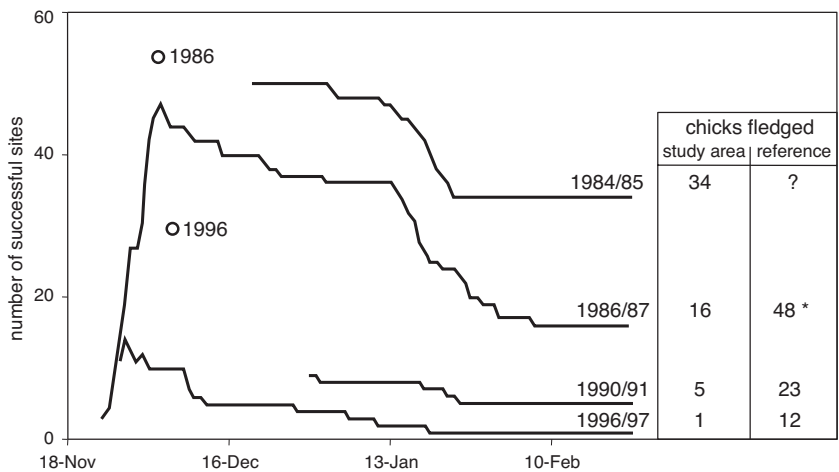


Figure 3. Antarctic Petrel breeding success in the Northern Plateau study area. Line graphs show numbers of successful sites (see methods) in the study area for all four seasons. For years with full seasonal coverage (1986 and 1996), the minimum number of eggs laid is shown by circles (note that these are underestimates since laying and loss may occur in between two subsequent checks). The box on the right compares final breeding success from the study area with that of the reference area. See text for details.

Proper records of such causes of failure were impossible because events during the egg laying period were totally chaotic. Giant petrels were regularly crash landing and strongly disturbed the breeding process. The giant petrels showed no interest in the eggs, but only went for the adults. However, the skuas were now constantly patrolling their territories in the petrel colonies and were taking advantage of the disturbance by stealing the temporarily deserted eggs. During a giant petrel attack on 26 November, a single skua was seen to take three eggs. Other eggs were deserted for over an hour, and just when adults resumed incubation, a second giant petrel landed and created a new panic. By 6 December, when the last egg laying was observed, only 10 of 30 pairs observed to have laid still had eggs. Considerably more than 30 eggs were undoubtedly produced within the study area, but many must have immediately been lost in between our daily checks. By 12 December, only five eggs remained. During the remainder of December, the snowdrift gradually melted and after 12 December no further giant petrel landings were seen. In the late egg phase and early chick phase some further 'normal' losses occurred in the study area. Of the five remaining eggs,

one was lost due to nest flooding, one 'rolled out' of the site, and a third disappeared for no apparent reason. Of the two chicks hatched, one disappeared probably due to skua predation, apparently unrelated to giant petrel disturbance.

The end result was that the 1996/97 breeding season was the poorest on record, with only one chick fledged from the study area and only 12 from the remainder of the Northern Plateau colony. The trend of declining success of earlier years was thus continued. Compared to fledging numbers in 1984/85, success in the study area fell to 47% in 1986/87, 15% in 1990/91 and 3% in 1996/97.

It is difficult to express such figures in terms of 'population success'. Breeding success is usually defined as the proportion of 'egg producing pairs' that succeeds in fledging a chick, but it is extremely hard to determine accurately the numbers of eggs laid (Warham 1990). The best estimate for numbers of eggs produced in our study area is from 1986/87. Daily nest observations indicated that at least 54 eggs were produced in 1986, although at no time were there more than 47 eggs present (Fig. 3). During egg laying, some eggs are rapidly lost, even in the absence of giant petrel disturbance like in 1996/97. Poor nest site quality (covered with snow, flooding with melt water, or eggs easily rolling out) or improper coordination of incubation duties between partners are common reasons for immediate egg loss. The skuas quickly remove any trace of these events. Observations once a day will definitely miss a number of such immediate losses, and thus underestimate both egg numbers and the breeding population. Initial loss rates as commonly seen in fulmarine petrels, suggest that the 50 eggs in the Antarctic Petrel study area on 18 December 1984, represented a much higher number of egg producing pairs. Some of the sites in which we never observed an egg, are definitely used by adults capable of breeding. From data in our first two seasons our best estimate of the 'potential breeding population' in our study area is 75 pairs. From numbers of birds attending the study area in 1986/87 and ten years later in 1996/97 (Fig. 2) there is no indication that the population significantly changed over that period: counts over the December egg period averaged 42 ± 8 birds in 1986, and 44 ± 13 in 1996 (t -test: $P = 0.66$, n.s.). In terms of an initial breeding population of 75 pairs, the population breeding success in fledging chicks was 45% in 1984/85, 21% in 1986/87, 7% in 1990/91 and 1% in 1996/97. The decrease over the years is highly significant ($t_{(298)} = -6.20$; $P < 0.001$) and largely due to egg losses before 31 December ($t_{(298)} = -7.43$; $P < 0.001$) with no clear effect of further egg or chick losses after that date ($t_{(98)} = -1.49$; $P = 0.139$).

A strong decrease in number of chicks fledged was also observed in the reference area (Fig. 3 inset). Chick numbers were not counted in 1984/85, but were definitely in the range of 100 to 150 chicks. The 1986/87 figure of 48 chicks in the reference area is from a count made from distance: a tentative correction for 10% to 20% 'hidden' sites suggests that around 55 chicks could have fledged. The decrease in

fledgling numbers in the study area after 1986/87 was stronger than that in the control area. According to the 1986 to 1996 trend in the reference area, expected numbers to fledge from the study area would have been 7 chicks in 1990/91, and 3 in 1996/97 (5 and 1 respectively were observed; Chi-square test n.s., but observed frequencies too low for proper testing).

Survival/Mortality

Survival and mortality were analysed from cohorts of adult birds banded in 1984/85 and in 1996/97 and their live resightings or dead recoveries (Table 1). From these, average annual survival rates were calculated (Fig. 4). The fulmarine petrels have high loyalty to established sites and apparently attend the colony annually (whether breeding or not). We interpret 'resighting' data directly as survival data. However, four out of eight 'non-breeding' females in 1984/85 disappeared immediately after banding and were never resighted. As survival of non-breeding males was 100% from 1984 to 1986, it seems likely that the disappeared females were only visitors, prospecting for a male partner with a site, and that they 'emigrated' to another part of the colony or another area after banding. This biases the 1984-86 survival figure for non-breeders in Fig. 4 and represents the only instance where resightings are inappropriate to calculate 'survival'. Otherwise we have found no significant differences in survival between the sexes (overall breeder survival over 12 years: 13 out of 38 males, and 13 out of 37 females).

Table 1. Colourbanding and resightings of Antarctic Petrels on Northern Plateau study area. Numbers of birds colourbanded in 1984/85 and in October-December 1996 and their subsequent resightings. See methods for the breeder versus non-breeder distinction. Resightings were used to calculate survival rates shown in Fig. 4.

	numbers (<i>banded</i>)/resighted			
	1984/85 cohort			1996 cohort
	all	breed	nonbreed	
banded 1984/85	90	75	15	
resighted 1986/87	80	69	11	
resighted 1990/91	64	54	10	
resighted start 1996/97	34	26	8	71
end 1996/97 *	30	22	8	64

* 'Resighted' figures for the end of the 1996/97 breeding season have been calculated from numbers of colourbanded birds found dead, assuming that others were still alive.

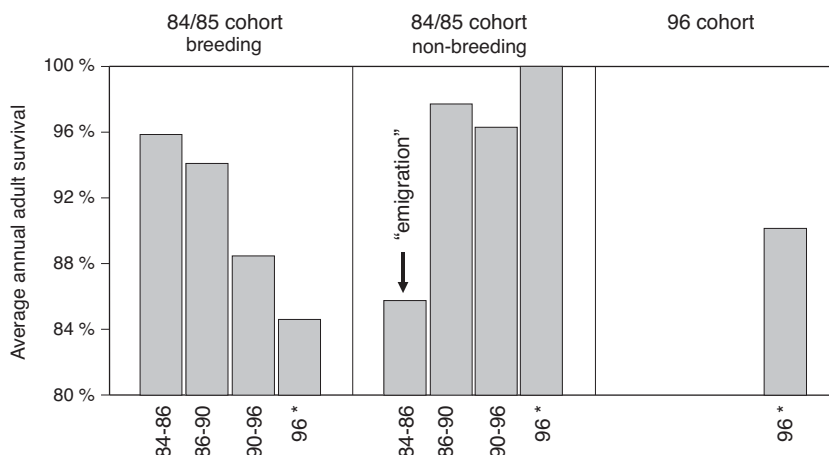


Figure 4. Survival rates of adult Antarctic Petrels. Average annual survival rates in between study years were calculated from live resightings of birds colourbanded as adults in 1984/85. The breeding and non-breeding categories refer to the status of the birds in 1984/85 (see methods). Survival within the 1996/97 breeding season (96*) was derived from dead recoveries of banded birds. Within season survival is also given for a new cohort of birds first colourbanded in October – December 1996. As not all killed birds may have been recovered, the 96* survival figures are maximum values. See Table 1 and text.

No distinction between breeders and non-breeders could be made in the new '96-cohort' of birds first banded in October-December 1996. The chaotic predation events and snowdrift complicated records of individual site-locations, pair bonds and breeding.

Survival of breeders in the 1984/85 cohort started with an average annual survival of 95.9% over the 1984-86 period, but decreased to 94.1% between 1986 and 1990, and 88.5% over the 1990-96 period. Within the 1996/97 summer, observed breeder mortality due to giant petrel predation was at least 15.4%! Very different results were obtained for the non-breeding component of the 1984/85 cohort. As indicated, the low average 'survival' for non-breeders over the 1984 to 1986 period in Fig. 4 (females 71%; males 100%) probably reflects 'emigration' of prospecting females. Over later periods, mean annual survival in this group was consistently high (97.7% and 96.3%). Within the 1996/97 breeding season, no mortality from giant petrel predation was observed among the non-breeder survivors of the 1984/85 cohort.

Using 96% as an expected survival figure for Antarctic Petrels (Warham 1996) for all periods, Chi-square tests show highly significant lowered survival for breeders of the 1984/85 cohort ($P < 0.001$), but not for the non-breeders ($P = 0.89$ if 1984-86 period included; $P = 0.72$ if excluded).

The within-season survival figure for the 1996 cohort is merely indicative. Birds were banded gradually over time, and thus could only be detected as victims of giant petrels for the part of the breeding season after the date of banding. Furthermore, the sample contained a mix of breeders and non-breeders. Out of 71 new birds banded from October to December 1996, seven were recovered dead the same season demonstrating at least 9.9% mortality within a few months due to giant petrel predation.

Climate data

The large snowdrift on Northern Plateau in 1996 that persisted well into December had not been observed in previous years. However, only in 1986 had observations started early enough (24 November) for a comparison. It is known that not much snow was present and none of the nest-sites was snow-covered that year. Snowdrifts on several other places on the northern side of the island were also larger in 1996 than in any of the previous years, and persisted well into December and January.

Snowfall showed a strong increase over the observed period. Total annual precipitation over the 17 years significantly increased (Fig. 5A; linear regression $P = 0.01$) in spite of considerable interannual variation. The increase was not evenly distributed over the year. A comparison of average monthly precipitation figures during the 1980s to those in the 1990s (Fig. 5B) shows that summer snowfall had not much changed, it may have even slightly decreased in December and January in later years. For the separate months, increases over 17 years were only significant for August ($P = 0.008$) and November ($P = 0.036$). Seasonal precipitation totals significantly increased in winter (June-August: $P = 0.023$) and especially spring (September-November: $P = 0.005$), but not in summer (December-February; $P = 0.760$) and autumn (March-May: $P = 0.212$). The four-month period prior to the egg laying

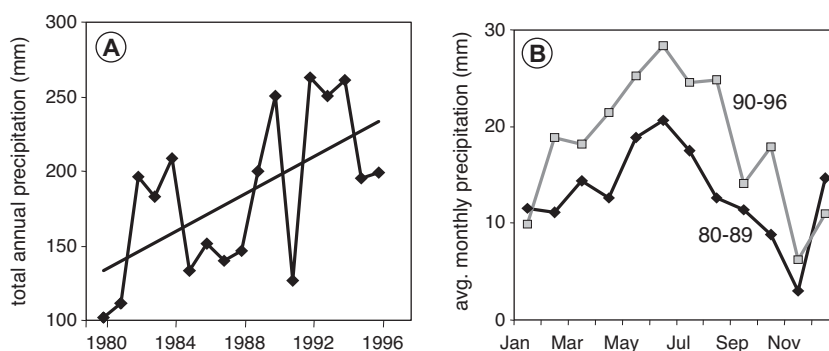


Figure 5. Increased precipitation in the Casey area over the period 1980-1996.

of the Antarctic Petrel showed a highly significant increase (August-November: $P < 0.001$).

Air temperatures in the Casey area showed no clear changes over the 1980-1996 period. Trends over 17 years for the annual mean maximum ($P = 0.09$) or the mean minimum ($P = 0.08$) were not significant (Fig. 6A). Monthly mean maximum air temperatures during the 1980s are compared to those 1990s in Fig. 6B. Except for an apparent cooling of May temperatures (linear regression over 17 years $P = 0.016$) none of the months showed a significant increase or decrease. We also tested annual and monthly temperature trends over a longer period 1970-96, and these confirmed the absence of significant trends in mean, minimum or maximum temperatures. The

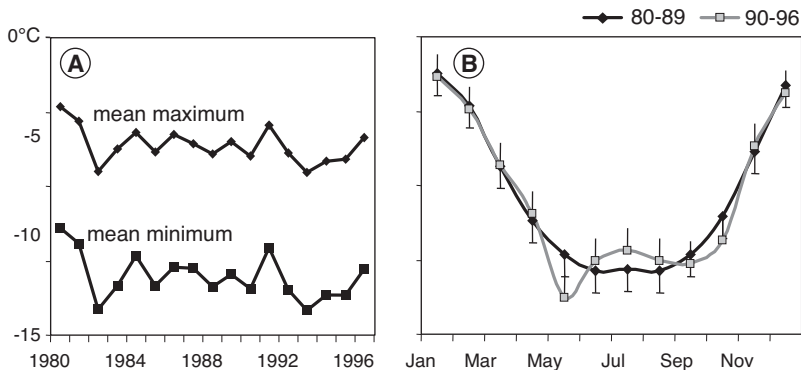


Figure 6. Temperatures at Casey station over the period 1980-1996. Annual mean maximum and minimum temperatures in Fig. 6A show no clear trend. Monthly data in Fig. 6B are pooled for the 1980s (standard deviation in downward bars) and 1990s (standard deviation in upward bars).

drop in mean maximum May temperatures remained the only significant finding (over 27 years $P = 0.002$).

Analysis of the annual tables for wind speed and direction (Fig. 7) revealed a significant shift in wind direction from a predominantly south-eastern quarter during the 1980s to a more north-easterly one in later years (Fig. 7A: linear regression on 17 year trend in E-SSE winds $P < 0.001$; on N-ENE winds $P = 0.004$; other directions n.s.). At the same time, the frequency of moderate wind speeds in the range of 10 to 30 km h^{-1} increased ($P < 0.001$), whereas those of calm weather decreased ($P < 0.001$). No significant change occurred in the frequency of high wind speeds (Fig. 7B).

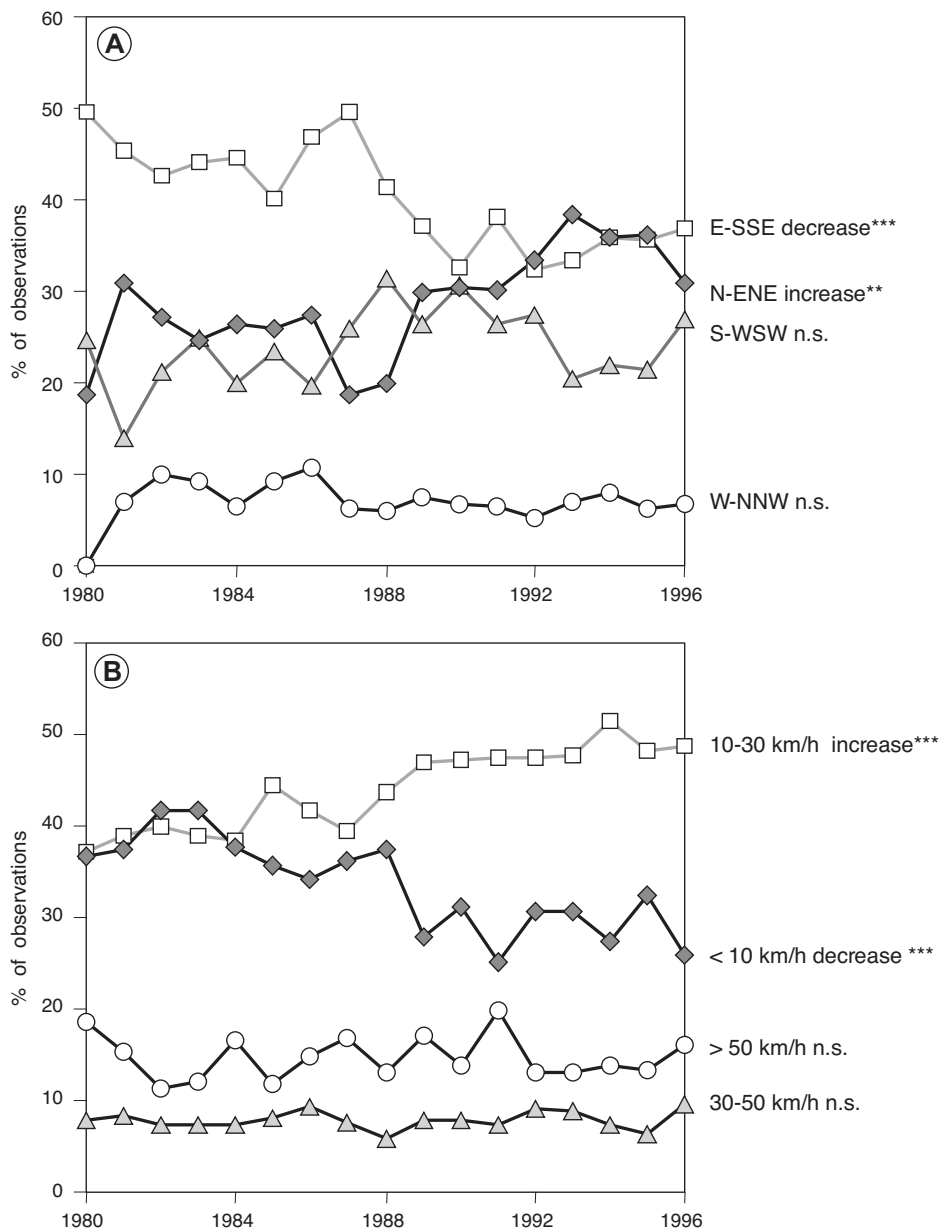


Figure 7. Wind-directions and speeds at Casey station over the period 1980-1996. Data expressed as percentage contribution to the total of observations. Original data for directions and speeds have been pooled in smaller number of categories which are described alongside the respective data. The significances of linear regressions over 17 years of data are alongside each category (n.s. = not significant; ** = $P < 0.01$; *** = $P < 0.001$).

DISCUSSION

Our observations in 1996 showed that Antarctic Petrel breeding success and survival on Ardery Island were dramatically lowered as a consequence of predation by the Southern Giant Petrel during the prelaying and egg laying periods.

Survival/mortality

Survival was directly affected by giant petrel predation, most seriously so among experienced breeders. Within the 1996/97 summer, observed mortality among breeders was 15.4%. Average annual mortality of such birds had been 11.5% from 1990/91 until October 1996, a significant increase in comparison to earlier periods. "Normal" mortality of adult petrels with life strategies like the Antarctic Petrel is in the order of 4% (Warham 1996), a level only observed over the initial two years of our study.

Remarkably different mortality was recorded for non-breeding birds, whose numbers seemed unaffected throughout the period of observation (1984-86 emigration period not considered). Overall mortality levels among non-breeders remained at a "normal" level for the 1986-96 period, and no mortality from predation was observed within the 1996/97 breeding season. The differences between breeding and non-breeding Antarctic Petrels can be explained by the observed hunting technique of the giant petrels. Successful kills were only made when they followed the 'surprise attack' strategy. As a consequence, the Antarctic Petrels with the strongest site-tenacity became the victims.

In the newly banded cohort of birds, 10% mortality within the 1996 season is in between the figures for the 'old' breeder and non-breeder groups. The similarity shows that high mortality in our older cohort is not a matter of birds dying of old age. Furthermore, the change in mortality rate, is much stronger than could be expected from published examples of old age in petrels (Warham 1996).

Breeding success

The almost total breeding failure of Antarctic Petrels in 1996/97 was an indirect result of giant petrel predation. Disturbance during their attacks caused intense predation on deserted eggs by skuas. Most eggs had already disappeared by the end of the two-week laying period, and this determined the final breeding success. The decline in breeding success in our study area appeared sharper than that in the reference area, probably due to local topography. The study area at Northern Plateau was situated in between the snowdrift and the remainder of the colony, which means that the giant petrels had to walk through or closely past the study area at every approach to the reference area.

Population trend

As yet, no significant change in bird numbers attending the study area was detected between 1986 and 1996 (Fig. 2). Seabird life strategies are able to withstand many years of unfavourable conditions but complicate early detection of population change (Anker-Nilssen & Røstad 1993, Anker-Nilssen *et al.* 1996). Large 'backup' populations of immatures and non-breeding adults form 'strategic reserves' (Warham 1996) that may long obscure adverse effects, especially if the species' loyalty to the natal colony is low. Indeed, in the study area of the roughly 200 regularly attending birds, there are three immigrants banded as chicks on Haswell Island and the Rauer Islands, thousands of kilometres to the west. Nevertheless, if adult mortality and breeding failure in the Northern Plateau colony continue at the 1996 level, there seems little doubt that the colony will gradually disappear.

Southern Giant Petrel as predator

The hunting technique of giant petrels on Ardery Island is that of an efficient predator capturing healthy adult prey on land. We know of no earlier reports of such behaviour. Both *Macronectes* species are considered to be scavengers (e.g. Conroy 1972, Johnstone 1977, Hunter 1983, 1985, Voisin 1991, Emslie *et al.* 1995, Warham 1996) taking dead, injured, and weak or defenceless prey among marine mammals and birds, and are persistent ship-followers. They do take apparently healthy penguin chicks too, but the taking of chicks that can neither escape nor defend themselves is very different from the predatory behaviour witnessed on Ardery Island. Few records have been made of predation on smaller petrels at sea, e.g. of burrowing petrels (Johnstone 1977, Hunter 1990) although most refer to the taking of birds that were somehow impaired. Observations most similar to ours were described by Punta & Herrera (1995) on Isabel Island where Southern Giant Petrels scared Imperial Cormorants *Phalacrocorax atriceps* (King) off their nests by low flights over the colony. They did not land but chased and attacked cormorants when flying over sea or on the water. The success rate was relatively low (two kills in 85 attacks). As on Ardery Island, other birds, in this case gulls and sheathbills, took advantage of the disturbance by taking the cormorant eggs from the deserted nests.

Predation and petrel breeding distribution

We have no indications that our presence in the colony or food shortage have led to this predatory behaviour as a newly acquired technique. If the behaviour was due to our activities, similar predation events would have been expected in earlier years, and not only in, and immediately at the start of the 1996 season. In addition, there is no

evidence of food scarcity for the giant petrels. Expected local food sources have either been growing (Adélie Penguin *Pygoscelis adeliae* (Hombron & Jacquinot): Woehler *et al.* 1994; Elephant Seal *Mirounga leonina* (L.): Murray & Luders 1990) or not known to have undergone major changes (e.g. Weddell Seal *Leptonychotes weddellii* Lesson). In our opinion the predatory behaviour is an 'old' and normal event, which is simply rarely observed.

This view is based on the knowledge that the colonies of all four smaller fulmarine petrels (Southern Fulmar and Antarctic, Cape and Snow Petrels) are largely, but not completely, restricted to steep slopes and cliffs. We believe that the nesting distribution of petrels shows all signs of long-term adaptation to the presence of predators that approach from land. In the schematic cross section of Ardery Island (Fig. 8) three types of terrain may be distinguished:

Type A: steep cliffs;

Type B: moderately sloping terrain found in inland slopes (B1), along cliff tops (B2), and subsections in the cliffs (B3); and

Type C: flat areas.

Dense nesting of all petrel species breeding on Ardery Island occurs on the cliffs (terrain type A) and on slope sections within the cliffs (type B3). This is especially true for the Antarctic Petrels and Southern Fulmars. Cape Petrels and particularly Snow Petrels also occur on some of the inland slopes (B1) and the higher cliff edges (B2) but usually more scattered and in lower numbers.

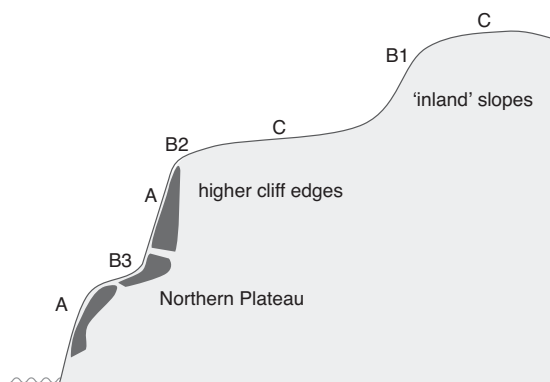


Figure 8. Schematic cross section of Ardery Island showing main petrel nesting areas (dark) in relation to the type of terrain (A = steep cliffs; B = boulder slopes; C = level terrain). Normally, giant petrels can only land in the flat areas (C) from where adjacent slopes (B1, B2) can be reached by foot.

We reject the idea that such nesting distributions are determined by limited flying skills of the smaller petrels, necessitating a strong vertical drop for nest access or departure. Antarctic Petrels have little problems in taking off from relatively flat ground (Cowan 1979; personal observation). Also Snow Petrels and Cape Petrels nest on more level surfaces. None of the species seems to have problems at locations like

the Northern Plateau. If flying skills were the major factor, similar dense nesting of all petrels would be seen on all type B locations and not just on type B3.

Two land predators, skuas and giant petrels, have to be considered as potentially limiting nesting distributions of petrels. From our observations, skuas are unlikely to exert such a predation pressure. Skuas were never seen to attack adult petrels at nests, but only in air. Even hovering over nest sites, a common skua threatening behaviour in penguin colonies for stealing eggs or chicks (e.g. Emslie *et al.* 1995), is infrequent in petrel colonies (personal observation; Haftorn *et al.* 1991). Weidinger (1998) showed that Cape Petrel eggs and chicks were more frequently taken if skuas could attack from the ground. Many spots on Ardery Island do allow 'ground attacks' by skuas, but are nevertheless densely populated with nesting petrels. Northern Fulmars (*Fulmarus glacialis* (L.)) can also be found nesting on flat ground in the presence of skuas, but usually only in places where access for other land predators is impossible. Thus, in our view, skua predation pressure does not explain the current limits of petrel nesting areas.

The behavioural pattern of the only other predator, the giant petrel, does explain the nesting distributions of the smaller petrels. Unlike the skuas, giant petrels need relatively large, flat and smooth surfaces for landing, occurring only on the type C locations in Fig. 8. Potential petrel nesting slopes that border these are accessible for giant petrels by foot (type B1 and B2) and are void of colonies of Antarctic Petrels and Southern Fulmars. Snow and Cape Petrels can only extend some of their nesting to such areas by breeding in inaccessible holes in between rocks or scattered in otherwise sheltered sites (Green 1986). In addition, both species have a particularly well developed defensive oil-spitting behaviour that would discourage predators from preying on them on the nest (Johnstone 1977). Only when type B locations are surrounded by steep cliffs and have a rough surface, access for giant petrels (not for skuas) is impossible, as they can not land nor approach on foot. In such areas all smaller petrels are nesting in high densities. We conclude that nest locations of the fulmarine petrels in the area are determined by long-term predation pressure from giant petrels. Under stable conditions, predatory actions will be infrequent, and restricted to the margins of areas where giant petrels can land (type C). Our very few observations of giant petrels along the cliff tops in earlier years, might in retrospect be interpreted in such a way. Only when changed conditions create new landing spots in previously inaccessible locations, does predation become frequent enough to be regularly witnessed.

Climate change

Our analysis showed important changes in the *local* climate in the Casey region since 1980. For the Wilkes Land coast, Morgan *et al.* (1991) used ice-cores to look at longer

term changes over a wider area. They concluded that snow accumulation rates had significantly increased from 1960 to the mid 1980s, to 20% above the average long-term level. Apparently, this trend is still in progress. They also noted that increases were due to 'winter' precipitation (cf. Fig. 5B) and linked this to intensified cyclonic activity and a more oceanic type of climate (cf Fig. 6). Morgan *et al.* (1991) suggest that increased precipitation occurs over a wide Antarctic region and Jacobs (1992) links such increased precipitation to global atmospheric warming.

The key factor for predation in 1996 was the presence of a large snowdrift adjacent to, and partly over our study area. The snow provided a new landing area that was previously inaccessible. The reduction in the giant petrel visits during melt of the drift in December confirmed the crucial role of the snow in providing access. Visits did not stop because of lack of prey, because Antarctic Petrels continue to attend their nest sites until late January irrespective of earlier breeding failure. Critical for the effects on Antarctic Petrels in 1996 was persistence of the snowdrift persisted into the egg laying period. This totally influenced the year's breeding success in the population, and aggravated adult mortality.

Because of the lack of data on the annual persistence of the snowdrift and our small sample of only four study seasons, no statistical significance can be demonstrated for correlations between Casey snowfall and the number of remaining eggs or fledged chicks in study years, nor for the survival rates in between those periods (Fig. 9). Nevertheless, the significant trend in local climate and our observations of predation events suggest strongly that giant petrel predation has increased in response to snow conditions and is the background of steadily decreasing survival and breeding success among the Antarctic Petrels.

Concluding remarks

The effects of increased snowfall on a local population of Antarctic Petrels should not be interpreted as a general consequence of global warming for Antarctic seabirds. General increases in snowfall are not necessarily followed by proportional increases in local snow accumulation. Snow Petrels are known to have used the same nunatak nesting areas over periods up to 35,000 years (Hiller *et al.* 1988, Ryan *et al.* 1992) in spite of the many climatic variations that must have occurred over such a period. On the other hand, part of the Adélie Penguin colonies near Palmer station was abandoned because of increased snowfall (Fraser & Patterson 1997).

Our concern from the Ardery Island events is not so much the changes faced by the local population of Antarctic Petrels. Natural climate changes, both short- and long-term, will continuously alter suitability of bird nesting areas in many ways. It was the extreme complexity and unpredictability of ecosystem response to such change, that surprised us. The predictable effect of increased snowfall would have

been a relatively minor reduction in breeding success by the freezing of eggs laid in snow. It is the unpredictable chain of secondary events that followed (access for bird-predator, mortality, disturbance, egg predation and total breeding failure) that leaves us uncomfortably aware of limitations in predicting the effects of environmental change on ecosystems.

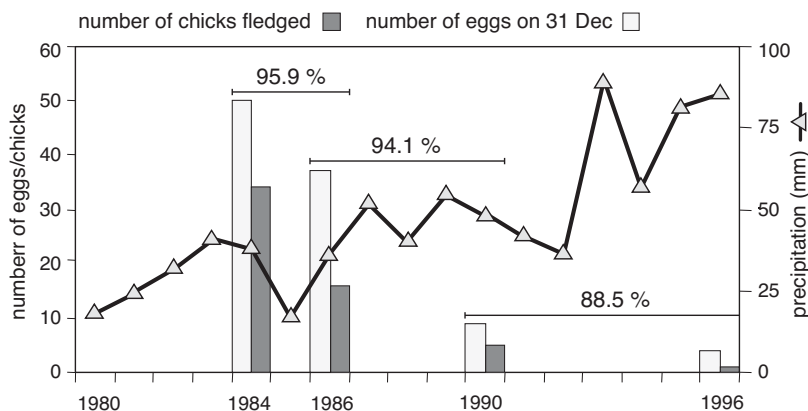


Figure 9. Snowfall in relation to breeding success and survival of Antarctic Petrels. Annual data for precipitation at Casey during the prelaying period (August-November) since 1980 plotted in relation to changes in breeding success and average annual survival of Antarctic Petrels in the Northern Plateau study area.

ACKNOWLEDGEMENTS

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CHAPTER

5

**MONITORING OF A SOUTHERN GIANT PETREL
MACRONECTES GIGANTEUS POPULATION
ON THE FRAZIER ISLANDS, WILKES LAND,
ANTARCTICA.**

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ABSTRACT

Since 1956, Southern Giant Petrels on the Frazier Islands, Antarctica, have been counted with different census techniques, sometimes varying within seasons and among islands, which hindered analysis of the data. Protective measures for the islands from 1986 onwards have increased the need for reliable long-term census data, but reduced the ways to collect these data. Published and unpublished data were re-examined, and population trends were reconstructed based on two relatively standardised techniques: the number of Active Chicks (AC) and the number of Apparently Occupied Nests (AON) around hatching. AC-values from Nelly Island from 1959 to 1998 indicate substantial periodical fluctuations, but no consistent long-term change. Since the late 1970s, AC-values on the other two islands and AON-values suggest that the breeding population may have grown by 35%. This recent growth, however, is within the extent of periodic fluctuations observed in the Southern Giant Petrel population that is stable over the long term.

INTRODUCTION

Southern Giant Petrels are considered as a 'vulnerable' species according to IUCN guidelines (Birdlife 2000). The global population has probably decreased by 18% between the early 1980s and the late 1990s, although local population trends may have been positive (Patterson *et al.* in preparation). Human disturbance is often blamed for this global population decrease. Southern Giant Petrels are easily disturbed at their nest and readily leave their nest when humans approach at close distances (Warham 1962), which leads to decreases in reproductive success (Conroy 1972, Hunter 1984, Peter *et al.* 1991, Chupin 1997). Some colonies close to research stations have disappeared or decreased dramatically (Micol & Jouventin 2001, Nel *et al.* 2002).

Most Southern Giant Petrels breed on Sub-Antarctic islands and in the area around the Antarctic Peninsula (Hunter 1985, Patterson *et al.* in preparation). The Antarctic continental coast holds only about 1% of the global breeding population (Woehler *et al.* 2003). Here, along the southern limit of its habitat only four breeding localities are known: Giganteus Island (67°35'S 62°30'E), Hawker Island (68°38'S 77°51'E), Frazier Islands (66°17'S 110°32'E) and Pointe Géologie (66°20'S 140°01'E). All these colonies are small and therefore probably vulnerable to catastrophic events or environmental variability (Shaffer 1987) including human disturbance. The largest of these four continental breeding populations exists on the Frazier Islands 17 km offshore the Australian research station Casey. Here, Southern Giant Petrels have probably experienced relatively infrequent human disturbance because the islands are difficult to reach from the station. Since 1986, additional protective measures have been taken by banning helicopter flights and only allowing access by watercraft. The banding of Southern Giant Petrels has been discontinued, and only non-invasive observations from outside the colony boundaries are currently permitted (Woehler *et al.* 2003). Earlier analyses suggested that the population on the Frazier Islands decreased till the 1980s and has been recovering after banding of chicks had stopped (Woehler *et al.* 1990, Woehler *et al.* 2003).

Detectability of long-term population change depends on the quality of census data. The accuracy of each census is influenced by the bias and precision of the counting technique (Verner 1985, Bibby *et al.* 2000). Especially in historical long-term datasets, biases may occur due to differences in study designs, aims, or techniques. On the Frazier Islands, until the mid 1980s the main purpose of many visits was to band chicks for study of dispersal and longevity. Since then, the interest has shifted towards population monitoring for conservation purposes.

The first census of the Southern Giant Petrel population on the Frazier Islands was carried out in 1955. Since then, at irregular intervals, data have been collected by different and sometimes poorly described census techniques. Methods

varied from superficial aerial surveys to exact chick counts by banding. In some years, multiple visits to the islands allowed estimates on breeding performance. Annual reproductive success, together with the number of breeding pairs, will determine future population trends and is thus an important parameter for long-term monitoring (Croxall & Rothery 1991). Comparisons with less marginal populations living under more moderate climatic conditions might reveal how well the Frazier Islands population is performing. Breeding performance might also differ among colonies, due to differences in breeding habitat quality (*cf.* Patterson *et al.* 2003) such as snow deposition, elevation for fly-off possibilities, or distance to a main feeding source consisting of Adélie Penguins *Pygoscelis adeliae*.

From the start of the breeding season onwards, Southern Giant Petrels experience an accumulating number of breeding failures (Hunter 1984). This will result in a decreasing number of active nests (AN) over the season. In earlier analyses of the Frazier Islands population (Woehler *et al.* 2001, 2003), however, this date effect was not taken into account due to the low number of censuses. In this study, more census data were available because data were analysed for each island separately instead of only total numbers of breeding pairs on the Frazier Islands.

The purpose of the present paper was to review and re-examine all available census data, checking both published and unpublished information sources in order to select reliable time series based on comparable methods, locations and accuracy. Monitoring seabird populations is usually done by counting 'breeding pairs' although the meaning of this definition varied between researchers and studies. Thus for a reconstruction of the population trend of Southern Giant Petrels on the Frazier Islands it was necessary to establish what had actually been counted, and also how it was counted. Such a classification of census methods and census units will help to standardise future monitoring of this population and possibly of other seabird populations as well.

METHODS

Study area

The Frazier Islands (66°23'S, 110°17'E) are situated in Vincennes Bay, Wilkes Land, Antarctica, approximately 17 km WNW of the Australian base Casey. The island group consists of: Nelly Island, Dewart Island and Charlton Island which are separated from each other by 50-100 m wide sea channels (Figs. 1 and 2). The three islands have a similar topography with ridges running NW to SE at the northern and the southern part of the islands. The northern ridges have steep slopes to the North and Northwest. The southern ridges are lower, except on Nelly Island, where the

southern peak is 70 m high and very steep (Fig. 2). Colonies are found on higher and lower ridges, which were classified ('high' or 'low') as to their position relative to their surroundings.

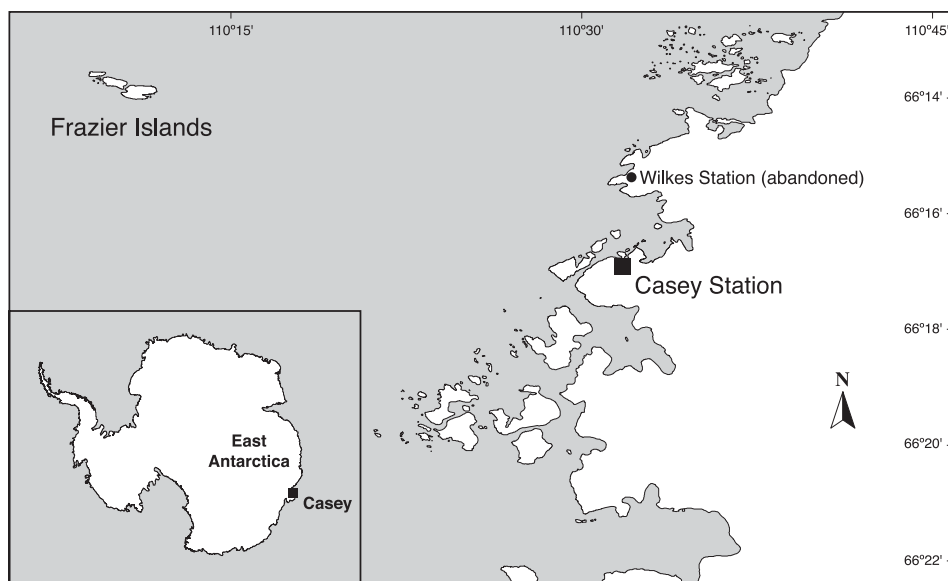


Figure 1. Situation map of Frazier Islands, situated in relation to Casey Station and to the Antarctic continent.

Mapping of colonies

Colonies were defined as an aggregation of nests of a single species (either Southern Giant Petrel or Adélie Penguin) less than 15 m apart. Locations of colonies were mapped during a census on 26 December 1998. Boundaries of the colonies were recorded by walking slowly 15m from the most peripheral nests of each colony with a mobile Trimble GPS Pathfinder system and locations were retrieved every 10 s. Coordinates were differentially corrected afterwards with a reference base station at Casey, resulting in a position determination accurate to a couple of decimetres. Solitary nests (more than 15 m away from a colony) were also mapped as stationary positions. Colony area was computed with ArcView software. The density of each colony was calculated by dividing the number of AN by colony area. Distances between the centre of each Southern Giant Petrel colony to the centre of the nearest Southern Giant Petrel colony, as well as to the closest edge of the Adélie Penguin colony were determined using ArcView.

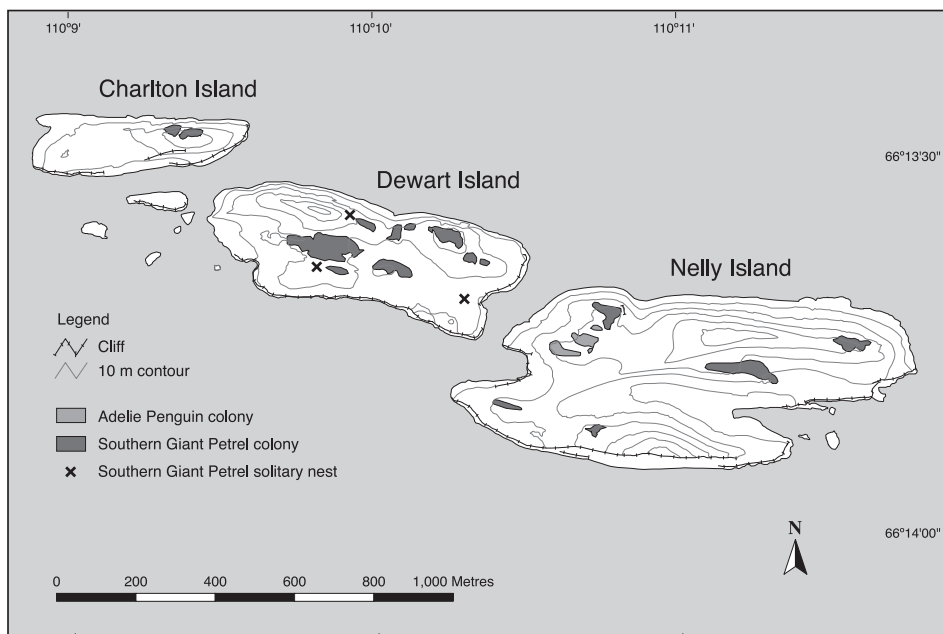


Figure 2. Locations of Southern Giant Petrel and Adélie Penguins colonies on the Frazier Islands.

Census

Data in this study come from censuses on the Frazier Islands conducted since the 1955 season. All authors, except the last author of this paper have been personally involved in censuses since 1984 and their data were supplemented with information from published sources and unpublished information in files of the Australian Antarctic Division and Australian Bird and Bat Banding Schemes. When confusion consisted on the actual numbers (see Table 1), data were taken, if possible, from field notes or from published data by the surveyor who did the census. Numbers based on extrapolations or estimations were not used for analysing population trends. Breeding seasons are named after the year when the eggs were laid. For example the 1959 season started in October 1959 and lasted till May 1960.

Over the years, different census methods and census units have been used to estimate the breeding population, unfortunately often poorly documented. Census methods have been classified as follows:

Unknown - No details on the census method are given. Data were not used for analyses.

Air - Counting birds from air. Numbers represent only crude estimates of the population, and are not used for analyses.

Land - Counting birds while walking on the island. Unfortunately this category could not be subdivided by censuses from close distance (unaided eye) and those from a viewpoint (use of binoculars), because this was often not documented. Furthermore both techniques are probably used within one census between different colonies on the island (e.g. from close distance for small colonies and from viewpoint for large colonies).

Census units represent what was actually counted such as nests, chicks, or adults. The census units have been classified in four categories:

Unspecified census units (unspec.) - Number of birds counted without attention to breeding status or where no details on the census method were given. In this census method it is likely that non-breeding birds are included in the number of counted birds. Aerial censuses were included in this category.

Apparently Occupied Nests (AON) - Number of well-constructed nests occupied by at least one, apparently breeding, bird. Non- or failed breeders normally occupy a proportion of the AON; thus AON will include a certain proportion of failed or non-breeding nest-sites. AON-censuses are possible during the egg and early chick phases without causing disturbance (see Walsh *et al.* 1995, Bibby *et al.* 2000).

Active Nests (AN) - Number of nests observed to contain an egg or chick. The method implies checking all nests with apparently breeding birds for the presence of an egg or chick, to determine the actual number of breeding sites at the date of the count. Because of the disturbance involved with AN-censuses, the method was abandoned after 1983.

Active Chicks (AC) - Number of chicks after the initial chick phase, when most chicks are not brooded or guarded anymore by their parents. AC-censuses are possible without disturbance, however till 1986 they often coincided with chick banding.

Within a particular season, census methods often differed for the separate islands. Therefore, when analysing population trends the islands had to be treated separately. Breeding Southern Giant Petrels have a very high fidelity to their nesting colony (Ingham 1959, Warham 1962, Conroy 1972, Voisin 1988) making exchange of individuals between the islands unlikely.

Evaluation of AON type counts

During the 1997 and 1998 seasons, after counting the number of AON in a colony during a short time period (5 - 10 min), observations were continued for prolonged periods in order to assess the actual breeding status for as many nests as possible in each colony. It was recorded whether the nest content became visible, and if so, whether it contained an egg, chick, or nothing. It was assumed that in continued observations, birds sitting on failed or non-breeding sites would stand up or move

around in such a way that nest content became visible. If large pieces of eggshells were observed just out of the nest, it was judged to be successful and counted as having a hatched chick. For all AON it was also noted whether the attending adults were singles or pairs. If a second adult was sitting or standing near the nest, within the reach of the bird sitting on the nest, it was counted as a 'pair'.

Breeding performance

Breeding performance was defined as the number of AC (in the chick period) in proportion to the number of AN (before or around hatching) in the same season. These data were only available for two early seasons (1959 and 1983). For the 1998 season we estimated the number of AN by subtracting the number of occupied nests that were observed to have no egg or chick from the number of AON.

Statistical analysis

Since the census data are counts, a Poisson regression framework was used to investigate population trends. Residual analysis was used to identify influential points (Cook & Weisberg 1999). For data sets with fewer than ten points only linear regression (LR) models were used, otherwise also Generalised Additive Models (GAM) and polynomial regression (PR) models were used (see Woehler *et al.* 2003). The percentage of variance explained (%VE) was calculated using [(residual deviance/null deviance)*100]. Dates of AC-censuses varied widely; thus it was tested whether a date effect existed. Comparisons between proportions (such as breeding performance or nest content) were tested using log-likelihood tests (G-statistics, see Sokal & Rohlf 1995). Seasons were separately analysed if proportions differed significantly between the seasons. Correlations between breeding performance and environmental variables were tested with Pearson product-moment coefficients. Differential population trends between colonies on the Frazier Islands (e.g. as result of differences in size, or in exposure to snow and wind) could not be established because the number of accurate datapoints was too low for statistical analyses. Statistical analysis was done using S+2000 and SPSS 10.0. All statistical tests were two-tailed and significance level was set at $\alpha = 0.05$.

RESULTS

Locations of Southern Giant Petrel colonies

Colonies were located on snow-free areas on the northern and southern ridges as well on low snow-free ridges protruding in the valleys (Fig. 2). The colonies on high ridges have steep slopes with easy fly-off points in northerly or northeasterly directions. The GPS-locations of colonies were compared with older maps. Location of most colonies

matched well with those observed in December 1989 (Woehler *et al.* 1990), apart from a few minor topographical differences likely due to less accurate mapping techniques in the past.

Trends in numbers of breeding Southern Giant Petrels

From all standardised censuses on the Frazier Islands, only counts of AC and AON had been done frequently enough to allow analysis of long-term trends in the breeding population of Southern Giant Petrels (Table 1).

On Nelly Island, the number of AC was counted during 13 seasons. This constitutes our longest data-series for this population, as AC counts for the other islands were available only for a reduced number of more recent years. The number of AC on Nelly Island fluctuated strongly between an unusual minimum of 11 chicks in 1996 and a maximum of 72 chicks in 1967 (Fig. 3A). Linear and PR models indicated no significant trend in the population over the full time period (LR model: 0.3% VE, $P = 0.624$; PR model: 4.3% VE, $P = 0.207$). However, a GAM model demonstrated that values around the long-term average are not random, but show significant periodic fluctuations (29.0% VE, $P < 0.001$) (Fig. 3A). The 1996 census on Nelly Island was identified as a potential influential point (residual value of -6.3) with a number of surviving chicks that was depressed to around 10-20% of the expected value. Removal of this point improved fit of linear and polynomial models (LR model: 15.7% VE, $P = 0.031$; PR model: 17.6% VE, $P = 0.073$). However, from a biological viewpoint the 1996 datapoint should not be removed since there is no doubt that the observation is fully reliable. The Nelly Island data series was also checked for a date effect, as the dates of census varied between 18 January and 22 March (see Table 1). No significant relationship between census date and number of AC existed (LR model: 3.8% VE, $P = 0.092$; PR model: 3.9% VE, $P = 0.239$).

On Dewart Island an AC-census was conducted seven times (Fig. 3B), the first complete one being in the 1976 season with 43 chicks. The numbers increased to 82 chicks in the 2001 season, which was highly significant (LR model 77.9% VE, $P < 0.001$). On Charlton Island an AC-census was conducted only four times, starting with 6 chicks in 1977 and ending with 11 chicks in 1998 (Fig. 3B). This increase was not significant due to the low sample size (84.0% VE, $P = 0.116$). However, totals of all islands together over the time period 1976-1998 increased 35% significant though there were only four datapoints (Fig. 3B; 93.7% VE, $P = 0.001$). Data for 1996 were lacking for both Dewart and Charlton Island.

Data of the type 'AON' were collected for the first time in the 1989 season. In 1989, 193 AON were found on the Frazier Islands, which increased to 248 AON in the 2001 season (Fig. 3C). Increases for separate islands were 27.4% on Nelly Island, 27.4% on Dewart Island and 42.9% on Charlton Island but none of these changes

Table 1. Overview of Southern Giant Petrel censuses on the Frazier Islands. Data in bold are used for population trend analyses in this article (Figs 3-5), census values followed by a ‘+’ are minimum estimates, and data or references mentioned between brackets are not used in article.

Season	Date	ISLANDS				CENSUS ^b		
		Day n ^a	Nelly	Dewart	Charlton	Method	Unit	references ⁱ
1955	21, 22 Jan 1956	94	250			AIR?	unspec.	1,3
1958	27 Jan 1959	99	80-100	20+		LAND	unspec.	1,2
1959	15 Dec 1959	56	60			LAND	ANc	1,8
1959	12 Feb 1960	115	46			LAND	AC	1,2,8
1960	21, 22 Mar 1961	153	34	10+		LAND	AC	1,2
1963	21 Jan 1964	93	10+			unknown	AC	1
1967	07 Mar 1968	139	72			LAND	AC	1,2,4
1971	20, 21 Jan 72	93	52	53+ ^d		LAND	AC	[1],[2],5
1971	20, 21 Jan 72	93			10-20	AIR	unspec.	[1],[2],5
1973	31 Jan 1974	103	76+ ^e			unknown	unspec.	1,2
1974	29 Jan 1975	101		29 ^f		LAND?	unspec.	1,[2],7
1976	13 & 17 Feb 1977	118	27+	43		LAND	AC	[1],[2],6
1977	24 Jan 1978	96	48	48	6	LAND	AC	1,2,6
1978	30 Jan & 2 Feb 1979	103	37	46	5	LAND	AC	1,[2],7
1979	20, 21 Jan 1980	93	44	55		LAND	AC	1,7
1982	18 Jan 1983	90	43	[10] ^g	[0] ^g	LAND	AC	1,7
1983	28, 29 Nov 1983	40	63	68	9	LAND	AN	1,7
1983	28, 29 Nov 1983	40	69 ^h	68+	9+	LAND	AON	1,7

1983	25, 26 Jan 1984	98	52		LAND	AC	1
1984	3 & 6 Mar 1985	135	64	69	LAND	AC	1,9
1985	14 Feb 1986	117	59 ⁱ	50 ⁱ	LAND	AC	[1],[7]
1989	23 Dec 1989	64	73	106	LAND	AON	1
1996	18 Feb 1997	121	11		LAND	AC	10
1997	23 Dec 1997	64	96	104	LAND	AON	10
1998	26 Dec 1998	67	95	103	LAND	AON	10
1998	14 Mar 1999	145	66	82	LAND	AC	10
2001	26 Dec 2001	67	93	135	LAND	AON	11

^a Daynumber is (an average of) the number of days after 20 October (estimated mean laying period)

^b See Material and Methods for description of census methods and units

^c Penney mentioned "approximately 60 nellies incubating eggs"

^d One colony could not be banded. Murray (1972) estimated c.20 another chicks in this colony

^e No details known; in this season only 27 chicks ringed

^f Data uncertain: Murray & Luters 1990 give 26+; Woehler *et al.* 1990 give 29; ABBBS give 12 chicks banded

^g Census data from Dewart Island and Charlton Island confused with number of banded chicks

^h 63 AN and 6 occupied nests with empty nest content is mentioned (Woehler *et al.* 1990), but it is not fully sure

ⁱ Data from banding records ABBBS are use and differ slightly from earlier published values: Nelly Island: 55 chicks

^j References: 1 = Woehler *et al.* 1990; 2 = Murray & Luters 1990; 3 = Ingham 1959; 4 = Shaughnessy 1971; 5 = Murray 1972; 6 = Cowan 1979; 7 = Australian Antarctic Data Center; 8 = R.L. Penney unpublished data; 9 = J.A. van Franeker unpublished data; 10 = J.C.S. Creuwels unpublished data; 11 = E.C. Woehler & F. Olivier unpublished data

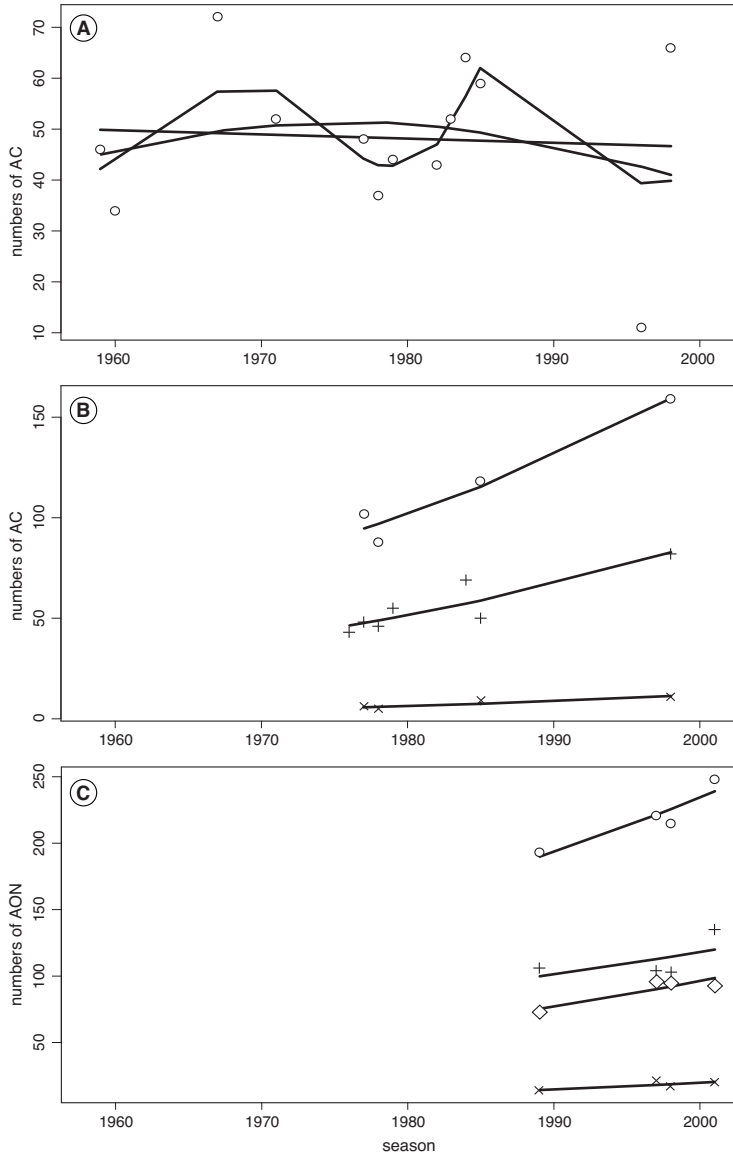


Figure 3. Population trends on the Frazier Islands. Graphs show the number of AC and fitted models for a) Nelly Island and for b) Dewart Island, Charlton Island as well as Totals for all Frazier Islands together. Furthermore is shown c) the number of AON and fitted models. Used symbols are: *diamonds* for Nelly Island, *crosses* for Dewart Island, *x-es* for Charlton Island, and *circles* for Totals of the Frazier Islands together. LR-models are shown in all three graphs, and in uppergraph (A) also PR-models and GAM-models are shown (for details, see text).

was significant (LR-models with only 4 censuses for all islands; Nelly Island: 79.5% VE, $P = 0.07$; Dewart Island: 32.5% VE, $P = 0.159$; Charlton Island: 65.0% VE, $P = 0.292$). When all islands were taken together, however, the trend was significant (87.2% VE, $P = 0.014$).

Breeding performance

For Nelly Island, there are three seasons for which there exists the combination of a census conducted just before or around hatching plus a later AC, allowing an estimate for breeding performance (Table 2). On other two islands such comparative censuses were performed only in the 1998 season. Despite a variable interval and different timing of the censuses, no differences in the breeding performance were found. Breeding performance between the late egg / early chick phase and the later chick phase averaged 80.4% ($G=1.27$, $P=0.530$). In the 1998 season the breeding performance on the three Frazier Islands averaged 81.1% with no significant differences between the islands ($G = 3.37$, $P = 0.185$).

Geographic data on the colonies were used to explain the differences in reproductive success among colonies in the 1998 season. The breeding performance of lower elevation colonies (82.2%) was similar to higher elevation colonies (80.7%; $G = 0.08$, $P = 0.780$). No correlations were found between the breeding performance and colony size by number of AON ($r^2 = 0.11$, $P = 0.258$), by colony surface area ($r^2 = 0.13$, $P = 0.298$), or by nest-density (AON/area; $r^2 = 0.06$, $P = 0.499$). Neither was breeding performance affected by distances to nearest penguin colony ($r^2 = 0.03$, $P = 0.660$), nor to the nearest neighbour Southern Giant Petrel colony ($r^2 = 0.02$, $P = 0.714$).

Table 2. Breeding performance of Southern Giant Petrels during three seasons.

season	island	first census		second census		breeding performance	time between censuses
		date	AN	date	AC		
1959	Nelly Island	15 Dec 59	60 ^a	12 Feb 60	46	83.6% ^b	59 days
1983	Nelly Island	28,29 Nov 83	63	23/28 Jan 84	52	82.5%	58 days
1998	Nelly Island	26 Dec 98	86 ^c	14 Mar 99	66	76.7%	78 days
1998	Dewart Island	26 Dec 98	95 ^c	14 Mar 99	82	86.3%	78 days
1998	Charlton Island	26 Dec 98	15 ^c	14 Mar 99	11	73.3%	78 days

^a Penney (unpublished fieldnotes) wrote 'approximately 60 nellies were incubating eggs and there were at least 20 more which were associated with nests but which took off when we neared'

^b in December 1959 5 eggs were taken for albumin sampling, therefore breeding performance calculated from 55 AN

^c see Methods for estimation of AN

Evaluation of AON type of counts in the 1997 and 1998 seasons

Detailed observations on the nest contents after the AON-census revealed the breeding status for almost half of the nests in our censuses. In the 1997 season, nest contents became more often visible (55.7%) than in the 1998 season (37.7%; $G = 14.24$, $P < 0.001$; Table 3). Despite the difference in the proportions of revealed/unrevealed nests, the proportion of AON found to contain no egg or chick stayed equal in both seasons (9.4% of all AON; $G < 0.01$, $P = 0.943$). Where the content became visible, 20.1% of the nests were empty and 79.9% nests were successful (11.3% with egg and 68.6% with chick), which was consistent over the two seasons ($G = 2.15$, $P = 0.142$).

Pairs did not reveal their breeding status more frequently than single birds, despite substantial differences in both seasons (Table 3). In the 1997 season 25.0% of the pairs and 45.5% of the singles did not show their nest content ($G = 2.04$, $P = 0.154$) and in the 1998 season this was 42.1% of the pairs and 64.3% of the singles ($G = 3.50$, $P = 0.061$). AON sites attended by pairs were more likely to contain no egg or chick (no egg or chick in 38.7% of all sites attended by pair and 7.2% of all sites with a single bird; $G = 22.30$, $P < 0.001$), which was consistent between the seasons ($G = 0.62$, $P = 0.431$). Consequently, pairs had relatively fewer chicks (16.1%) than single birds (33.3%; $G = 4.38$, $P < 0.036$), which was consistent between the seasons ($G = 0.66$, $P = 0.416$).

Table 3. Additional observations on nest contents of AON sites, obtained during outside-colony censuses.

single/pair	nest content revealed			unrevealed
	empty	egg	chick	
1997 season (221 AON)				
single	16	13	85	95
pair	5	0	4	3
total	21 (9.5%)	13 (5.9%)	89 (40.3%)	98 (44.3%)
1998 season (215 AON)				
single	13	7	50	126
pair	7	3	1	8
total	20 (9.3%)	10 (4.7%)	51 (23.7%)	134 (62.3%)

DISCUSSION

Census techniques

In published reviews on Antarctic birds it is often not fully clear which census methods or which census units were used to estimate the number of 'breeding pairs' (e.g. Woehler & Croxall 1997, Woehler *et al.* 2001). The number of breeding pairs can be derived from counts or estimates of the number of (apparently occupied) nests in different breeding phases, or of counts of either AN or AC. These options can give quite different results. The purpose of the study will usually determine the choice of a census method, but there might be constraints due to logistic, financial, and time limitations. The aim of the Frazier Islands censuses is to establish a long-term population trend of Southern Giant Petrels. For such purpose, consistency in the monitoring procedure (the combination of census method, census unit, timing, and effort) is of greater importance than the actual values.

At the Frazier Islands, two relatively standardised methods were recognised to allow trend analysis: AC- and AON censuses. Counts of AC have the advantage of being relatively easy and accurate, but are conducted late in the season and thus may suffer from strong variability in breeding success among seasons. Counts of AON are conducted earlier in the season, but are less accurate because a proportion of the nests counted will have no egg or chick. Since mid-1980s, protective measures for the Frazier Islands (e.g. no more chick banding) have resulted in a shift from AC- towards AON censuses. Furthermore, restriction of access to small boat transport will usually allow annual mid-summer visits (AON censuses around hatching) but late AC censuses will be often impossible due to sea ice conditions.

During a workshop on the statistical assessment of population trends of Antarctic seabirds it was concluded that developing standardised population surveys should get high priority (Woehler *et al.* 2001). For a few species selected for the CCAMLR Environmental Monitoring Program (CEMP) detailed methods for the collection of population data are available (<http://www.ccamlr.org/pu/E/pubs/std-meth04.pdf>). Most species, however, like the Southern Giant Petrel, still lack an appropriate census protocol. The analysis of a historical long-term population dataset, as well as indicating where problems arise during data collection, is a first step in developing standardised census procedures for this species, and possibly for other seabird species as well.

Population trends

Earlier analyses of the Frazier Island data (Woehler *et al.* 2001, 2003) suggested that the local Southern Giant Petrel population was declining from 1955 until the early 1980s due to human disturbance and recovery was the result of protective measures since

the mid-1980s. In re-examining the dataset and the sources of the data, some of this population trend could be attributed to inconsistency of census methods. Firstly, the highly influential census in 1955 was probably performed from the air (helicopter). Such a census is very inaccurate and likely to include many non-breeding birds, and therefore removed from the analysis. Secondly, different census methods were used. Before starting with AON censuses in 1989, most data came from AN- and AC censuses, which will be lower than from AON censuses because of the proportion of unsuccessful but attended nests. Thirdly, some surveys were incomplete and had to be excluded. Some colonies had been overlooked, because detailed colony maps were lacking in past. For example, Cowan (1979) noted a colony on Nelly Island that he apparently had missed in the previous season.

A critical review of all available census data led to the data selection shown in Table 1 and Fig. 3, which suggests a basically stable long term population with some periodic fluctuations over the period 1959–1998 (Fig. 3A). As in the earlier analysis by Woehler *et al.* (2001, 2003) a dip in the population is seen in the 1970s. The second fluctuation in the 1990s could be not detected in earlier analyses, because the 1996 datapoint, which concerned only Nelly Island, was not selected for the Woehler *et al.* (2001, 2003) dataset. Datasets on AC- as well as AON censuses for the other islands, and for all the islands combined are limited to a more recent time period (Figs. 3B, C). All trends suggested an increasing population since the late 1970s, but only three out of eight were significant. More censuses, and preferably over a longer time span, are needed to infer real population trends. Trends derived from such small datasets should be treated cautiously because removing or adding one or two data points might lead to different conclusions.

In the 1996 season all surface-breeding petrel species in the Windmill Island area performed very badly due to extreme snowfall (Van Franeker *et al.* 2001, J.C.S. Creuwels & J.A. van Franeker, unpublished data). Unfortunately, only Nelly Island was visited in this season, but trends for Dewart and Charlton Island would have been quite different, if census numbers had been available for this season. We noted that snow cover had decreased in consecutive seasons, and observed that birds in the valleys ('low colonies') started to breed in recently uncovered areas just outside the former colony boundaries. High annual variation in numbers of fledged chicks or numbers of 'breeding pairs' is also known from other continental Antarctic colonies of Southern Giant Petrels (Woehler *et al.* 2001, Micol & Jouventin 2001). Seasons with infrequent and irregular mass mortality of eggs or chicks could represent 10% or more of the reproductive life of most seabird species (Wooller *et al.* 1992).

Breeding performance and number of non-breeders

Breeding failures of Southern Giant Petrels are most frequent shortly after egg-laying

and around hatching (Mougin 1968, Conroy 1972, Hunter 1984). Thus after the egg-laying period, any census method based on active nests (AN- or AC censuses) will always give an underestimate of the actual number of breeding efforts. On the Frazier Islands averaged over three widely spaced seasons (1959, 1983 and 1998), about 20% of Southern Giant Petrel nests had failed between the first AN census around hatching and the second late-AC census. Similarly, Hunter (1984) recorded on South Georgia that two thirds of the losses (almost 20% of all breeding attempts) occurred in this period (from 1 week before until 4 weeks after the mean hatching date). At localities with more moderate climatic conditions most chick mortality occurs in this period (Hunter 1984, Cooper *et al.* 2001). At the Frazier Islands, however, it was found that at least in one season 10% of chicks died just before they were ready to fledge (Cowan 1979). Within one season a similar breeding performance was found between the colonies differing in their geographic position, colony size and distance to the Adélie Penguin colony.

In order to establish the proportion non-breeders in AON censuses, extensive observations were made in 1997 and 1998 following the initial AON counts (Table 3). In both seasons, censuses were conducted somewhat after the median hatching peak, as seen in the high proportion of chicks recorded. Eggs recorded in these censuses might also include failed eggs, which are sometimes incubated unsuccessfully for long periods. All observed chicks were very young. At the end of December, 9.4% of the AON did not contain an egg or chick, which is close to 8.7% at end November 1983 and ca.10% at end December 1989 (Woehler *et al.* 1990). The proportion of nests with no chick or no egg, expressed as a percentage of only those nests of which contents were revealed, was 20.1%. This percentage is probably an overestimate because the persistent incubation behaviour at nests where contents remained invisible suggests the presence of egg or chick. Birds without an egg or chick are much more likely to stand up or move around, and thus revealing their nest contents. Interestingly, the proportion of empty nests was equal in both seasons, in spite of the fact that the proportion of unrevealed nests was much higher in the 1998 season.

Unfortunately, there are no data for the Frazier Islands to estimate loss rates of eggs prior to the AN censuses around hatching. If Southern Giant Petrels experience similar losses in the early incubation period as other surface-nesting fulmarine petrels, which breed one to two months later in the season, then 30% of early breeding failures could be expected (Creuwels & Van Franeker 2003). This figure is much higher than the 10% losses observed under more temperate climatic conditions at South Georgia (Hunter 1984). Thus, at this stage we cannot reliably estimate the actual number of breeding pairs, although population trends can well be monitored with AON- and AC censuses.

Disturbance

Giant Petrels are highly sensitive to human presence, and leave their nest much faster than other procellariiforms (Warham 1962, Chupin 1997). Their uncovered eggs and small chicks are vulnerable to predation by skuas *Catharacta spp.* (Warham 1962, Conroy 1972, Hunter 1984, Peter *et al.* 1991), thus repeated human visits to colonies may cause low reproductive success (Prévost 1958, Conroy 1972, Peter *et al.* 1991, Chupin 1997). Chronic human disturbance, such as aircraft flights, presence of nearby research stations, and continuous research activities in the colony can cause population declines (Croxall 1984, Rootes 1988, Peter *et al.* 1991, Micol & Jouventin 2001, Woehler *et al.* 2003). Difficult access to the Frazier Islands, however, has caused relatively low and infrequent human disturbance levels. Some disturbance certainly came from visits of ornithologists for censuses or to band birds, although we did not detect any negative effects of increased banding efforts. During 11 seasons from 1971 through 1986, chicks were banded on the Frazier Islands, and personnel were transported to the islands mostly by helicopter (Murray & Luders 1990). In this period the number of AC increased on both Nelly Island and Dewart Island. The possibility cannot be excluded that this increase would have been higher without disturbance, but it is more likely that one or two visits per year fall within the range of each individual to deal with stress. For another Antarctic seabird, the Adélie Penguin, Fraser and Patterson (1997) argued that although short-term studies often found negative effects of human disturbance, this was rarely found in studies with long-term demographic datasets (but see Woehler *et al.* 1994). Recent work by Patterson *et al.* (2003) confirmed that at this stage no significant detectable human impact could be shown for the Adélie penguin population decline at Palmer Station.

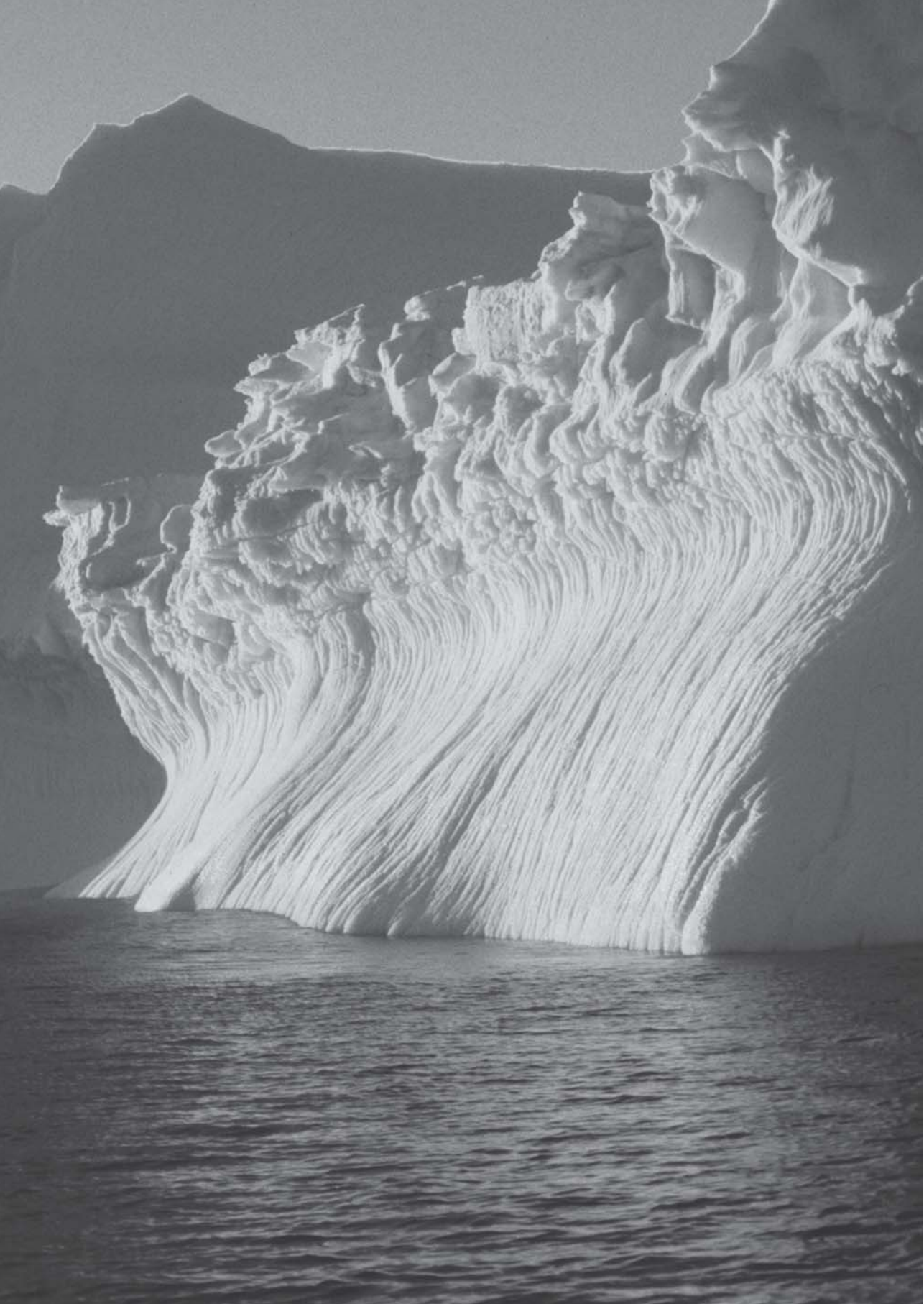
Conclusions and recommendations

This study detected no negative effects of human disturbance on the Southern Giant Petrel population on the Frazier Islands. The global vulnerable status of this species, however, justifies a precautionary approach as taken since 1986. Since transport to Frazier Islands is limited to small boats, research access is limited to good weather and ice conditions, which mostly occur during the mid-summer period. For long-term monitoring of the Southern Giant Petrels we suggest continuation of AON censuses at a standardised date (on Frazier Islands: around hatching). Due to the extreme variability in breeding performance and/or breeding efforts, monitoring is best attempted at annual rather than at multi-year intervals. Our analysis reveals no objections to opportunistic study visits, such as chick banding or an additional AC census late in the nestling period. A late AC census makes an estimation possible of the reproductive output and would improve comparisons with historical AC-values. Generally, to improve data quality of bird censuses it is recommended to

specify census methods, census units, viewing positions, distances to the colony, and if binoculars are used. Furthermore, specifying numbers for separate colonies and using accurate maps would further increase accuracy and makes analysis possible at colony level.

ACKNOWLEDGEMENTS

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CHAPTER

6

**SOUTHERN GIANT PETRELS
MACRONECTES GIGANTEUS
STARVE TO DEATH WHILE INCUBATING
ON THE ANTARCTIC CONTINENT**

Jeroen C.S. Creuwels, Jonny S. Stark, Wolfgang Petz and Jan A. van Franeker

INTRODUCTION

Procellariiforms are seabirds with life histories characterised by a long life span, 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 is 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. 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 three banded adult Southern Giant Petrels on their breeding grounds in the Antarctic that died while incubating their eggs.

RESULTS

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 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).

Table 1. Summary of details of Southern Giant Petrels recovered on the Frazier Islands

BANDING DETAILS			
Band number	CSIRO 131-34208	CSIRO 131-34191	OIS Museum Paris CF8226
Location	Dewart Island	Dewart Island	Ile des Pétrels
Date	27 Jan 1978	24 Jan 1978	01 Feb 1986
Age	Adult	Pullus	Pullus
RECOVERY DETAILS			
Location	Dewart Island	Dewart Island	Dewart Island
Date	08 Feb 1994	26 Dec 1998	26 Dec 1998
Age, sex, status	Adult, female ^b breeding	Adult, female breeding	Adult, male breeding
MEASUREMENTS			
Bill length (mm)	86.0 ^c	81.2	97.9
Bill depth (at gonys; mm)	31.2 ^c	24.8	32.7
Head length (mm)	157.7 ^c	154	175
Tarsus length (mm)		89.5	96
Wing length (mm)		517 ^d	531 ^d
Body mass (g)		2300	2100

^a measurements were taken according to van Franeker & ter Braak (1993)

^b sex derived from skull measurements (see Marchant & Higgins 1990)

^c only head of bird had been taken and measured afterwards; head length measured from bare skull

^d both birds showed no moult of primaries

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 Pétrels (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 ($\pm 10 \times 18$ mm) indicating death during the early breeding phase.

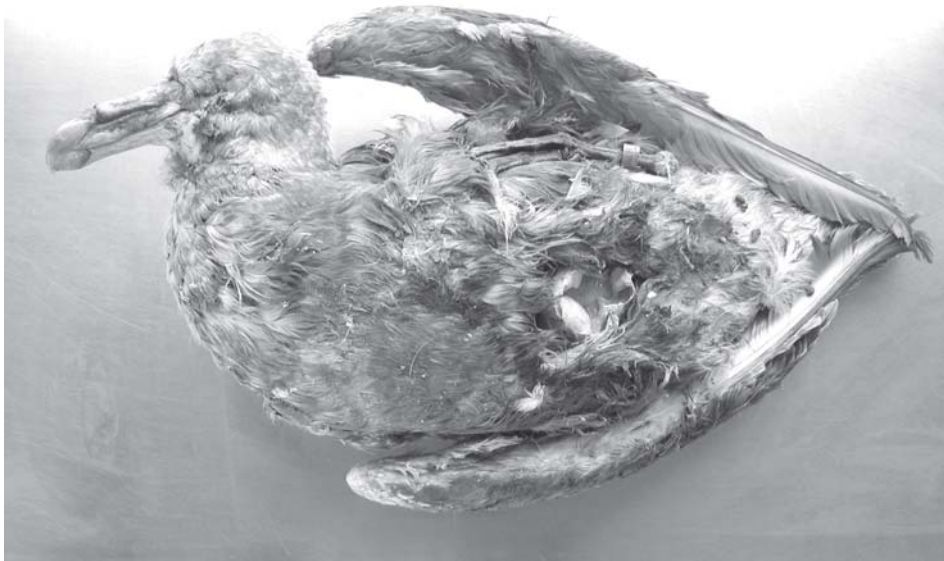


Figure 1. Corpse of the French-banded Southern Giant Petrel (Paris CF8226) before dissection. The egg is still positioned in the brood patch between the belly feathers. (Photo by J.A. van Franeker)

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 well, as evidenced by emaciated breast muscles. Stomachs contained no fresh food, but hard prey remains such as squid-beaks, penguin feathers and seal hairs were present in both. Furthermore, the French-banded male had remains of what was probably a large crustacean in the 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).



Figure 2. Damaged and decaying egg of the French-banded Southern Giant Petrel. (Photo by J.A. van Franeker)

DISCUSSION

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 only reported at Pointe Géologie, Adélie Land (Prévost 1953, Mougin 1975) and Fraziers 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 1-2 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 5 periods of 3 days with moderate to heavy snowfall or blowing snow, and another 5 periods longer than 3 days. The period of snow conditions on 23-30 October 1993 stood out for its long duration and severity. This may have attributed to the mortality of the bird found in February 1994. In spring 1998, however, there were no snow periods longer than 2 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 begin or end of the incubation shift, which lasts on average 4-6 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 Fulmar *Fulmarus glacialis* and Antarctic Petrel *Thalassoica antarctica*, regularly allow themselves to be buried under sometimes thick layers of snow during incubation. This appeared to have no effect on survival or reproduction because wind and melt usually limits the duration of such snow coverage. (Mougin 1968, J.C.S. Creuwels & J.A. van Franeker unpublished data). Northern Giant Petrels *Macronectes halli* on Bird Island, South Georgia breed 5-6 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 personal communication). During blizzards at Pointe Géologie, ice formed temporarily around the heads of Southern Giant Petrels that protrude from the snow cover (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 with no fatal consequences for the incubating birds have 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%; Hunter 1984, Mougín 1975) and even a slight reduction in the 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 personal communication). In the Palmer Archipelago a blizzard on 20-21 November 1975 caused c. 30% breeding failures due to abandonment of the nests (Parmelee 1992).

The age of the recovered birds suggested that 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 mass (Table 1). The average body weight 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 a good breeding condition to be able to lay an egg and start incubation, and thus their body weight 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 suggested that the dry cold air and windy conditions might quickly 'freeze dry' 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 had 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.

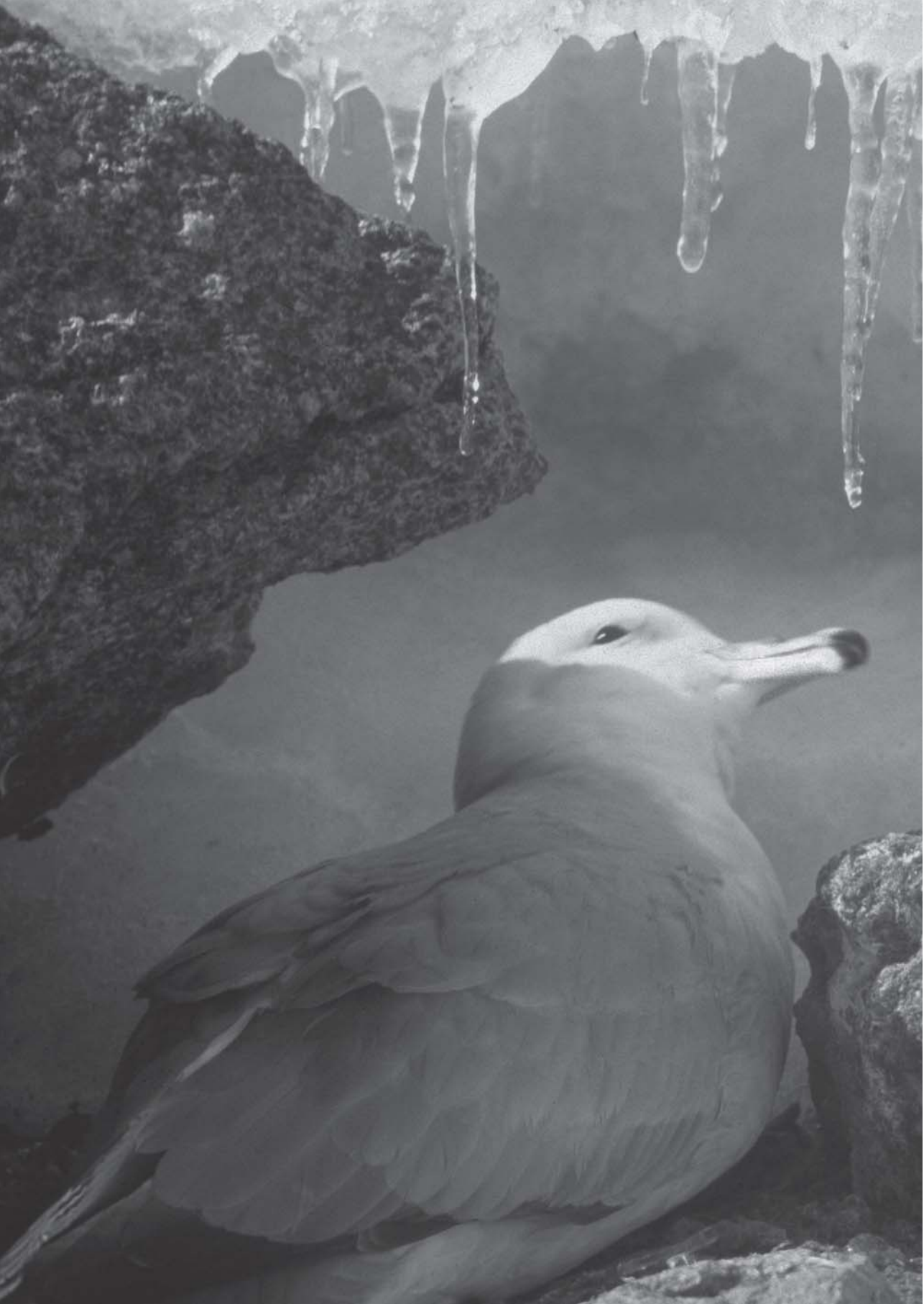
Why the two Southern Giant Petrels continued incubating until reaching the lethal starvation level remains uncertain. Snow and ice cover may possibly have prevented them from leaving their nests. Also, the upper snow layer might have been iced, because of increasing temperatures. In such conditions low 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 period (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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CHAPTER

7

**DISTRIBUTION AND ABUNDANCE
OF THE
SOUTHERN FULMAR *FULMARUS GLACIALOIDES***

Jeroen C.S. Creuwels, Sally Poncet, Peter J. Hodum and Jan A. van Franeker

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ABSTRACT

We reviewed published and unpublished literature to establish the status of the breeding distribution and abundance of Southern Fulmars *Fulmarus glacialisoides*. The species breeds widely throughout the Antarctic and on peri-Antarctic islands. From breeding population data collated from 73 of these localities, we estimated the minimum global population to be about 400,000 breeding pairs. After adjusting for seasonal variation in numbers of breeding pairs based on studies at Ardery Island, East Antarctica, the total global population is estimated to be at least one million breeding pairs. Of this, 72% nest on islands of the Scotia Sea arc and the South Atlantic Ocean. The precision of the estimate on the total number of breeding pairs is low, as several colony estimates were only available as orders of magnitude. Furthermore, different timing of the surveys and the difficulties of censusing colonial cliff-nesting birds reduced the count accuracy. Currently, there are no known threats to the global population, although the effects of fishery activities are not fully known.

INTRODUCTION

Southern Fulmars (*Fulmarus glacialisoides*) are found in great numbers in the Southern Ocean and they are an important consumer in the Southern Ocean ecosystem (Van Franeker *et al.* 2001). It has been estimated that 1.7 million individuals gather in the Prydz Bay area in East Antarctica (Cooper & Woehler 1994) during the summer months, and the breeding population of the Scotia Arc area and the Antarctic Peninsula has been estimated at 'several million' breeding pairs (Croxall *et al.* 1984). Southern Fulmars are known to disperse widely from Antarctica to subtropical waters, and they occasionally migrate along cool currents to tropical latitudes (Marchant & Higgins 1990). Many birds migrate north during the winter months when individuals have been recorded along the coasts of the Falkland Islands, South America, South Africa, Australia and New Zealand (Marchant & Higgins 1990).

Accurate knowledge of the breeding distribution and abundance of seabird populations is essential in order to assess population trends and to evaluate the potential impact of changes in the Antarctic ecosystem on seabirds. Consequently, the Group of Experts on Birds of the Scientific Committee on Antarctic Research (SCAR-GEB) is attempting to compile comprehensive syntheses of all Antarctic and sub-Antarctic breeding seabirds (Woehler 1993, Croxall *et al.* 1995, Van Franeker *et al.* 1999, and various others in preparation). Until the early 1980s, population estimates of Southern Fulmars were often derived from broad-scale surveys (Croxall *et al.* 1984), and many breeding localities had been rarely visited. Recently, new systematic censuses have been carried out in important breeding areas and new areas have been surveyed, enabling a more accurate appraisal of the current population and conservation status of the species.

The aim of this paper is to present a detailed review of published and unpublished information on the breeding distribution and abundance of Southern Fulmars. This is the first comprehensive estimate of the entire global breeding population of this species. We evaluated the accuracy of the population estimate by assessing the reliability of the range of different census methods employed.

METHODS

Study species

Southern Fulmars are also known as Silver-grey / gray Petrel, Silver-grey / gray Fulmar and Antarctic Fulmar. In 1949, the species' scientific name *Procellaria glacialoides* was changed to *Fulmarus glacialoides*, thereby placing it in the same genus as its sibling species the Northern Fulmar *Fulmarus glacialis* (Voous 1949). This decision was recently justified by mitochondrial DNA research (Nunn & Stanley 1998).

Diet studies of Southern Fulmars indicate a great variability in prey species ingested. The main prey species are fish (*Pleuragramma antarcticum*, *Electrona antarctica*), Antarctic Krill (*Euphausia superba*) and various squid species (Bierman & Voous 1950, Ainley *et al.* 1984, 1991, 1992, Ridoux & Offredo 1989, Arnould & Whitehead 1991, Norman & Ward 1992, Hodum & Hobson 2000, Van Franeker *et al.* 2001). Southern Fulmars forage opportunistically and have been observed feeding at a sewage outfall (J.A. van Franeker, personal observation) or feeding on discards from fishing vessels (Watson 1975) and on whale and seal carrion (Gain 1914, Murphy 1936, Bierman & Voous 1950, Holdgate 1963).

Studies conducted at breeding localities in East Antarctica (Hop Island, Haswell Island, Ardery Island, and Ile des Pétrels; see Table 1, Fig 1) indicate highly synchronised breeding. Birds return to colonies during the first half of October (Falla 1937, Prévost 1953, Mougin 1967, Pryor 1968, Luders 1977). The pre-laying exodus occurs during November and into the first week of December, but is less pronounced than in other petrel species (Luders 1977, Warham 1990, Brooke 2004). Egg-laying occurs between 3 and 23 December (mean approximately 11 December) and eggs are incubated for 45-47 days (Mougin 1967, Van Franeker *et al.* 1990, Hodum 2002, Creuwels & Van Franeker 2003). Incubation shifts are on average about 4 days, although the first few shifts are much longer and the last couple of shifts are shorter (Mougin 1967, Weimerskirch 1990a). Hatching occurs between 20 January-8 February (mean: 25-27 January) (Hodum 2002, Creuwels & Van Franeker 2003). The duration of the chick guard period varies widely among colonies and seasons, averaging 14-24 days (Mougin 1967, Hodum 2002). Fledging occurs between 10 and 28 March (mean: 15-20 March) (Prévost 1964, Mougin 1967, Hodum 2002, Creuwels & Van Franeker 2003). The chick-rearing period is 50-53 days, and chicks fledge on average 97-99 days after egg-laying. (Mougin 1967, 1975, Hodum 2002, Creuwels & Van Franeker 2003). Anecdotal data on the breeding biology of Southern Fulmars seem to confirm that breeding seasons of Southern Fulmars advance with decreasing latitude. Hatching occurred between 20 January-8 February in East Antarctica (66 to 68°S) (Hodum 2002, J. Creuwels unpublished data) between 15-24 January on Gibbs Island (61°S) (Furse 1977) and between 10-17 January on Bouvetøya (53°S) (O. Huyser, personal

communication). Little is known of the breeding biology of Southern Fulmars in the Antarctic Peninsula and the Scotia Sea area.

Census methods

Historically, the accuracy of seabird census methods and census metrics have varied widely due to such factors as survey time constraints, topography of the breeding area and research objectives. Due to the inaccessibility of many Southern Fulmar breeding areas, nests and birds are typically surveyed from vessels or estimated from a vantage point located at some distance from the colony. In a few cases, especially where colonies were small, observers were able to enter the colony, and nests were counted individually and checked for eggs and chicks. Details on the precise census methodology employed are often lacking, but in most cases we were able to categorise studies according to the different census metric(s) used:

Unspecified number (*Unspec.*). No information available on the type of count. In most cases, it is assumed to represent the number of *apparently occupied sites* (see below).

Total number (*Total*). The total number of birds present in the colony, irrespective of their breeding status. This number may include birds sitting on a nest, birds sitting as a pair and birds not attached to a nest site. In general, the total number of individuals has been rarely recorded in seabird colony surveys.

Apparently Occupied Sites (*AOS*). The number of individuals or pairs sitting tightly on an area that seems suitable (relatively horizontal and large enough to hold an egg) for successful breeding (Walsh *et al.* 1995, CCAMLR 1997, Bibby *et al.* 2000). AOS are normally counted from a distance, and therefore no distinction can be made between active and failed nests. In many studies, AOS-counts have also been reported as 'breeding pairs', or 'nesting pairs'.

Active Nests (*AN*). The number of nests containing an egg or chick, present on the day of census. AN are counted any time after egg-laying when all nests may be approached on foot and their contents individually checked.

Active Chicks (*AC*). The number of nests containing a chick on the day of census. AC can be counted individually by checking nest content, or by counting from a distance (distance-count) later in the season when chicks no longer brooded and therefore visible. Very late in the season when most chicks are unattended and often difficult to distinguish from adults, these distance-counts are less reliable.

The most commonly used metric for measuring the size of a breeding population is 'breeding pair'. The total number of breeding pairs in a colony may be defined as

the total number of pairs that laid an egg during the season. However, this number is difficult to determine for Southern Fulmars for a number of reasons: occasionally another breeding pair may lay an egg in an abandoned nest during the same breeding season, eggs may roll into adjacent nests, un-paired females may lay an egg and even an incubating trio was observed. In order to record the actual number of eggs laid in one season, birds have to be individually marked and nests monitored at least twice daily, particularly since birds may also abandon the nest site within 24 hours after losing their egg (Prévost 1953, J. Creuwels & J. van Franeker unpublished data).

A Southern Fulmar colony or 'breeding locality' is defined here as the smallest geographically distinct area for which we have some data on the number of breeding birds. Due to the typical loosely scattered distribution pattern of Southern Fulmar nest sites along a coastline, colony boundaries are often difficult to identify. In this review, most estimates were of populations of entire islands (in some cases: archipelagos) rather than specific colonies.

Where surveys were very approximate, population size estimates were often recorded as a range rather than a precise figure, and in these cases, the mean of the upper and lower data is presented as the population estimate. Where no estimates of the number of breeding birds were available, the breeding location was recorded as 'breed'. Those sites that were listed as possible or probable but where breeding was unconfirmed were recorded as 'possibly breed'. The 'census season' is the year during which the breeding season ended (i.e. the 1998/99 season is given as 1999), following the CCAMLR convention (Woehler *et al.* 2001).

A full overview containing all census data including many historical surveys and additional notes will be made available through the SCAR-GEB website (<http://www.birds.scar.org>). Latitudes and longitudes of the breeding localities were obtained from the SCAR Composite Gazetteer of Antarctica (<http://www.scar.org/information>).

Intra-seasonal variation in colony attendance

One of the important factors that influence the outcome of censuses is how bird numbers in a colony vary over the season. The intra-seasonal variation in numbers of breeding pairs and birds attending the colony was investigated in a study area on Ardery Island, Wilkes Land, East Antarctica, during three consecutive seasons (1997-1999) from the spring arrival of birds through to fledging. Southern Fulmars were counted on an almost daily basis, first by distance-counts and subsequently by individual nest checks (active nests) in the colony. The distance-counts of apparently occupied sites and total numbers of birds present were conducted from a viewpoint about 30-60 m away from the boundaries of the colony.

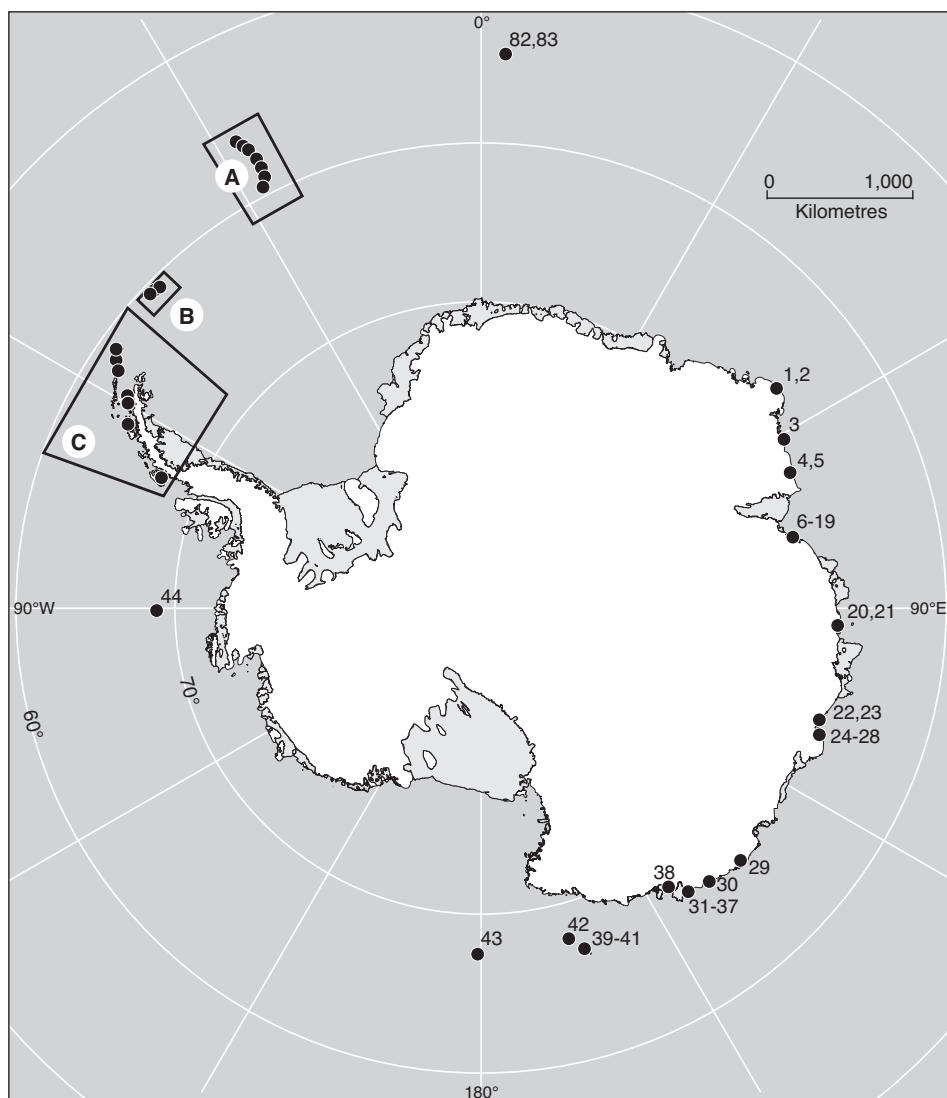


Figure 1. Distribution of breeding localities of Southern Fulmars. Area A (Antarctic Peninsula and environs) is given in detail in Fig. 2, area B (South Orkney Islands) in Fig. 3, area C (South Sandwich Islands) in Fig. 4. Numbers near the dots correspond with numbers in Table 1.

RESULTS

Distribution and abundance

An overview of the most recent and reliable census data for all breeding localities of Southern Fulmars is presented in Table 1. In total, 80 confirmed and 3 possible breeding localities have been recorded and the global breeding population estimated at a minimum of 400,000 breeding pairs. Census data are lacking for seven of 80 breeding localities, but descriptive notes (Falla 1937, Robertson *et al.* 1980, Convey *et al.* 1999) suggest that their total breeding population probably comprises less than 1% of the estimated global breeding population. The current population estimate of 400,000 breeding pairs, based on the most recent and reliable counts (Table 1), should be interpreted as a *minimum estimate*. Below we discuss the historic population estimates for 14 areas around the Antarctic (Fig. 1) and island archipelagos in the Southern Ocean, and compare these with this study's estimates in Table 1.

Areas I-VIII: East Antarctica and adjacent islands

East-Antarctica (Fig.1) has previously not been reviewed as a whole, although three separate reviews have been compiled for this area: Robertson *et al.* (1980) estimated 15,000-20,000 breeding pairs for the Balleny Islands in the Ross Sea sector; Jouventin *et al.* (1984) mentioned about 50 breeding pairs on Ile des Pétrels in Terre Adélie; and Woehler & Johnstone (1991) estimated 29,000 breeding pairs for the Australian Antarctic Territory.

Estimates from more recent surveys (see Table 1) indicate no significant change in population size. A recent survey of part of King George V Land (area VII), revealed many new breeding localities with almost 7,000 previously unrecorded breeding pairs (Barbraud *et al.* 1999). In total, we estimate that 59,000 breeding pairs or 15% of the estimated global breeding population breed in East Antarctica.

Area IX: West Antarctica (excluding Antarctic Peninsula)

Only one breeding locality is known from West Antarctica, located on Peter 1 Øy (Fig. 1). Southern Fulmars were recorded by the first expedition to land on the island in 1929 (Olstad 1929, Holgersen 1945). In 1948, Holgersen (1951, 1957) estimated a minimum of 3,500 'nesting pairs'. During a recent circumpolar survey, Gavrilov (1997) estimated that thousands of breeding pairs were present on the island. We estimate that 10,000 breeding pairs or 3% of the estimated global population breed on Peter 1 Øy.

Area X: Antarctic Peninsula

Southern Fulmars were first recorded to breed on the Antarctic Peninsula (Fig. 2) in

Table 1. Overview of breeding localities and the estimated number of breeding pairs.

Locality	Latitude	Longitude	Census date	Season	number of breeding pair			References
					estimation	min	max	
I. ENDERBY LAND								
1 Proclamation Island	65°51' S	53°41' E	13 Jan 1930	1930	B	-		Falla 1937
2 Aagaard Island	65°51' S	53°40' E	15 Dec 1996	1997	B	-		Gavrilo unpublished report
II. MAC. ROBERTSON LAND								
3 Kidson Island	67°12' S	61°11' E	24 Jan 1989	1989	2000	unspec.		Robertson 1991
4 Scullin Monolith	67°47' S	66°42' E	1-6 Feb 1987	1987	1350	unspec.	1080	Alonso <i>et al.</i> 1987
5 Murray Monolith	67°47' S	66°53' E	17 Feb 1997	1997	30	unspec.	10	50 Gavrilo unpublished report
III. PRINCESS ELIZABETH LAND								
6 Svenner Islands	69°02' S	76°50' E		1981	2800	unspec.		ANARE unpubl. report
7 Hop Island	68°50' S	77°42' E	2-3 Jan 1985	1985	2576	AN [†]		Green & Johnstone 1986
8 McNab Island	68°49' S	77°40' E	2-3 Jan 1985	1985	320	AN [†]		Green & Johnstone 1986
9 "Island A" west of Hop Island	68°50' S	77°36' E	15 & 21 Dec 1981	1982	900	AOS		Green & Johnstone 1986
10 "Island B" west of Hop Island	68°50' S	77°36' E	15 & 21 Dec 1981	1982	150	AOS		Green & Johnstone 1986
11 "Island C" west of Hop Island	68°50' S	77°37' E	15 & 21 Dec 1981	1982	150	AOS		Green & Johnstone 1986
12 "Island D" west of Hop Island	68°50' S	77°37' E	15 & 21 Dec 1981	1982	950	AOS		Green & Johnstone 1986
13 Buchan Island	68°47' S	77°46' E	10 Feb 1984	1984	2378	AN [†]		Green & Johnstone 1986
14 Small island North of Buchan Island	68°47' S	77°46' E	15 & 21 Dec 1981	1982	400	AOS		Green & Johnstone 1986
15 Filla Island	68°49' S	77°50' E	5-6 Jan 1985	1985	4007	AN [†]		Green & Johnstone 1986
16 Islands North of Strelka Island	68°46' S	77°45' E	15 & 21 Dec 1981	1982	400	AOS		Green & Johnstone 1986
17 Kryuchok Island	68°48' S	77°45' E	15 & 21 Dec 1981	1982	20	AOS		Green & Johnstone 1986
18 "Northern Island" NW of Forpost I.	68°51' S	77°33' E	15 & 21 Dec 1981	1982	730	AOS		Green & Johnstone 1986

Table 1. Continued.

	Locality	Latitude	Longitude	Census date	Season	number of breeding pair			References
						estimation	min	max	
19	Forpost Island	68°52'S	77°35'E	15 & 21 Dec 1981	1982	750	AOS		Green & Johnstone 1986
IV. QUEEN MARY LAND									
20	Haswell Island	66°31'S	93°00'E	20-24 Jan 1979	1979	3150	AOS	2950	3350 Starck 1980
21	Fulmar Island	66°32'S	93°00'E		1963	1500	unspec.	1300	1700 Pryor 1968
V. WILKES LAND									
22	Hudson Island	66°39'S	108°25'E	mid Dec 1993	1994	200	unspec.		Melick <i>et al.</i> 1996
23	"Island A" South of Hudson Island	66°40'S	108°25'E	mid Dec 1993	1994	80	unspec.		Melick <i>et al.</i> 1996
24	Nelly Island	66°14'S	110°11'E		1962	500	unspec.		Orton 1963
25	Dewart Island	66°13'S	110°10'E		?	B	-		Murray & Luders 1990
26	Ardery Island	66°22'S	110°30'E	20-31 Dec 1995	1996	3860	AOS		Barbraud & Baker 1998
27	Odbert Island	66°22'S	110°33'E	Dec 1984	1985	2000	AOS		Van Franeker <i>et al.</i> 1990
28	Holl Island	66°25'S	110°25'E	Dec 1977-Jan 1978	1978	400	unspec.		Cowan 1979
29	Lewis Island	66°06'S	134°22'E	18 Jan 1960	1960	86	AOS		Law 1962
VI. TERRE ADÉLIE									
30	Ile des Petrels, Pointe Géologie	66°39'S	140°01'E	c.20 Dec 1962-2001	1963-2002	53	AN ²		Jenouvrier <i>et al.</i> 2003
VII. KING GEORGE V LAND									
31	Cape Pigeon Rocks	66°59'S	143°47'E	Dec 1997-Jan 1998	1998	501	AOS	476	526 Barbraud <i>et al.</i> 1999
32	Four Islets	66°56'S	143°54'E	Dec 1997-Jan 1998	1998	65	AOS	62	68 Barbraud <i>et al.</i> 1999
33	"Island D"	66°58'S	143°54'E	Dec 1997-Jan 1998	1998	1015	AOS	964	1066 Barbraud <i>et al.</i> 1999
34	"Island C"	66°57'S	143°55'E	Dec 1997-Jan 1998	1998	708	AOS	673	743 Barbraud <i>et al.</i> 1999

35	"Island B"	66°56'S	143°57'E	Dec 1997-Jan 1998	1998	920	AO5	874	966	Barbraud <i>et al.</i> 1999
36	"Island A"	66°58'S	143°57'E	Dec 1997-Jan 1998	1998	1497	AO5	1422	1572	Barbraud <i>et al.</i> 1999
37	Stillwell Island	66°55'S	143°48'E	Dec 1997-Jan 1998	1998	2155	AO5	2047	2263	Barbraud <i>et al.</i> 1999
38	Penguin Point	67°39'S	146°12'E	31 Dec 1912	1913	24	AO5			McLean in Falla 1937
VIII. ROSS SEA SECTOR										
<i>Balleny Islands (39-42)</i>										
39	Young Island	66°25'S	162°24'E		1964; 1965	B	-			Robertson <i>et al.</i> 1980
40	Row Island	66°31'S	162°38'E	10-18 Feb 1965	1965	5500	unspec.	5000	6000	Robertson <i>et al.</i> 1980
41	Borradale Island	66°35'S	162°45'E		1964; 1965	PB	-			Robertson <i>et al.</i> 1980
42	Sturge Island	67°28'S	164°38'E	27-31 Jan 1965	1965	15,000	AO5	10,000	20,000	Robertson <i>et al.</i> 1980
43	Scott Island	67°24'S	179°55'W	7 Jan 1982	1982	PB	-			Wilson & Harper 1996
IX. BELLINGHAUSEN SEA										
44	Peter I Island	68°47'S	90°35'W	19 Jan 1997	1997	10,000	unspec.	5000	15,000	Gavrilo 1997
X. ANTARCTIC PENINSULA										
45	Pourquoi Pas Island	67°41'S	67°28'W	27 Feb 1986	1986	7500	AO5	5000	10,000	Poncet & Poncet unpublished data
46	Anvers Island, NW coast	64°32'S	62°53'W	30 Jan 1987	1987	5000	AO5	1000	10,000	Poncet & Poncet unpublished data
47	Brabant Island	64°15'S	62°20'W	2 Feb 1987	1987	1000	AO5	300	1500	Poncet & Poncet unpublished data
48	Davis Island	64°06'S	62°04'W	2 Feb 1987	1987	5000	AO5	1000	10,000	Poncet & Poncet unpublished data
49	Trinity Island	63°48'S	60°45'W	21 Jan 1987	1987	10,000	AO5	2000	20,000	Poncet & Poncet unpublished data
50	Tower Island	63°35'S	59°49'W	21 Jan 1987	1987	75	AO5	50	100	Poncet & Poncet unpublished data
51	Cape Kjellman	63°44'S	59°24'W	31 Jan 1990	1990	B	-			Poncet & Poncet unpublished data
52	Otter Rock	63°38'S	59°12'W	1 Feb 1990	1990	5000	AO5	1000	10,000	Poncet & Poncet unpublished data
53	Cape Roquemaurel	63°33'S	58°57'W	18 Jan 1987	1987	2000	AO5	1000	5000	Poncet & Poncet unpublished data
54	Young Point	63°36'S	58°57'W	21 Jan 1987	1987	PB	-			Poncet & Poncet unpublished data
55	Astrolabe Island	63°17'S	58°40'W	18 Jan 1987	1987	5000	AO5	1000	10,000	Poncet & Poncet unpublished data

Table 1. Continued.

	Locality	Latitude	Longitude	Census date	Season	number of breeding pair			References
						estimation	min	max	
XI.	SOUTH SHETLAND ISLANDS								
56	Greenwich Island	62°34'S	59°34'W		2000	PB	-		Naveen 2003
57	Bridgeman Island	62°03'S	56°45'W		1977	100	unspec.		Furse 1978
58	O'Brien Island	61°30'S	55°58'W		1977	7880	unspec.		Furse 1978
59	Eadie Island	61°28'S	55°57'W		1977	8500	unspec.		Furse 1978
60	Aspland Island	61°28'S	55°55'W		1977	9800	unspec.		Furse 1978
61	Gibbs Island	61°28'S	55°34'W		1977	18,830	unspec.		Furse 1978
62	Rowett Island	61°17'S	55°31'W	Dec 1970-Mar 1971	1971	40	unspec.		Furse & Bruce 1975
63	Cornwallis Island	61°04'S	54°28'W		1977	550	unspec.		Furse 1978
64	Clarence Island	61°12'S	54°05'W		1977	25,475	unspec.		Furse 1978
XII.	SOUTH ORKNEY ISLANDS								
65	Inaccessible Islands	60°35'S	46°40'W	31 Dec 1986	1987	50,000	AOS	10,000	Poncet & Poncet unpublished data
66	Monroe Island	60°36'S	46°01'W	6 Jan 1984	1984	7500	AOS	5000	Poncet & Poncet unpublished data
67	Coronation Island, Sandefjord Bay	60°38'S	46°00'W	6 Jan 1984	1984	15,000	AOS	10,000	Poncet & Poncet unpublished data
68	Coronation Island, East Cape	60°39'S	45°16'W	24 Nov 1956	1957	3000	unspec.		Hall 1957
69	Powell Island	60°41'S	45°03'W	31 Dec 1983	1984	3500	AOS	1200	Poncet & Poncet unpublished data
XIII.	SOUTH SANDWICH ISLANDS								
70	Zavodovski Island	56°18'S	27°35'W	30 Jan 97; Feb 98	1997; 1998	B	-		Poncet 1997, Convey <i>et al.</i> 1999
71	Visokoi Island	56°42'S	27°09'W	30 Jan 1997	1997	26,000	AOS	15600	Poncet 1997, Convey <i>et al.</i> 1999
72	Candlemas Island	57°04'S	26°41'W	29-30 Jan 1997	1997	500	AOS	450	Poncet 1997, Convey <i>et al.</i> 1999
73	Vindication Island	57°06'S	26°46'W	29 Jan 1997	1997	2200	AOS	1320	Poncet 1997, Convey <i>et al.</i> 1999

74	Saunders Island	57°47'S	26°27'W	29 Jan 1997	1997	10	AOS	9	11	Poncet 1997, Convey <i>et al.</i> 1999
75	Montagu Island	58°25'S	26°20'W	28 Jan 1997	1997	20,000	AOS	12000	28000	Poncet 1997, Convey <i>et al.</i> 1999
<i>Bristol Island and environs (76-79)</i>										
76	Bristol Island	59°02'S	26°37'W	27-28 Jan 1997	1997	7000	AOS	4200	9800	Poncet 1997, Convey <i>et al.</i> 1999
77	Freezland Rock	59°03'S	26°37'W	27 Jan 1997	1997	1300	AOS	780	1820	Poncet 1997
78	Wilson Rocks	59°02'S	26°38'W	27 Jan 1997	1997	7000	AOS	4200	9800	Poncet 1997
79	Grindle Rock	59°02'S	26°38'W	27 Jan 1997	1997	5000	AOS	3000	7000	Poncet 1997
80	Thule Island	59°27'S	27°22'W	25-26 Jan 1997	1997	3500	AOS	2100	4900	Poncet 1997, Convey <i>et al.</i> 1999
81	Cook Island	59°28'S	27°12'W	26-27 Jan 1997	1997	14,000	AOS	8400	19600	Poncet 1997, Convey <i>et al.</i> 1999
XIV. SOUTH ATLANTIC ISLANDS										
<i>Bouvet Island and environs (83-84)</i>										
82	Bouvetøya	54°26'S	03°24'E	Jan-Feb 1997,1999	1997; 1999	50,000	unspec.	20,000	100,000	K. Isaksen, personal communication
83	Larsøya	54°28'S	03°24'E	17-21 Dec 1928	1929	B	-			Olstad 1929
All breeding localities						Total:	396,385			

¹ Estimated number of currently breeding pairs, based on the proportion 'active nests (AN) / apparently occupied nests (AOS)' in a few reference areas

² Maximum number of active nests (AN), no data available on number of apparently occupied nests (AOS)

in 1902 (Anderson 1905) when Nordenskjöld explored this area. The first review of breeding population data included three breeding localities with a total of 100 to 1,000 breeding pairs (Croxall *et al.* 1984).

Between 1986 and 1989, S. Poncet and J. Poncet (unpublished data) undertook detailed seabird distribution and abundance surveys of the Antarctic Peninsula and recorded over 40,000 breeding pairs of Southern Fulmars. We estimate that 41,000 breeding pairs or 10% of the estimated global breeding population breed on the Antarctic Peninsula.

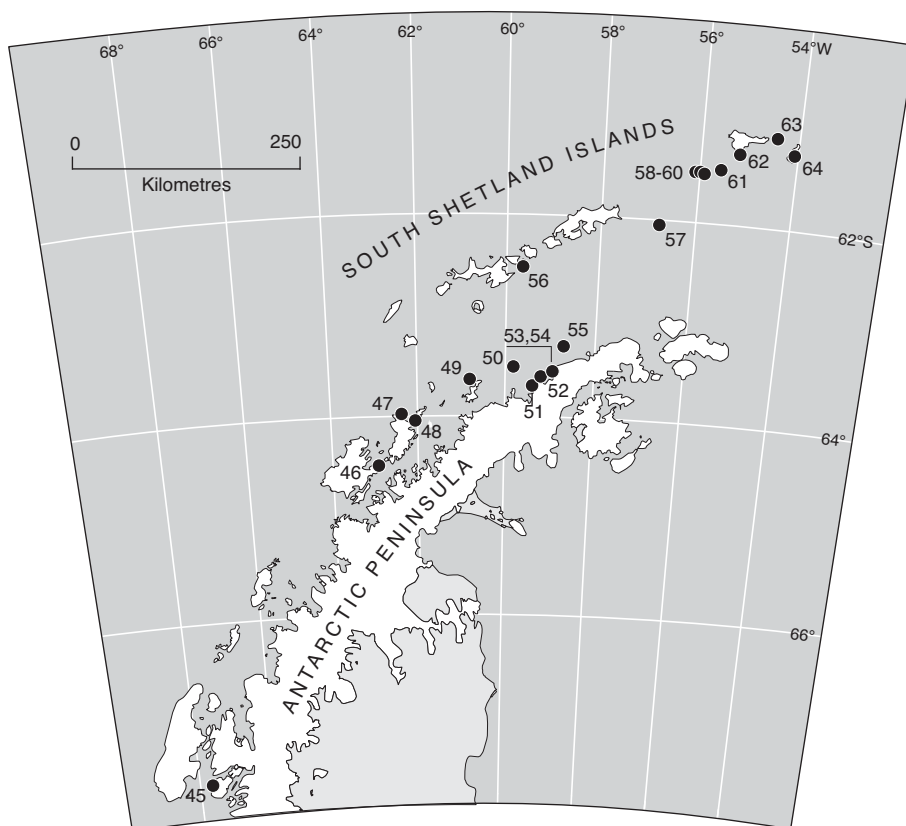


Figure 2. Distribution of breeding localities of Southern Fulmars on the Antarctic Peninsula and Shetland Islands. Numbers near the dots correspond with numbers in Table 1.

Area XI: South Shetland Islands

The South Shetland Islands (Fig. 2) consists of two main island groups. The southern group lies relatively close the Antarctic Peninsula and includes Deception Island, which was mentioned historically as a possible breeding locality (Anderson 1905, Gain

1914). Increased numbers at sea probably occurred due to whaling activities around Deception Island (Gain 1914, Murphy 1936), but we found no evidence that breeding may have occurred here. Croxall *et al.* (1984) mentioned no confirmed breeding here. Recently, Naveen (2003) suggested Greenwich Island as a possible breeding locality.

The northern group, also called the Gibbs and Elephant Island Group, appears to be an important breeding area. Detailed surveys in the 1970s showed that many birds breed here, especially on Gibbs and Clarence Islands (Furse & Bruce 1975, Furse 1978). In total, 71,000 breeding pairs are estimated (Croxall *et al.* 1984), this being 18% of the estimated global breeding population.

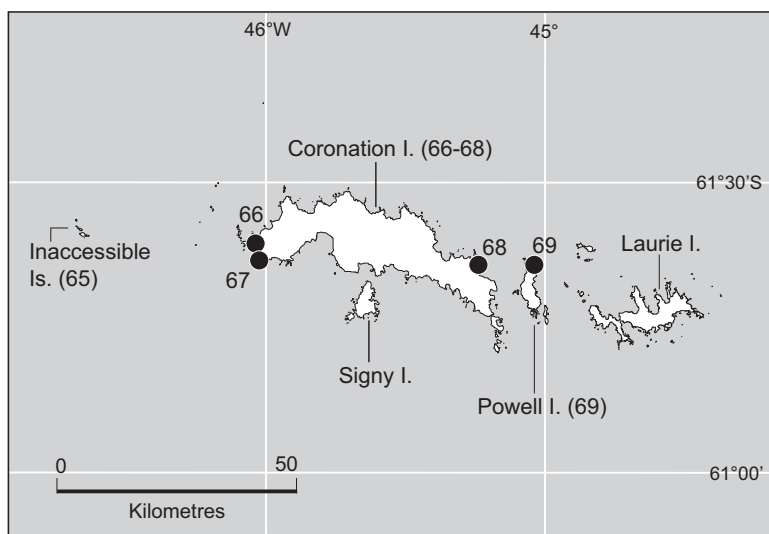


Figure 3. Distribution of breeding localities of Southern Fulmars on the South Orkney Islands. Numbers near the dots correspond with numbers in Table 1.

Area XII: South Orkney Islands

The South Orkney Islands (Fig. 3) were first surveyed in the early 1930s (Ardley 1936), when more than 500,000 breeding pairs were estimated to nest on the Inaccessible Islands and 25,000 breeding pairs on Coronation Island. Croxall *et al.* (1984) estimated 100,000 – one million breeding pairs for the South Orkney Islands.

J. Poncet and S. Poncet (unpublished data) censused about 25,000 breeding pairs on three islands of the South Orkneys in 1984 and a further 50,000 breeding pairs on Inaccessible Islands in 1986 (Table 1). No recent estimates are available for the east coast of Coronation Island, last surveyed in 1957 (Hall 1957). On the basis of these data, we estimate the current population of this area to be about 80,000 breeding pairs, representing 20% of the estimated global breeding population.

Area XIII: South Sandwich Islands

The South Sandwich Islands (Fig. 4) have been rarely visited (e.g. Larsen 190Wilkinson 1956, 1957) and only anecdotal information was available until recently. Kemp & Nelson (1932) and Holdgate & Baker (1979) gave detailed descriptions of each island's topography, geology and biology, but did not attempt to estimate the breeding population of birds. From these reports, it appeared that Southern Fulmars nested here in high numbers. Croxall *et al.* (1984) mentioned roughly one million breeding pairs.

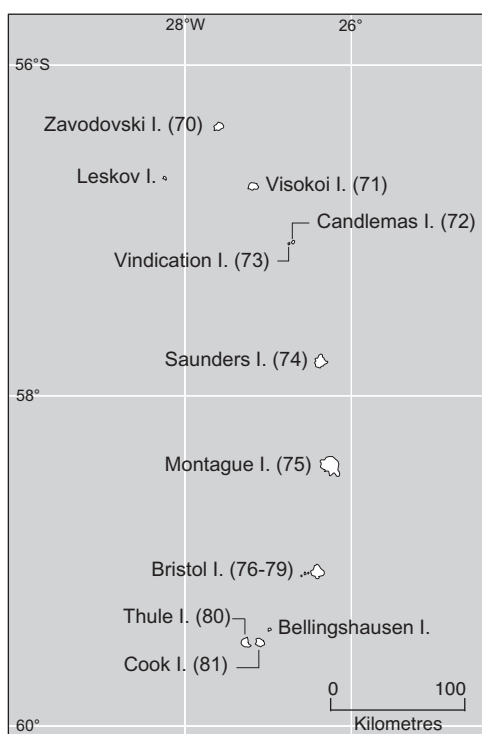


Figure 4. Distribution of breeding localities of Southern Fulmars on the South Sandwich Islands. Numbers behind the islands' name indicate that breeding occurs on the island, and correspond with numbers in Table 1.

Detailed systematic surveys have been undertaken recently (Poncet 1997, Convey *et al.* 1999), confirming the importance of this island group for the global population. Many islands contained numerous breeding pairs, notably Visokoi Island, Montagu Island, Bristol Island (including Wilson, Grindle, and Freezland Rocks) and Cook Island. These recent population estimates total about 90.000 breeding pairs, this being 22 % of the estimated global population.

Area XIV: South Atlantic Islands

In the South Atlantic Ocean, only Bouvetøya and adjacent rocks and islets (Fig. 1) are known to contain breeding pairs of Southern Fulmars. Based on high numbers of Southern Fulmars observed at-sea near Bouvetøya, it has been suggested that this species may breed on the island (e.g. Bierman & Voous 1950, Holgersen 1951), although no systematic survey has been conducted.

K. Isaksen (personal communication) estimated between 20,000-100,000 breeding pairs in 1996-1998, based on rough extrapolations. In contrast to colonies in East Antarctica where birds disperse after each breeding season, high numbers of Southern Fulmars (50,000 individuals) are seen around Bouvetøya during the winter months (Augstein 1987). We have assumed that 50,000 pairs may nest here, or 13% of the estimated global population.

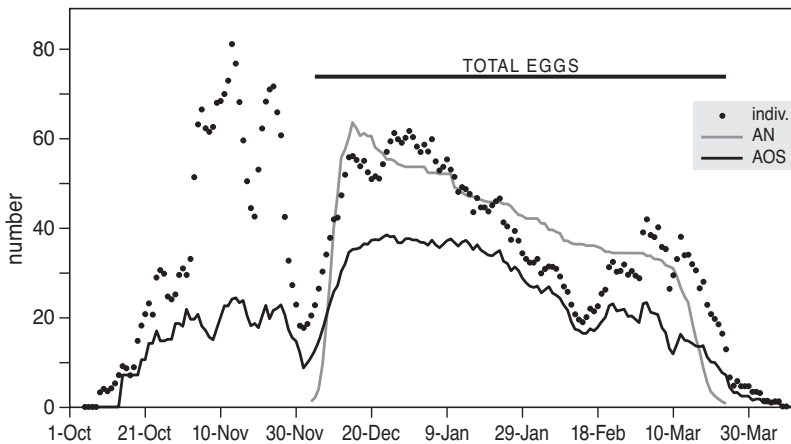


Figure 5. Intra-seasonal trends in numbers of breeding Southern Fulmars. Distance-counts (AOS and total of individuals) are counted before entering the study area. In the colony, the nest contents of each individual nest was checked and number of AN counted. Data are averaged over three seasons, and distant censuses are presented as running averages over 7 days. On average 74 eggs were laid per season.

Intra-seasonal variation in the Ardery Island study colony

During three consecutive seasons (1997-1999), the intra-seasonal variation in breeding population numbers was investigated on Ardery Island, East Antarctica. On average, the number of eggs laid (i.e. the number of breeding pairs) in this colony was 74 per season. The population trends according to the three census methods (see Fig. 5) can be summarised as follows:

- i) The number of *active nests* was always lower than the number of eggs laid

due to many nest failures occurring immediately after laying. The number of active nests was highest at peak egg-laying (15 December), by which time 14% of the total number of eggs laid had been lost. Just before fledging, the number of active nests had decreased to 33% of the total number of eggs laid.

ii) The number of *apparently occupied sites* was lower than the number of active nests due to undercounting of birds on nests, as not all were visible from the viewpoint. During the first half of incubation (15 December – 15 January), the number of apparently occupied sites was about half the number of breeding pairs and decreased further to about 20% just before fledging.

iii) The *total number of individuals* was highly variable and fluctuated around the total number of active nests during much of the season. The greatest number of birds in the colonies was recorded before the pre-laying exodus. As the season progressed, numbers of birds fluctuated widely due to influxes of non-breeding birds or failed breeders. Consequently, numbers of individual birds are not considered to be reliable indicators of breeding pairs.

In conclusion, all three methods underestimated the number of breeding pairs on Ardery Island. The number of apparently occupied sites in the period between egg-laying and hatching (c. 20 December – 20 January) was relatively stable and in that period represented approximately 40% of the number of eggs that actually had been laid in the colony.

DISCUSSION

Based on available census data, the sum of colony estimates in Table 1 produces a global population of Southern Fulmars of about 400,000 breeding pairs. This is certainly an under-estimate of the real number of breeding pairs as it is largely based on the number of AOS or active nests. The actual number of breeding pairs (producing an egg) was obtained from data provided by the detailed colony study at Ardery Island. During much of the incubation period until hatching, the number of AOS represented only 40% of the number of eggs known to be laid in the colony, and rapidly decreased thereafter (Fig.5). In Terre Adélie, Jenouvrier *et al.* (2003) found that by late December, 43% of the breeding population not breeding, but known to be alive.

The number of AOS in the Ardery Island colony has been derived from counts conducted from a nearby vantage point. Many of the counts in Table 1 were made during incubation, but some were made well after hatching, and from distant viewpoints. It is likely therefore that the number of AOS is around 40% of the actual number of egg-producing pairs. This proportion has been applied to the total figure of 400,000 pairs in Table 1, and the global breeding population of Southern Fulmars estimated to be at least a million pairs.

The current global estimate breeding pairs of one million breeding pairs is considerably lower than the previous estimate of 'several millions' pairs which was estimated for only a part of the distributional area (Croxall *et al.* 1984). In particular, the population estimates for important breeding areas such as the South Orkneys and South Sandwich Islands (Table 1) are much lower than previously reported, while those for the Antarctic Peninsula and King George V Land (which are relatively small on the global scale, Table 1) are considerably higher.

In translating breeding estimates to overall numbers of birds it has to be kept in mind that bird populations contain many non-breeders. In an earlier study on Ardery Island, Van Franeker *et al.* (1990) found that the number of regularly attended sites was twice as high as the number sites where eggs were produced. Furthermore, intensive ringing studies indicated that for every breeding individual, two non-breeders attended the colony.

Below we discuss in further detail why a global breeding estimate of one million breeding pairs is not very precise, why it should be interpreted as a minimum estimate, and whether the global population of Southern Fulmars is likely to change in the near future.

Precision and accuracy of the counts

The precision and accuracy of a count are the two principal sources of errors when counting birds (Bibby *et al.* 2000). Count precision is a measure of the natural variation in census values, and reflects the variation in results obtained during repeated counts under similar conditions. Estimated count precision, indicated by minimum and maximum reliable values is available for counts at 39 breeding localities (Table 1). Details on how the count precision was estimated are often lacking. Large colonies are typically counted by extrapolating estimates of snapshots of representative parts of the colony. Such estimates may deviate 40% or more from the estimated count (Poncet 1997, Convey *et al.* 1999). The use of photography in future surveys could increase count precision if individual birds are counted from high quality images.

Count accuracy is a measure of the bias present in the count data, and indicates how much the estimated value deviates from the true value. The accuracy of counts performed from a distance (distance-counts) can only be determined if they are compared with precise count data, preferably collected in the colony or at short distance from the nests. As most censuses in Table 1 were of inaccessible colonies counted from a distance, count accuracy is mostly unknown. Important factors that influence count accuracy are weather and colony location (especially colony topography). Colonies on cliffs and in coastal areas can often only be surveyed from sub-optimal viewpoints (e.g. from water or sea-ice), resulting in reduced numbers of birds being visible (Walsh *et al.* 1995, Bibby *et al.* 2000). Even under relatively

favourable census conditions, many nests can be missed. In a study colony on Ardery Island, Wilkes Land, East Antarctica, where nests were counted from an elevated viewpoint overlooking the colony, an estimated 30-50% of the nests appeared to be hidden among boulders (Van Franeker *et al.* 1990, Fig. 5).

Aerial or yacht-based photography is a census method that has not been used before to carry out Southern Fulmar censuses. Photography has many advantages for census surveys, such as the possibility of archiving images and the assessment of the count error by repeating the counts from the images. Furthermore, data on colony boundary and colony size can be obtained from photographic prints or digital images and used for future comparisons. Ideally, estimates derived from photos should be adjusted in order to take into account the proportion of birds not on nest and the proportion of nests without an egg. This requires count data obtained at close distance to the colony or by shore parties. For a detailed description on the methodology, we refer to Poncet *et al.* (2006) and Robertson *et al.* (2006).

In situations where more detailed repeated censuses are possible, we refer to standard methods developed (for Antarctic Petrels) by CCAMLR (1997).

Undiscovered colonies

The breeding localities are not evenly distributed over Antarctica (Fig. 1), which in some areas might also be related to differences in surveying efforts. Particularly in East Antarctica, the clustered distribution probably reflect a higher search effort around research stations. Thus, small colonies in these areas have a higher chance to be detected, and further away the research stations there are possibly still colonies to be discovered. For example, Barbraud *et al.* (1999) recently surveyed the coast along Terre Adélie and a part of King George V Land and found six new breeding localities.

Several at-sea distribution studies have reported high densities of Southern Fulmars close to the breeding grounds (Falla 1937, Bierman & Voous 1950, Holgersen 1957, Ainley *et al.* 1984, Montague 1988, Veit & Hunt 1992, Whitehouse & Veit 1994). However, high densities at sea may not necessarily indicate the proximity of breeding localities. For example, the discrepancy between at-sea numbers of 1.7 million birds (Cooper & Woehler 1994) and 16,500 breeding pairs on land, both recorded in the highly productive and well-surveyed Prydz Bay area, remains to be resolved. For example, the rich food supply in the Prydz Bay area attracts many seabirds (Woehler 1997) and possibly also non-breeding individuals or birds that are not breeding in the area. On the other hand, the breeding population estimates in this area are conservative and might underestimate the true size of the local population (E. Woehler, personal communication). The presence of Southern Fulmars in the Amundsen and Bellingshausen Seas during the breeding season (Gain 1914, Zink 1981, Hunt and Veit

1983, Gavrilov 1997) possibly indicates that there are still colonies to be discovered in the coastal area of West Antarctica. More systematic surveys are needed for these relatively poorly surveyed areas in addition to major breeding localities.

Possible threats

Currently, there is no evidence of serious threats to the global Southern Fulmar breeding population. Chemical contaminants such as organochlorine compounds and mercury have been found in eggs and adults of Southern Fulmars, but levels are generally low (Luke *et al.* 1989, Van den Brink *et al.* 1998). Plastic particles have been recorded in the stomachs of Southern Fulmars, but their rates of occurrence are low (Van Franeker & Bell 1988, Ainley *et al.* 1990). Long-term population trend data are available only for Ile des Pétrels in East Antarctica. This small colony has been monitored annually for more than 40 years, during which time its breeding population has increased slightly due to immigration from colonies elsewhere (Jenouvrier *et al.* 2003). The species usually breeds on precipitous cliffs and inaccessible rock ledges, and the largest breeding concentrations are found on remote oceanic islands that are rarely visited (Poncet 1997, Naveen 2003, IAATO 2005). At the few sites where visitors (including tourists, researchers and station support personnel) are able to access breeding sites, no disturbance impacts have been recorded and should they occur, are unlikely to affect the global population, although they may have an effect on the local population.

Fishery vessels attract Southern Fulmars (Whitehouse & Veit 1994, Weimerskirch *et al.* 2000, Wienecke & Robertson 2002) and frequent interactions with fishing gear have been observed (Marín 2004). Apart from one mortality in the South Atlantic Ocean (Vaske 1991 cited in Brothers *et al.* 1999) no fatal accidents of Southern Fulmars with long-lining vessels and trawlers have been recorded (White *et al.* 1999, Weimerskirch *et al.* 2000, Kock 2001, Wienecke & Robertson 2002, Sullivan 2004). Increasing fishery activities could have positive effects due to increasing supply of discards, and negative effects due to increased competition for food resources. Pelagic krill fisheries operate in areas close to major breeding grounds in the Scotia Sea and Antarctic Peninsula (Croxall & Nicol 2004). The Antarctic Krill *E. superba* is the only food source that Southern Fulmars share with commercial fisheries (CCAMLR 2005) but it is probably not a major component of the Southern Fulmar diet (Van Franeker *et al.* 2001). Reduced krill stocks could affect breeding success and population growth, via effects on intermediate trophic levels such as fish and squid.

RECOMMENDATIONS

In order to facilitate future comparative surveys, it is essential that census methods are clearly described, and boundaries of breeding colonies be identified. Standardising the timing of the censuses (e.g. as close to hatching as possible) is recommended, but will be difficult due to logistical constraints. More studies are needed on intra-seasonal variations in population numbers in order to interpret censuses conducted at different times. Due to the inaccessibility of most colonies, most censuses need to be done by boat or aerial surveys. If possible, verification of distance-counts with censuses at closer distance is highly recommended to enhance the accuracy. The use of photography in censusing Southern Fulmar populations should be explored.

From Table 1, it follows that more detailed systematic surveys should be conducted, especially of the Clarence and Elephant Islands group, South Orkney Islands, South Sandwich Islands, Balleny Islands and Bouvetøya. We recommend that any information on the breeding distribution and abundance of Southern Fulmars be forwarded to the SCAR – GEB (<http://www.birds.scar.org/contacts>) and/or to the first author to enable the public database to be updated and revised.

ACKNOWLEDGEMENTS

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Where do breeding Southern Fulmars and Antarctic Petrels forage?

Studying the breeding biology of seabirds on land reveals many intriguing aspects of their breeding ecology, but also invokes questions about their behaviour in the habitat where they live most of their time. We were particularly interested to find out whether the longer durations of the foraging trips of Antarctic Petrels meant that they were covering longer distances or that their foraging areas were located further away than those of Southern Fulmars. A pilot study was set up to investigate the possibilities of tracking Southern Fulmars and Antarctic Petrels, which also gave the opportunity to elucidate some of these issues of the foraging strategy.

We used Microwave Telemetry satellite transmitters (Platform Transmitter Terminals) weighing 20 gram. With TESA[®]-tape the transmitters were attached to a couple of mantle feathers on the back of the birds and the total added mass amounted to 2.5 - 5% of the individual body mass. In total, 9 devices were available, which were attached to a bird for on average 13 days (range: 2-31 days). Because the trackers could be easily removed and applied again, most devices were used at least on two different birds. Between 23 January and 23 March 1999, we were able to fit satellite transmitters on 8 Antarctic Petrels and 12 Southern Fulmars, equally divided over both sexes. All individuals receiving a satellite transmitter had a chick at the moment of employment and per animal different foraging trips were recorded. Due to technical failures position data could not always be generated by each PTT.

Microwave PTTs use ARGOS satellites to calculate the location of the PTT and ARGOS also classifies the accuracy for each calculated position. We showed only satellite fixes of a highest category (0, 1, 2, 3) and filtered the dataset to remove most of the improbable locations (see McConnell *et al.* 1992).

The preliminary results of this pilot project are shown Fig. 1. Although some of the positions might not be fully accurate, the overall picture is clear. The areas where both species forage are clearly separated, if we compare Fig. 1A with Fig. 1B. Southern Fulmars stay closer to Ardery Island and virtually all foraging occurred below 66°S in a relatively small area within 100 km of the breeding colony. Fig. 1A showed five foraging trips that were recorded north of 65°S, which were different from the usual routine in Southern Fulmars. Two of these trips were of birds that left Ardery Island in March and were moving to their winter areas. One of these adult left its chick after heavy snowstorms early in March (the chick was fed by

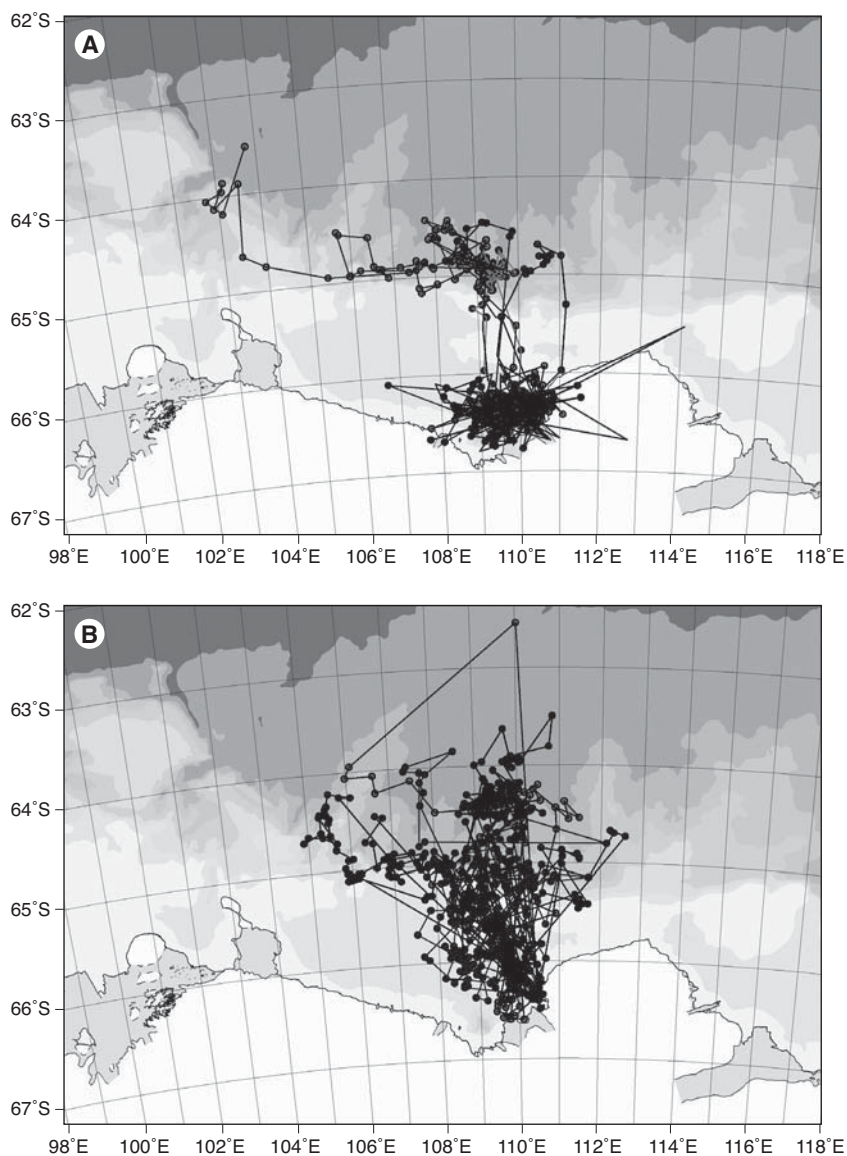


Figure 1. Distribution of foraging Southern Fulmars (a) and Antarctic Petrels (b) in the chick-rearing period. Plotted are data of satellite transmitters of individual birds that were applied on their breeding colony on Ardery Island (66°22'S 110°27'E) between 23 January 1999 and 23 March 1999. Grey shades indicate changes in the bathymetry. North of Ardery Island the continental shelf (light grey) extends roughly until 65°S, where the continental shelf break is situated. Deep waters (more than 1000m deep, darker grey) are found north of this area. Sea-ice cover is not indicated in this figure. For more explanation on individual foraging trips, see text.

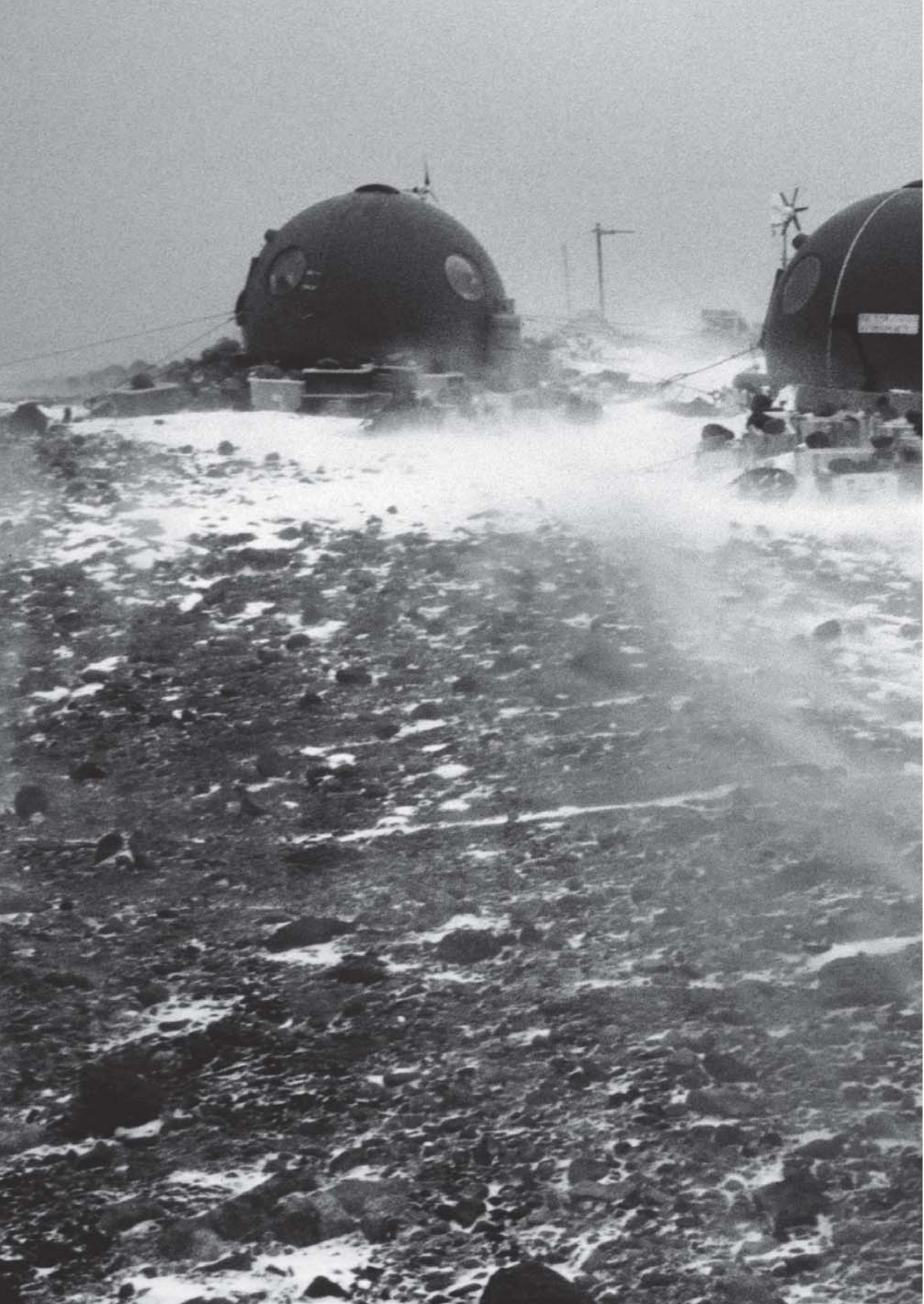
one partner, but predated just before fledging), the other one left the day after the chick successfully fledged. Two trips were of individuals that made an unusual large loop in mid February, which appeared to be just after the highly demanding chick guarding period. These individuals returned to the colony after 2 days and resumed their normal foraging regime with short trips. The fifth bird made a long trip end February and returned after two days. Possibly, Southern Fulmars also take occasionally long breaks ("bimodal foraging strategy") when their body condition is low, or when parents have to recuperate.

Antarctic Petrels have not only longer durations of foraging trips, but they also forage further away. It is not clear whether these feeding grounds are more productive and thus contain more food or that these grounds are the typical ice-habitat where Antarctic Petrels prefer to forage. Possibly, further investigation of the satellite tracker data combined with detailed data on the cover and concentration of sea-ice might clarify this relationship. Although Antarctic Petrels have satellite positions around Ardery Island, their foraging ranges are generally between 64°S and 66°S. Probably most positions close to Ardery Island are of birds that are commuting between the feeding and breeding grounds, although some opportunistic feeding might occur on the way when they encounter large patches of prey. The distance to the furthest foraging ranges was much more than 300 km away.

The area where most Antarctic Petrels were foraging and the five deviating Southern Fulmar tracks were found appeared to be in the vicinity of the continental shelf break, which is here situated at around 65°S. The minimum sea-ice edge (in February) is located a bit closer to the continent, roughly at 65°30'S, and thus the main foraging area for Antarctic Petrels is situated within the highly productive, seasonal sea-ice zone. Interestingly, when a large part of the coast of East Antarctica was surveyed in 1996, the highest peak of krill density and especially seabird numbers in this area of Antarctica was observed north of Ardery Island, between 63° and 65°S along the 110°E north-south transect (Nicol *et al.* 2000).

Temporal differences in foraging, except for Southern Fulmars very late in the season, were not found. However a closer look to individual birds and individual foraging tracks is needed to verify this. The data of this pilot study also show that positions should be determined in a high temporal and spatial resolution, especially in Southern Fulmars that have short distances and short durations of their foraging trips.

Many thanks to Dave Watts of Australian Antarctic Data Centre of the Australian Antarctic Division for helping to plot the data in Figure 1.

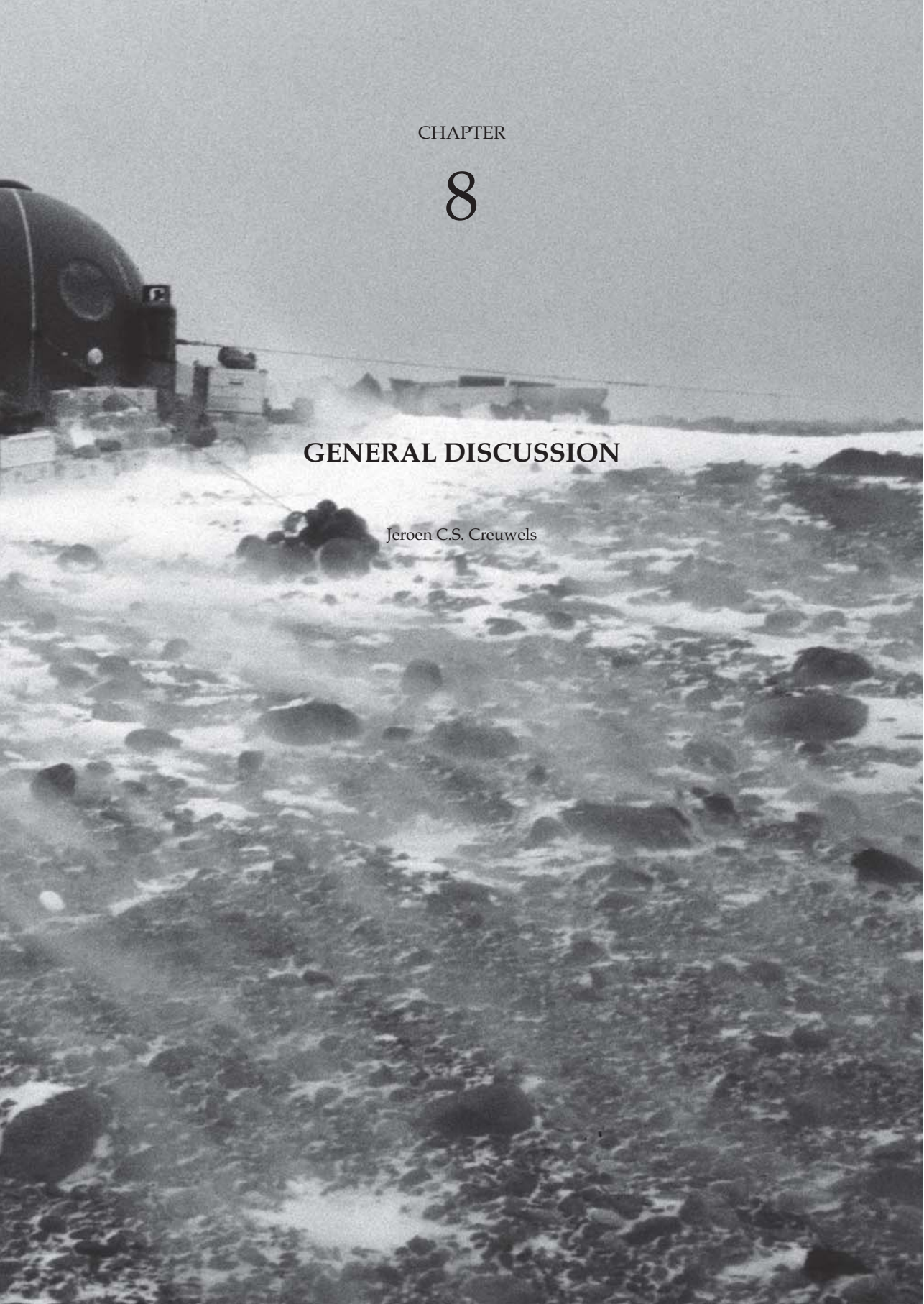


CHAPTER

8

GENERAL DISCUSSION

Jeroen C.S. Creuwels



INTRODUCTION

This study started as a component of a long-term research project on the ecology of fulmarine petrels, to provide basic information on their survival, recruitment, breeding success, and chick diets. The main focus of this research was on the Antarctic Petrel. This species is very well adapted to life in an extreme polar environment. It has the southernmost breeding distribution of any bird and the majority of this species breeds in far inland colonies. Antarctic Petrels collect their food within or close to the pack ice throughout the annual cycle and are faced with a very narrow time window that is available for reproduction at high latitudes. Breeding too early may be expected to lead to loss of eggs, and too late could result in loss of nearly fledged chicks.

The study site at Ardery Island offered the possibility of comparison with other fulmarine species. We decided to investigate two species being the earliest and the latest fulmarine species breeding since their breeding success might be expected to be most heavily affected by the short summer seasons in Antarctica. Therefore, it was decided to study the breeding and foraging ecology of Antarctic Petrels (*Thalassoica antarctica*) and Southern Fulmars (*Fulmarus glacialisoides*) with special emphasis on daily monitoring of nests during the whole breeding season.

The study showed that despite their close relationship, these two Antarctic fulmarine petrel species differ in several significant aspects of their breeding ecology. Earlier studies had already indicated differences in timing of breeding and foraging strategy (Norman *et al.* 1992, Hodum 1999, 2002, Van Franeker 2001). These and other differences between the species were investigated in Chapters 2 and 3, analyzing details in patterns of nest failures over time, colony and nest attendance and chick provisioning rates. Predation of the study species by visiting Southern Giant Petrels (*Macroneptes giganteus*) took us by surprise in terms of causes as well as consequences (Chapter 4). These events served to redirect research attention in part to population assessments of the predator (Chapter 5) which also revealed a remarkable type of mortality of that predator while breeding (Chapter 6). Finally, a compilation of breeding distribution and abundance data of Southern Fulmars was produced (Chapter 7) to complement similar reviews of the Antarctic Petrel and other fulmarines, and to illustrate the distributional background behind differences in breeding strategy from that of the Antarctic Petrel.

In Table 1 an overview is given of the main ecological variables for the breeding biology of the Antarctic Petrel and the Southern Fulmar, which are described in Chapter 2 and 3. The table is supplemented with additional information from other chapters and relevant similarities and differences between both species will be discussed in the appropriate sections below.

Table 1. Overview of variables on the breeding biology of Antarctic Petrels and Southern Fulmars. For each parameter average values are given over all seasons when available. Between parentheses is indicated in which chapter more specific details can be found.

	<u>Antarctic Petrel</u>	<u>Southern Fulmar</u>
ADULT WEIGHT		
Average adult weight	678g	800g
BREEDING SUCCESS (CH. 2)		
Overall breeding success	36.5%	35.0%
Egg failure during egg laying period	30.1%	17.7%
Overall hatching success	53.3%	52.5%
Fledging success	68.5%	66.7%
Chick mortality until 3 days after end of guarding	90.9%	14.8%
COLONY ATTENDANCE (CH. 2)		
Arrival adults at colony	Begin Oct	Mid Oct
Colony absence during pre-laying exodus	complete	partial
Presence of adults in colony in Feb -Mar	<5 %	20-30%
BREEDING BIOLOGY (CH. 2)		
Date of egg laying	25 Nov	11 Dec
Date of chick hatching	11 Jan	26 Jan
Date of chick fledging	01 Mar	17 Mar
Incubation period (days)	47.7	46.5
Guarding period (days)	14.3	20.1
Chick period (days)	48.7	50.1
Total breeding period (days)	96.6	96.6
FORAGING (CH. 2, 3, BOX 2)		
Foraging trip length during incubation (days)*	17.2	8.8
Foraging trip length during chick period (days)*	2.5	1.3
Distance to main foraging area (km)	150-250	<100
Meal size (g)	141	135
Chick provisioning rate (g/day)	140	265
CHICK GROWTH (CH. 3)		
Age at peak mass (days)	33.6	35.3
Date of peak mass	13 Feb	02 Mar
chick growth rate until peak mass (g/day)	29.3	33.9
Chick loss rate after peak mass (g/day)	20.4	21.1
Maximum chick mass (g)	920	1119
Maximum chick mass (of adult mass)	136%	140%

Table 1. Continued.

Fledging chick mass (g)	622	812
Fledging chick mass (of adult mass)	92%	102%
MOULT (BOX 1)		
Start primary moult non-breeding individuals	15 Jan	28 Dec
Start primary moult breeding individuals	4 Feb	21 Jan
First fully moulted bird in colony	-	9 Mar
BREEDING DISTRIBUTION (CH. 7)		
Distribution of breeding colonies (in latitude)	66° - 80°S	54° - 69°S
Main breeding distribution (geography)	continental	oceanic islands

* trip length is calculated as twice the mean incubation shift or fasting interval

BREEDING SUCCESS

Overall breeding success

Breeding success of Antarctic Petrels and Southern Fulmars was studied from egg-laying until fledging during three seasons. Large annual variation in breeding success (the percentage of eggs that results in fledged chicks) occurred, but the trend was similar in both species (Fig. 1) and within each season we found no differences between the species. Heavy snowfall and thick snow cover affected both species especially during the 1996-97 season, most evidently in Antarctic Petrels. The extremely poor success of Antarctic Petrels in this year continued a trend observed in preceding seasons (1984-85, 1986-87 and 1990-91) and was found to be connected to snow-related predation in especially the early egg phase.

Within the three study seasons of the present project, the trend of breeding success of both species changed direction and increased significantly to peak values in the last season of 48.1 % success for Southern Fulmars and even 57.4% success for Antarctic Petrels. Average values over three seasons were, respectively, 35.0% and 36.5% (Table 1). For these species, an average breeding success of c. 35% is probably normal. Hodum (2002) observed that Southern Fulmars had an overall breeding success of 30-55% and Antarctic Petrels of about 20-30% in two seasons on the Rauer Islands. At Terre Adélie, Southern Fulmars showed an average breeding success of 70% over 39 years (Jenouvrier *et al.* 2003), but this value is probably inflated because surveys appear to miss the egg-laying period and thus the early breeding failures in this period. Furthermore, nests in this colony are checked with large time intervals. We noticed that even a daily schedule is probably not sufficient to record all breeding attempts and failures, especially in an eventful season as 1996-97.

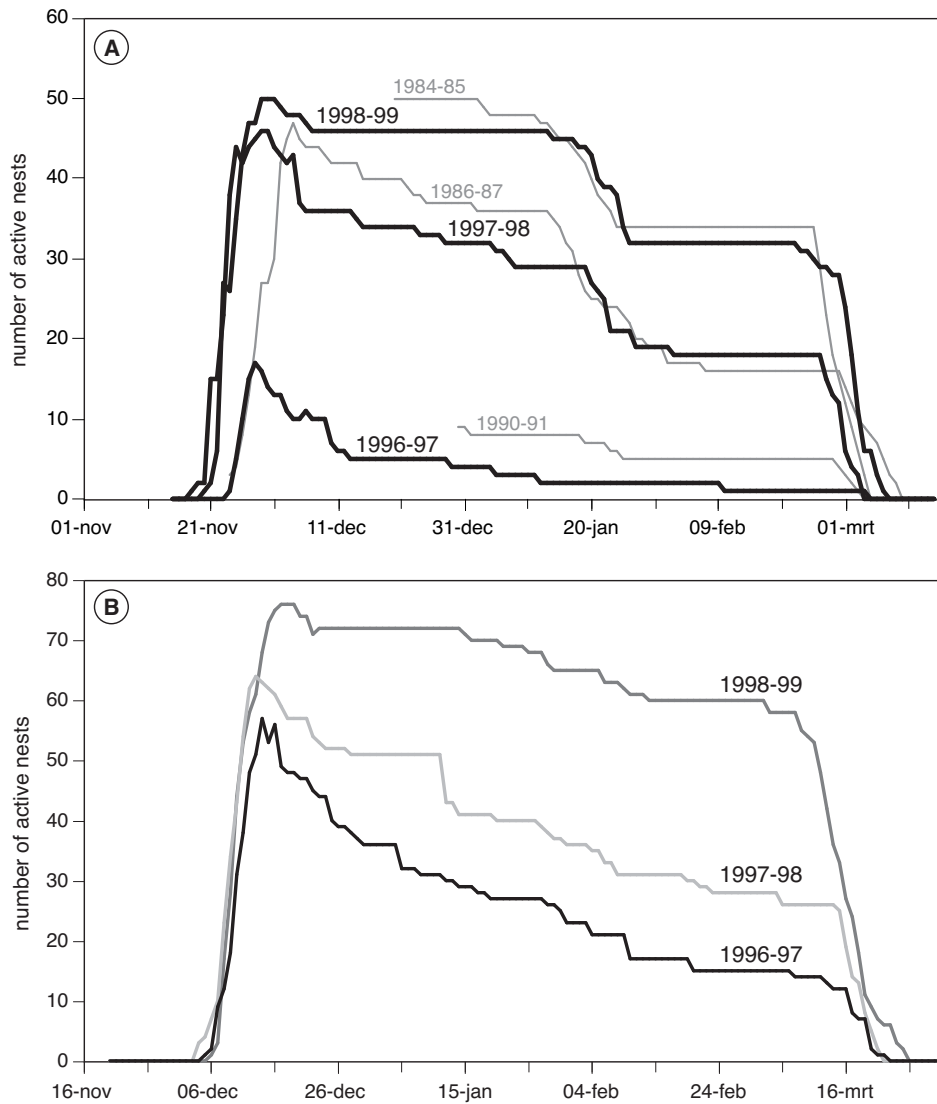


Figure 1. Number of active nests of Antarctic Petrels (A) and Southern Fulmars (B) in study plots on Ardery Island. For Antarctic Petrels, the values of seasons before 1996 are added. An active nest is a nest with an egg or chick that is not evidently failed or fledged. The exact date of egg failures is not easy to determine, and only when an egg has rolled out, has been deserted for prolonged time or has disappeared it was counted as being failed. Missing chicks less than 45 days old were considered as being failed, and older chicks as having fledged. Note the differences in both x-axes.

Egg failure

Egg failures occur through a variety of causes which are not always easy to disentangle. For example, a petrel egg that is left unattended and is consequently predated by South Polar Skuas (*Catharacta maccormicki*) may have been laid by an unpaired bird, or by a female that after egg-laying had to wait too long for her partner to return, or the incubating bird was scared off the nest by an other cause like a predating Southern Giant Petrel or a 'lost' penguin stumbling through the nesting area. What is then the ultimate cause? In only very few occasions the causes for failures are unambiguous, such as the occurrence of an avalanche or falling rocks as has been recorded for Arctic seabirds (Mallory *et al.* 2009). Especially in the beginning of the 1996-97 season, when snow made nest sites and painted rock numbers invisible and a considerable proportion of unbanded birds was involved, it was difficult to investigate in detail the causes of egg mortality. Another example is an egg that is unsuccessfully incubated and does not hatch: such an egg may simply be infertile, or maybe it was exposed too long to the cold, or it suffered a small but lethal crack because of lack of breeding experience, a nest dispute, or short panic flights for approaching predators.

Egg failure due to disturbance by our research activities is suggested to be negligible, as both species were usually highly tolerant to our entering of the colony and our slow and careful movements between nests. Furthermore birds in study plots became habituated to human presence and handling, e.g. to check bands and presence of eggs. Of course, occasionally nervous individuals (each year about one or two in the colony) were encountered which were subsequently avoided. In the very few cases where our activity led to temporary egg desertion, we always remained in the vicinity to protect the egg against skuas until the parent had returned. True control plots to investigate effects of researcher disturbance are very difficult to realize. However, over the early years up to 1996, the downward trends in breeding success in the Antarctic Petrel study area also occurred in a bordering reference area and no significant difference could be detected (Chapter 4).

From Fig. 1 it cannot be deduced exactly when the egg failures occur. In the early egg-laying period rapid failures immediately reduce the number of active nests counted in the daily surveys. Some eggs may be missed completely if they are laid and disappear in between two colony surveys on subsequent days. Failure dates later in the season are also often difficult to determine because parents stay on their nests and continue incubating even when the egg had already failed (infertile, cracked, frozen during temporary desertion). Some birds continue to incubate foul eggs, sometimes for long periods, even after all other eggs have hatched.

Chick mortality

In procellariiformes, elevated levels of chick mortality are generally found just

after chick hatching (Warham 1990). On Ardery Island this did not seem to be the case. Among Southern Fulmars only four out of 39 chick failures (10%) comprised young chicks (age five days or younger), and among Antarctic Petrels young chicks comprised only one out of 23 (4%) chick failures. We did on the other hand find enhanced mortality at the end of the guarding time among Antarctic Petrels chicks. Similar to all other breeding events, Antarctic Petrels stop guarding their chicks in a synchronized manner, and more than 90% of all chick failures occurred within three days after chicks were left unattended by their parents (Table 1). Such a strong synchronization and mortality was not found among Southern Fulmars chicks, whose parents guarded them on average 6 days longer.

Chick predation occurred by South Polar Skuas, which are known to take small chicks when they are unattended. South Polar Skuas quickly removed chicks from the colony, and only very occasionally we were able to witness such a predatory event. After a chick has been taken no traces were left in the colony, thus a chick less than about 15-20 days old that has suddenly disappeared, was generally assumed to be taken by skuas. We assumed therefore that most victims at the end of the guarding period were taken by skuas. In contrast, Southern Giant Petrels were in this stage not often seen predating on chicks, although these chicks seem an easy prey.

Late in the season, snow facilitated access to the study colonies for predatory Southern Giant Petrels. In a few cases in the second half of the chick period a Southern Giant Petrel walked into the colony and grabbed and partially ate 3-4 chicks. This was observed in the Antarctic Petrel reference colony and in the Southern Fulmar study area: foot prints in snow were clear proofs of the culprits. The left-over and at best half-eaten corpses of chicks were subsequently removed by skuas. In Southern Fulmars most of the chick failure in the last two weeks of the chick period could be contributed to Southern Giant Petrel predation.

Timing of breeding failures

The different timing of the breeding biology and breeding failures between both species on Ardery Island are summarised in Fig. 2. The graph shows how the breeding events and breeding failures are related:

Egg loss. Antarctic Petrels loose eggs at a higher rate in the early stage of the breeding cycle and consequently have fewer active nests in this period than Southern Fulmars.

Chick loss at the end of the guarding period. Antarctic Petrels experience elevated chick mortality when parents leave their chick unattended. Southern Fulmars guard their chicks longer and after egg laying, breeding failures occur at a relatively stable rate.

Chick loss at a later stage of the chick period. Antarctic Petrels have very little

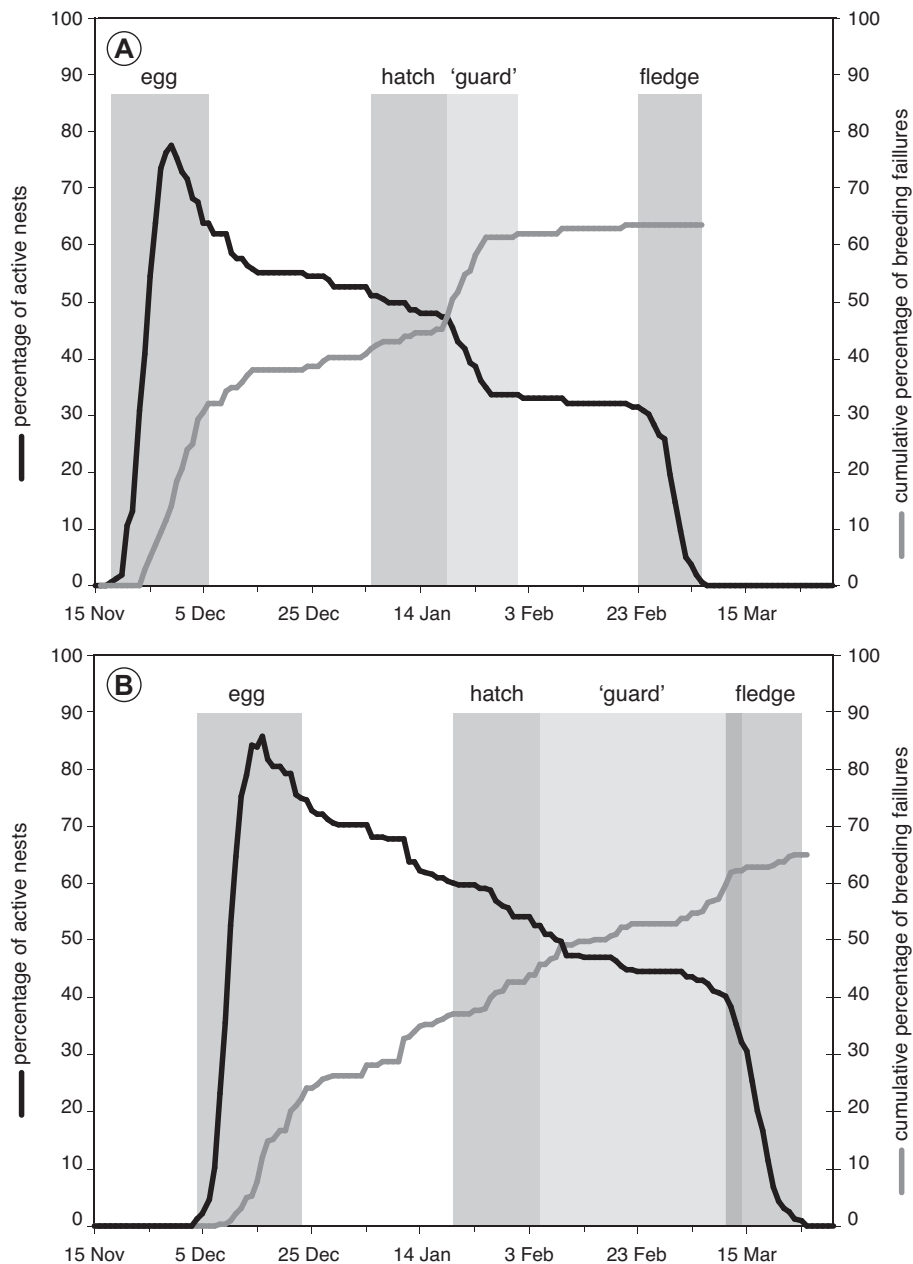


Figure 2. Overview of breeding events and breeding success in Antarctic Petrels (A) and Southern Fulmars (B). Percentage of active nests of each year were averaged over three years. The periods in which certain breeding events occurred are represented by grey bars: egg = egg laying, hatch = hatching of chick, 'guard' = the end of the guarding period, fledge = fledging of chick. See text for more explanation.

mortality in the second half of the chick period.

Percentage of breeding pairs

The number of pairs in a colony that is attempting to breed is often not very well correlated with the number of successful nests (Barbraud & Weimerskirch 2001, Olivier *et al.* 2005). We calculated therefore the 'percentage of breeding pairs', which is defined as the number of nests on which an egg was laid divided by the number of monitored nest sites times 100 (Barbraud & Weimerskirch 2001, Jenouvrier *et al.* 2003). We determined the number of monitored nest sites as those nests with an egg in at least one of the three study seasons. In total, Antarctic Petrels laid eggs on 70 different nest sites and Southern Fulmars on 100 different nest sites during three seasons. So we monitored respectively 70 and 100 nest sites.

The percentage of breeding pairs of Antarctic Petrels increased from 41 % in 1996-97 to 77 % in both 1997-98 and 1998-99. Such a large difference could be explained partly because the number of (potential) breeding individuals was reduced by predation by Southern Giant Petrels in the first season. There was, however, another reason that could explain the low number of eggs observed. Due to blizzard conditions we missed a few days of nest monitoring in the egg-laying period. Many eggs were laid in snow or on icy nests and due to the disturbance of visiting Southern Giant Petrels Antarctic Petrels were regularly temporarily leaving their nest. This may have offered opportunities for egg predation to South Polar Skuas. As a consequence, it is uncertain whether fewer eggs were observed because birds were skipping a breeding season due to the extremely unfavourable conditions in that year, or because eggs disappeared so fast that many were not seen at all. The situation was different in the last two seasons, when 54 eggs were laid. This number was identical to the number of eggs laid in 1985-86 and could suggest that in those years all favourable sites in the area were occupied. The Antarctic Petrel study colony was relatively small and physically bounded by steep cliffs and large boulders, but also by a neighbouring Southern Fulmar colony. The nests in this colony are thus packed in a small area with relatively few possibilities for new nests.

The percentage of breeding pairs of Southern Fulmars increased from 67% in 1996-97 to 81 % in the 1998-99 season. This species experienced much less Southern Giant Petrel predation and laid their eggs later, when more snow had disappeared. The Southern Fulmar study area extended over a large area (600 m²) with relatively much space between the nests. Most new nest sites, however, appeared at the boundaries of the colony, where breeding birds were often unbanded and less successful than birds in the core of the colony. Possibly these birds were young or inexperienced birds with little breeding experience. We noticed that these new nest sites were not always suitable, with eggs rolling regularly out of nests, sometimes resulting in birds

incubating two and in one case, three eggs. Petrels have a large urge to breed and easily accept extra eggs, although they have an incubation patch for only one egg. None of these multi-egg nests produced a chick.

Procellariiformes are generally known as birds that are very faithful to their nest sites (Warham 1990). Nevertheless, we found a relatively high variability in nest sites being used. This was reflected in the number of sites that were only used once during the three study seasons: 29% for Antarctic Petrels and 21% for Southern Fulmars. Furthermore, only 23% of the Antarctic Petrel nest sites and 44% of the Southern Fulmar had an egg in all three seasons.

TIME CONSTRAINTS FOR BREEDING IN ANTARCTICA

General observations

Compared to similarly sized relatives, the short time used by fulmarine petrels to complete their breeding supports the idea of a narrow time window available for these species in high Antarctic conditions. Synchronicity in breeding would be stimulated under such conditions. Indeed, both Southern Fulmars and Antarctic Petrels were highly synchronous in their egg-laying, with the latter species timing egg-laying even more tightly (Chapter 2). But the remarkable issue remains that Southern Fulmars and Antarctic Petrels exhibited a consistent difference of 16 days in the mean date of egg-laying. Van Franeker (2001) speculated that Antarctic Petrels can begin earlier because of their capability of flying longer distances over closed sea ice. Wing morphology studies by Dijkstra (2003) support such different flight specialization. Southern Fulmars would therefore have to wait for sufficient open water in the vicinity before commencing breeding. Although the time difference between the species did not result in differences in breeding success, we did find a clear difference in the timing of the breeding failures (Chapter 3). Mortality of chicks late in the season is relatively costly and occurred mainly in Southern Fulmars and less in Antarctic Petrels. Raising offspring is highly demanding and could lead to reduced post-breeding body condition during the moult and winter period, and can even lead to skipping the next breeding season. To which extent such 'sabbatical' years, i.e. years in which pairs refrain from breeding, occur in fulmarines is not yet very clear. It is worthwhile to continue to investigate the conditions, which affect the breeding success during the initial and final periods of the narrow time window and the potential impact it may have on the life cycle of breeding individuals.

Conditions in early season

Snowfall and accumulation of snow early in the breeding season are a fact of life for

petrels breeding in Antarctica. To some extent, birds are able to dig out their nest sites at their first arrival or after the pre-laying period of absence. However, as we clearly observed in the 1996-97 season, there are limits to this capability. When thick snowdrifts covered parts of the traditional nest locations it proved impossible for many birds to dig down to 'bare ground' and they had to lay eggs on snow. Especially in the first two seasons we found occasions when the warm egg was melting its way into the ice. When the bird still decided to breed on such an ice site, the egg melted itself deep into the ice through the warmth it transferred. On Ardery Island, the snowdrifts also allowed access for an unusual predator, the Southern Giant Petrel, which was in turn responsible for associated egg predation by skuas.

However, even without the snow issue, predation pressure might differ given the timing of egg-laying. Almost 30% of all breeding failures of Antarctic Petrels occurred before the Southern Fulmars even started to breed. Since the Antarctic Petrel is the earliest to breed, its eggs are the first available resource for South Polar Skuas which may exacerbate predation pressure on early breeding. Antarctic Petrels had a higher rate of failure in the early season than Southern Fulmars (Chapter 2) which gives support to the hypothesis that the narrow time-window causes a constraint for breeding for the early species.

Conditions in late season

The narrow time-window hypothesis also predicts that late breeders would face higher costs or risk of failure towards the end of the season. An obvious example of this was found in the last season when heavy snow showers occurred for about a week and high snow cover developed. Southern Fulmar chicks became buried and were deprived from parental feedings for prolonged periods of time, which led to early fledging in poorer condition. Antarctic Petrel chicks were about to fledge at that time and were more mobile and seemingly willing to leave the nest to move to a more sheltered spot as needed. Thus, the heavy snow had little consequences for their fledging. Although these extreme conditions were only found during one season, it does not mean that they are insignificant. Our results showed that in the season 1998-99 in Southern Fulmars almost half of all chick failures or almost a quarter of all breeding efforts failed in the final stages of the chick period due to snow. Heavy snow may cut off food provisioning by parents, may change predator access, and may act through melt water and refreezing. Catastrophic years with low breeding success are not unusual for long-lived species (Wooller *et al.* 1992, Chastel *et al.* 1993, Saether *et al.* 1997).

A late season condition that emerged from the chick feeding study (Chapter 3) was the obvious reluctance of both species to come into the colony during darkness. Frequency distributions of chick-feeding over different hours of the daily cycle

suggest that birds returning to the island during darkness wait with coming ashore until twilight, leading to peak numbers of adults feeding their chicks in morning dawn. Because of their early breeding, Antarctic Petrels experience almost continuous daylight. They therefore hardly have to take into account at what time of the day they return to the colony, allowing distant foraging and instant decisions to return to the chick. Southern fulmars are more restricted because they face more twilight and dark conditions, are less agile flyers and have more problems during landing (Cowan 1979, Orton 1968).

Chick growth

Southern Fulmars should complete the chick period before weather conditions deteriorate at the end of the season. One could expect that the late hatching Southern Fulmars might try to contract the chick period. We found a higher maximum growth rate in Southern Fulmars, and although the difference was small, it was significant (Chapter 3). Southern Fulmar chicks are about 20% larger than Antarctic Petrel chicks, and thus expected to have longer chick periods, which is not the case (Table 1). The slightly higher growth rate may have contracted the chick period but chicks of Southern Fulmars were still reaching peak weight and fledging at a later age and were heavier at the time of fledging than Antarctic Petrel chicks (Table 1). This could be interpreted as a way of how Southern Fulmars fit their chick period in the short time frame that is still left of the Antarctic summer. However, it is also possible that Southern Fulmar chicks need more body reserves because they face worse environmental conditions and a larger extent of frozen sea when they fledge. Thus the Southern Fulmar fledglings have to fly further to reach open waters to find their own food for the first time.

Moult

The timing of the moult is another aspect of the annual cycle that deserves attention in relation to early or late breeding. Feather synthesis is highly energy demanding and the moult of the wing feathers of the adults will reduce flight capacity. The high energetic costs of raising a chick and feather moult forces adult petrels to avoid overlap of both episodes when possible (Stresemann & Stresemann 1966). But postponing moult to autumn or early winter, when foraging conditions deteriorate, means a risk for adult winter survival. Southern Fulmars start moulting earlier than Antarctic Petrels (Table 1), especially if the difference in timing of breeding is taken into account. Based on their body size Southern Fulmars bring lighter meals to their chicks than Antarctic Petrels (Chapter 3). The start of the wing moult by parent Southern Fulmars relatively early in the breeding season, is probably related to other aspects of their breeding strategy. Overall, they have a more rate-maximising foraging strategy, with frequent

short foraging trips and spending more time in the colony in between the trips.

ADULT SURVIVAL

Being covered by snow is usually not a problem for adult birds. At various occasions in different seasons, birds were observed to be sitting under 10-15 cm snow cover, apparently quite undisturbed. Snow cover may even offer shelter, and there is apparently enough oxygen to breath. However, there is a risk attached to remaining on the nest when it becomes covered by snow. Evidence for this was discovered in two Southern Giant Petrels that we found on the Frazier Islands (Chapter 6). Their emaciated condition and the presence of their egg suggested that they were not sitting voluntary. Also, on Frazier Islands there was evidence that much snow cover had recently disappeared, especially from the valleys where the largest colonies were situated. Based on our observations of smaller fulmarine petrels, we suggest that other factors were leading to the death of both individuals. If the top layer for some reason gets icy the oxygen supply through the snow might fall below a critical level. Additionally, even when sufficient oxygen remains, an icy crust on the snow could trap the birds and prevent their escape.

On Ardery Island, all cases of adult mortality of the smaller fulmarines were caused by predation. In the ringed Antarctic Petrel population, mortality within the 1996-97 breeding season was over 15%, whereas normally it is less than 4% in a full year (Chapter 4). Even among new individuals gradually banded in 1996-97, about 10% died from predation by Southern Giant Petrels. Remarkably, even during chick periods, the Southern Giant Petrels seemed to prefer predation of adults over chicks, but our observations were infrequent. One reason to avoid chicks could be that the nestlings have much more stomach oil which can be successfully used in defending against predators.

CONTRASTING PROVISIONING STRATEGIES

The two species differ remarkably in the duration of their foraging trips, despite the similarity in chick diet (Chapter 3). Because the meal size did not differ much between the species, this resulted in a much higher chick provisioning rate in Southern Fulmars. However, the meal mass might not be a good indicator of the energy density of the meal. Most procellariiformes have the capability to process food in the stomach to produce an oil of high caloric value. In comparison to Southern Fulmars, Antarctic Petrels carry more highly processed food back to the colony, and the food delivered to

chicks contains larger proportions of stomach oil (Norman & Ward 1992, Van Franeker 2001), i.e. they deliver meals of higher energy density. Further research on this aspect could include investigating details of energy content of the meals delivered by both species.

Despite the large differences in chick provisioning between the species, the differences of chick growth were small and we suggest that the daily amount of energy in kJ delivered to chick is more related to growth rates than the amount of food in grams. Furthermore, allocation of energy within a chick might differ between the species e.g. due to differences in gut capacity, thermoregulation or tissue development. It has been shown that chicks of Southern Fulmars need more energy for thermoregulation and have a higher metabolism (Hodum & Weathers 2003, Weathers *et al.* 2000) than Antarctic Petrel chicks. Consequently, Southern Fulmar chicks are less efficient in converting food mass into chick mass. Antarctic Petrels chicks might have evolved ways to withstand longer fasting periods and colder temperatures, which probably relates to their breeding distribution.

BREEDING DISTRIBUTION

Differences in breeding and foraging strategies may explain why both species breed in different areas of Antarctica (summarized in Table 1). Antarctic Petrels breed along the Antarctic coast and especially in continental colonies, and its largest colonies are found between 72°S and 67°S (Van Franeker *et al.* 1999). In comparison, the highest concentrations of breeding Southern Fulmars are found at lower latitudes (64°S and more northerly) on the islands of the Scotia Sea arc and on Bouvet Island (Chapter 7). The coast of East Antarctica (between 50°E and 150°E) is therefore the only place where their breeding ranges overlap (Fig. 3). There are 18 known localities where both species breed sympatrically, although Southern Fulmars colonies in the area of overlap are relatively small (<5000 breeding pairs) and comprise only 3% of its global breeding population.

FORAGING AREAS

Based on differences in details of species composition in the diet of chick provisioning individuals, Van Franeker (2001) suggested foraging by Antarctic Petrels takes place in more distant offshore areas and by Southern Fulmars in the nearby shelf. This corresponds with the longer foraging shifts observed in the Antarctic Petrels (Table 1). Especially during early spring and during their incubation period when there

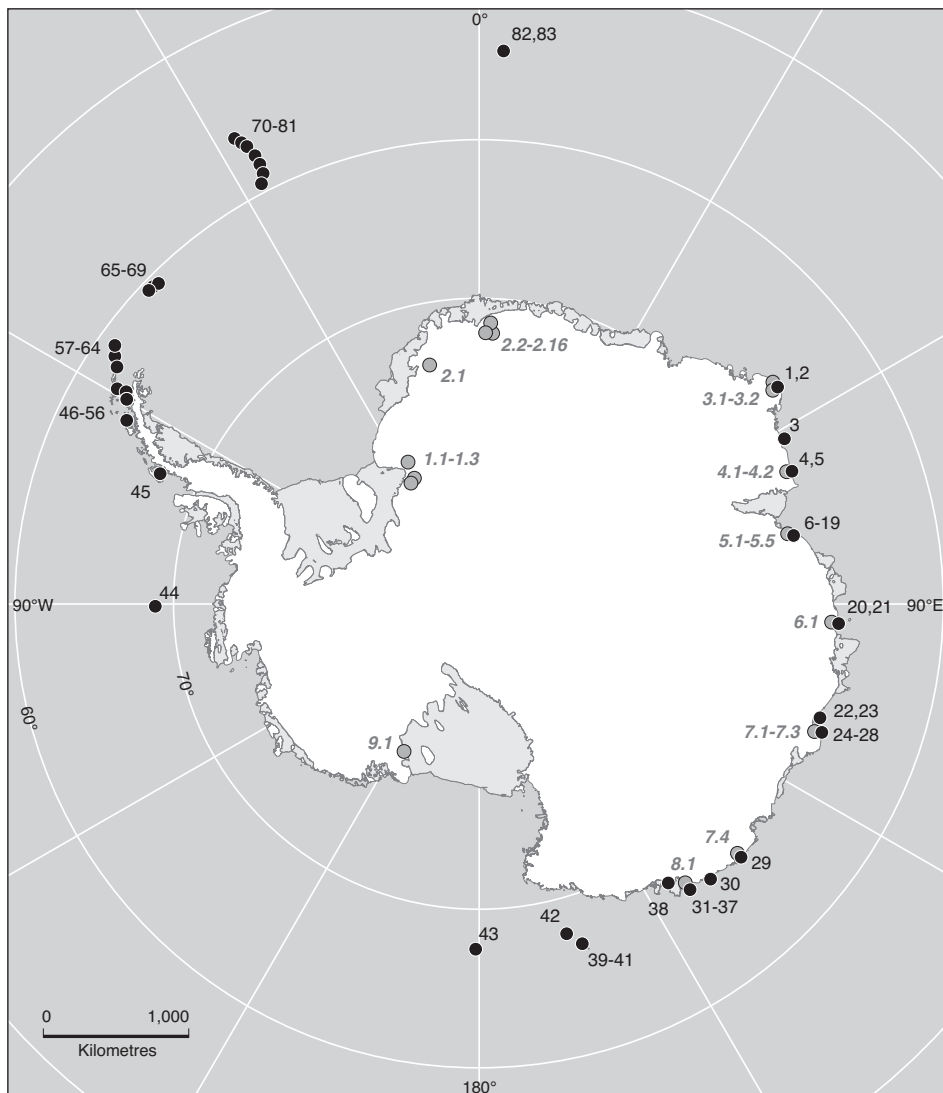


Figure 3. Breeding distribution of Antarctic Petrels (grey dots) and Southern Fulmar (black dots) and. Map shows that overlap of the breeding distribution only occurs along the coast of East Antarctica between 50°E and 150°E (numbers of breeding localities from Van Franeker *et al.* 1999, Chapter 7)

is still much sea-ice present, Antarctic Petrel make long extremely foraging trips (Chapter 2). However, prolonging the duration of foraging shifts might also be part of an efficiency-maximizing provisioning behaviour (Ydenberg 2007) in which the foraging areas are not necessarily at greater distance from the colony. By processing food into stomach oil Antarctic Petrels reduce the transport cost in terms of energy delivered to the chicks (Chapter 3). These foraging efforts might be further optimized by spending more time for self-feeding at the foraging grounds.

During a pilot project on foraging ecology of fulmarine petrels, a few individuals of both study species were fitted with satellite tracking devices. Preliminary tracking results confirm the hypothesis of further foraging in Antarctic Petrels as derived from the dietary differences (Box 2, Table 1). Spatial overlap in foraging areas of the two species does occur but is limited. Antarctic Petrels on the way to their foraging areas or on their return voyage cross the feeding grounds of Southern Fulmars around Ardery Island and may occasionally feed in these areas. Southern Fulmars were generally foraging closer to the colony (mostly within a circle of 50 km around the island) and making more short trips than Antarctic Petrels.

CONCLUDING REMARKS

We have shown that Southern Fulmars and Antarctic Petrels use different strategies to solve the problem of completing their breeding cycle in a narrow time window in Antarctica. Southern Fulmars are not able to start breeding early, suffer proportionally higher breeding failure late in the season after considerable energy investment, and therefore exhibit an overlap in their breeding and moult season. Although Antarctic Petrels breed earlier, they are probably also time constrained and hence they stop chick guarding earlier, deserting the chick long before it fledges. They possibly finish their rearing duties in this way in order to start moulting their wing feathers.

Climate change may affect the breeding and distribution of both species along the coast of East Antarctica differently. For example, a reduced extent of sea-ice in spring might favour Southern Fulmars as they would have less areas of sea-ice to cross to reach their breeding habitat, allowing a somewhat earlier start of breeding. Also, Antarctic Petrels could have shorter foraging distances because their favourite ice habitat might be situated closer to the breeding colonies. In East Antarctica, however, the temperature remained stable but sea-ice extent increased during the last 50 years, resulting in a later start of breeding in Antarctic seabirds (including Southern Fulmars and possibly Antarctic Petrels) (Barbraud & Weimerskirch 2006). A shift of breeding seasons might result in more or less interspecific competition for nest localities. Changes in snowfall patterns are likely to occur in a changing climate

and may seriously affect both species through effects on the suitability of current nesting areas and predation pressure.

Differences in sea-ice cover and temperatures can also alter the supply of food resources, such as krill and fish. A larger extent of sea-ice in winter is expected to improve food conditions and therefore affecting breeding performance and adult survival of fulmarine petrels in East Antarctica in different ways (Barbraud *et al.* 2000, Barbraud & Weimerskirch 2001, 2006, Jenouvrier *et al.* 2003, Olivier *et al.* 2005). Also different food supply might influence foraging and chick provisioning strategies of fulmarine petrels. Monitoring CEMP parameters in fulmarine petrels may generate results that reflect such changes in the ecosystem. The extent to which demographic parameters of seabird populations reflect the changes in harvestable food stocks requires more study since this thesis has shown that demographic parameters like breeding effort, breeding success and adult survival can be heavily influenced by changes in weather conditions at the local scale.

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SAMENVATTING

Antarctica is het droogste, koudste en ook meest winderige continent op aarde. Door het bijzonder onvriendelijke klimaat en vanwege het feit dat slechts 2% van het landoppervlak niet permanent bedekt is met sneeuw of ijs, zijn er maar weinig diersoorten die hier kunnen overleven. Echter, rondom Antarctica zijn de wateren uiterst voedselrijk en ze trekken elke zomer grote aantallen dieren die hier hun voedsel zoeken. Onder andere krill (*Euphausia superba*), een klein garnaalachtig diertje, komt hier in zeer grote zwermen voor. Het vormt een belangrijke voedselbron voor veel hogere diersoorten (vogels, zeehonden, walvissen) en is dus een belangrijke schakel in het Antarctische voedselweb. In de jaren zeventig begon men zich zorgen te maken over de toenemende krillvisserij in Antarctica.

In 1982 werd er een internationaal krillverdrag (Convention on the Conservation of Antarctic Marine Living Resources, CCAMLR) afgesloten om de invloed van visserij op het Antarctisch ecosysteem kritisch te volgen en te reguleren. Visserij, zowel op krill als vis, wordt toegestaan zolang het geen schade aanricht aan het ecosysteem. Langdurige en nauwkeurige studies moeten uitwijzen of dieren die afhankelijk zijn van krill en vis, nadelige gevolgen ondervinden van visserij. Hiervoor werd een aantal soorten aangewezen als indicatorsoort, waaronder diverse pinguïnsorten, pelsrobber en ook enkele stormvogelachtigen.

Stormvogels behoren samen met o.a. pijlstormvogels en albatrossen tot de orde van de stormvogelachtigen (Procellariiformes). Soorten in deze orde worden gekenmerkt door neusbuisjes op de snavel. De kleine subfamilie van de fulmariene stormvogels bestaat uit zeven soorten die speciaal aangepast zijn aan het leven onder polaire omstandigheden. Zowel in het Noord- als het Zuidpoolgebied broeden fulmariene stormvogels boven de 80^{ste} breedtegraad. In Antarctica vormen stormvogels de meest talrijke groep vogels die daar voorkomen.

Onderzoek aan fulmariene stormvogels op Ardery Island

Het onderzoek dat in dit proefschrift wordt beschreven, vormde een onderdeel van een langdurig Nederlands-Australisch onderzoek aan fulmariene stormvogels op Ardery. Dit eiland is gelegen in het oostelijk deel van Antarctica op 10 kilometer afstand van het Australische onderzoeksstation Casey. Op dit rotsachtige eiland broeden vier soorten fulmariene stormvogels: de Antarctische Stormvogel (*Thalassoica antarctica*), de Zuidelijke Stormvogel (*Fulmarus glacialisoides*), de Kaapse Duif of Kaapse Stormvogel (*Daption capense*) en de Sneeuwstormvogel (*Pagodroma nivea*). Een vijfde soort, de Zuidelijke Reuzenstormvogel (*Macronectes giganteus*), wordt ook regelmatig

waargenomen op dit eiland. Door deze rijkdom aan vogels heeft dit eiland een speciale beschermingsstatus gekregen. Het mag alleen onder bepaalde voorwaarden voor onderzoeksdoeleinden worden bezocht.

Het onderzoek richtte zich in eerste instantie vooral op de Antarctische Stormvogel, die als een indicatorsoort binnen het monitoringsprogramma van het krillverdrag is aangewezen, maar waarvan desondanks relatief weinig bekend is. Om te bepalen of parameters met betrekking tot de broedbiologie en populatiestatus van deze soort representatief zijn voor andere stormvogels, werd een vergelijking gemaakt met een verwante soort die op het eiland Ardery broedt: de Zuidelijke Stormvogel. Daarnaast werd in dit onderzoek getracht een verklaring te vinden voor het afnemende broedsucces van Antarctische Stormvogels op het eiland. Uit voorafgaand onderzoek bleek dat in de loop van drie seizoenen (1984-85, 1986-87 en 1990-91) het broedsucces in de kolonie drastisch afnam.

In 1996 werd een nieuwe fase van dit langdurige onderzoek gestart. Tijdens drie zomerseizoenen (1996-97, 1997-98 en 1998-99) werden de fulmariene stormvogels gedurende het broedseizoen (vanaf begin oktober / november tot en met april) intensief bestudeerd. Hiervoor werden in twee studiegebieden (voor elke soort één) alle potentiële nestlocaties gemarkeerd en werd een automatisch weegsysteem geïnstalleerd. Deze studiekolonies werden vrijwel dagelijks bezocht om het verloop van de broedcyclus en de aanwezigheid van broedende vogels nauwkeurig te volgen. Een groot deel van de oudervogels was gemerkt met een metalen vogelring van de Australische ringcentrale, met een plastic ring met een op afstand duidelijk te lezen nummer en met een 'transponder' die onder de huid werd aangebracht. Deze transponders bevatten een chip die afgelezen werd door het weegsysteem of door onderzoekers met speciale afleesapparatuur. Hierdoor konden de vogels in de studiegebieden individueel worden gevolgd.

Broedbiologie van Antarctische en Zuidelijke Stormvogels

In **hoofdstuk 2** worden de details van de broedbiologie van de soorten uitvoerig beschreven. Begin oktober kwamen Antarctische Stormvogels al in groten getale terug naar het eiland, terwijl Zuidelijke Stormvogels later en veel geleidelijker terugkwamen. Zoals gebruikelijk is bij stormvogelachtigen, verlieten beide soorten het eiland in de periode voordat een ei werd gelegd om lichaamsreserves op te bouwen voor het komende broedseizoen. In de eerste helft van november verlieten Antarctische Stormvogels massaal de kolonie en tijdens deze 'exodus' was de kolonie

2 tot 2,5 week volledig uitgestorven. Bij Zuidelijke Stormvogels gebeurde dit veel minder synchroon en minder lang en was de kolonie nooit volledig verlaten.

Het moment waarop vogels hun ei (slechts één per seizoen) legden bleek duidelijk te verschillen tussen beide soorten. De eileg bij Antarctische Stormvogels vond eind november plaats en gemiddeld 16 dagen later bij Zuidelijke Stormvogels. Het broedseizoen, dus de periode vanaf het moment dat het ei gelegd wordt tot aan het uitvliegen van het jong, was gemiddeld voor beide soorten even lang (96 dagen). Het bebroeden van het ei duurde circa 48 dagen bij Antarctische Stormvogels en 47 dagen bij Zuidelijke Stormvogels. De kuikenfase was circa 49 dagen bij Antarctische Stormvogels en 50 dagen bij Zuidelijke Stormvogels. Oudervogels wisselden elkaar af tijdens het uitbroeden van het ei. Een gemiddelde broedbeurt bij Antarctische Stormvogels duurde 9 dagen en bij Zuidelijke Stormvogels ruim 4 dagen.

Ondanks het verschil in tijdstip van broeden vonden we geen significant verschil in het broedsucces tussen beide soorten. Gemiddeld 37% van de eieren die gelegd waren door Antarctische Stormvogels bracht jongen voort die het nest uitvlogen, terwijl bij Zuidelijke Stormvogels 35% van de eieren succesvol was. Wel faalden zowel eieren als kuikens van Antarctische Stormvogels eerder, waardoor deze soort minder tijd en energie ‘verspilde’ aan verloren broedzorg dan Zuidelijke Stormvogels.

In het seizoen 1996-97 bleek de overvloedige hoeveelheid sneeuw in de kolonie de oorzaak van het mislukken van veel nesten vroeg in het seizoen. Dit speelde vooral bij Antarctische Stormvogels (maar dit kwam ook door een secundaire oorzaak die verderop besproken wordt). Laat in het seizoen 1998-99 werd het eiland Ardery getroffen door langdurige zware sneeuwbuien die uiteindelijk een aantal kuikens van Zuidelijke Stormvogels noodlottig werd. Hoewel dit incidentele waarnemingen waren, lijkt het niet onwaarschijnlijk dat dit soort catastrofale gebeurtenissen zich geregeld voordoen en deel uitmaken van het normale leven van stormvogels op dit eiland.

Antarctische Stormvogels hadden een duidelijke piek in de kuikensterfte, circa 10-20 dagen na het uitkomen van het ei, wat samen bleek te vallen met het tijdstip waarop ouders hun kuiken voor het eerst geheel alleen in het nest achterlieten. Wegens een nog niet geheel functionerende thermoregulatie van jonge kuikens en predatiegevaar door patrouillerende Zuidpooljagers (*Catharacta maccormicki*), worden kuikens een bepaalde periode in afwisselende beurten door hun ouders ‘bebroed’ en bewaakt. Omdat deze periode (‘guarding period’) bij Antarctische Stormvogels gemiddeld zes dagen korter is dan bij Zuidelijke Stormvogels, zijn de kuikens van eerstgenoemden op dat moment nog klein en daarom een gemakkelijke prooi voor Zuidpooljagers. In totaal werd meer dan 80% van de kuikensterfte van Antarctische Stormvogels waargenomen wanneer hun ouders hun jongen voor het

eerst alleen achterlieten, terwijl bij Zuidelijke Stormvogels geen verhoogde sterfte werd aangetoond.

Voeren en groeien van stormvogelkuikens

De groeifase van de stormvogelkuikens wordt in **hoofdstuk 3** in detail beschreven. Eerder werd geconstateerd dat de samenstelling van het voedsel dat ouders naar hun jongen brachten nauwelijks verschilde tussen beide soorten. Echter, de gemiddelde periode tussen de tijdstippen waarop jongen hun maaltijd kregen, varieerde wel sterk tussen beide soorten. Ouders voeren hun jong meestal onmiddellijk en in één keer als ze terugkomen van zee. Antarctische Stormvogelkuikens bleken over het algemeen ruim een dag te moeten wachten op een maaltijd en Zuidelijke Stormvogelkuikens maar ongeveer een halve dag. Door nauwkeurige metingen met het automatische weegsysteem konden we ook het gewicht van deze maaltijden bepalen. Het gewicht van de afzonderlijke maaltijden bleek niet zo veel te verschillen tussen beide soorten (jaargemiddelden varieerden tussen 111 en 152 gram). Door de verschillende voederfrequenties kregen kuikens van Antarctische Stormvogels veel minder voedsel (gemiddeld 122-140 gram) per dag dan Zuidelijke Stormvogelkuikens (gemiddeld 240-265 gram). Dit grote verschil kan maar ten dele verklaard worden door het veel geringere verschil (circa 18%) in kuikengewicht. Daarom onderzochten we of kuikens van beide soorten een zelfde groei vertoonden.

Bij alle stormvogelachtigen worden kuikens op een gegeven moment veel zwaarder dan hun ouders (sommige soorten worden zelfs twee keer zo zwaar) en verliezen vervolgens weer gewicht tot het moment dat ze uitvliegen. Het beschrijven van een dergelijke groeicurve is niet gemakkelijk. Daarom wordt vaak alleen gekeken naar de groei vanaf het moment dat een kuiken uit het ei komt tot en met het moment dat het kuiken het maximale gewicht bereikt. Zulke groeicurves zijn goed wiskundig te benaderen met een sigmoïde functie, maar negeren de periode van gewichtsafname volledig. Wij gebruikten daarom een nieuwe methode, de zogenaamde 'dubbele Gompertz'-curve, die het gehele traject van gewichtstoename en -afname beschrijft.

Kuikens van Antarctische Stormvogels bereikten hun maximale gewicht gemiddeld na 34 dagen, waarbij ze gemiddeld 136% zwaarder zijn dan hun ouders. Zuidelijke Stormvogelkuikens bereikten een piek van 140% van het oudergewicht. Op het moment van uitvliegen zijn Antarctische Stormvogelkuikens relatief lichter, vooral doordat hun ouders eerder stoppen met het voeren van hun jong. Door de vrij geringe aantallen kuikens in de studie konden niet veel significante relaties worden aangetoond tussen diverse groeiparameters en de hoeveelheid aangeleverd voedsel. Alleen bij de Zuidelijke Stormvogels vonden we dat ouders die meer voedsel per dag naar het nest brachten, kuikens hadden die sneller groeiden, een hoger maximaal gewicht bereikten en zwaarder waren bij uitvliegen.

De reden dat Antarctische Stormvogelkuikens minder voedsel nodig hebben om een vergelijkbare groeisnelheid te behalen als Zuidelijke Stormvogels moet nog beter worden uitgezocht. Op basis van eerder onderzoek waaruit bleek dat het voedsel van Antarctische Stormvogels verder verteerd was, veronderstellen we dat ze hun jongen maaltijden voeren van een hogere calorische waarde (minder water). Nader onderzoek moet uitwijzen of kuikens van beide soorten ondanks het gewichtsverschil van de maaltijden wel een vergelijkbare hoeveelheid energie krijgen.

Wanneer is het tijd voor stormvogels om hun vleugelpennen te wisselen?

Veren slijten hard en vogels moeten dus regelmatig nieuwe veren aanmaken. Veel vogelsoorten ruien hun veren één keer per jaar en beginnen met de rui van de vleugelpennen meteen nadat ze hun jong(en) hebben grootgebracht. Aangezien de aanmaak van nieuwe veren veel energie kost en extra nutriënten vraagt, valt dit vaak niet goed te combineren met het grootbrengen van hun nageslacht. Het vliegen wordt door het ontbreken van veren in de vleugel minder efficiënt en kan daardoor aanzienlijk meer energie kosten. Vanwege de korte tijdsduur van de Antarctische zomer en het duidelijke tijdsverschil van de broedseizoenen van beide soorten, waren we geïnteresseerd in het vraagstuk hoe fulmariene stormvogels het probleem van rui en broedzorg opgelost hadden. Hiervoor bepaalden we de mate van rui van de vleugelpennen bij alle volwassen vogels die we ringden of vingen voor ander onderzoek en in **Box 1** beschrijven we onze resultaten.

Antarctische Stormvogels bleken het standaardpatroon te volgen en te wachten met het ruien van hun vliegpennen. Pas in de tweede helft van de kuikenperiode begon deze soort langzaam met de vervanging van de eerste vleugelpennen. Zuidelijke Stormvogels volgden een andere strategie. Ze startten de rui gemiddeld 30 dagen eerder, nog voordat de eieren uitkwamen. Dus hoewel ze later begonnen met broeden, waren Zuidelijke Stormvogels veel verder gevorderd met de vervanging van vleugelpennen aan het eind van het seizoen. Sommige (niet-broedende) individuen hadden tegen die tijd zelfs volledige nieuwe vleugelpennen aan het eind van het broedseizoen. Bij beide soorten bleek de groep vogels van onbekende broedstatus (vermoedelijke niet-broedende of vroeg gefaalde individuen) de rui van de vleugelpennen twee tot drie weken eerder te beginnen dan de succesvol broedende soortgenoten.

Verskil in foerageerstrategieën tussen beide soorten

Het feit dat oudervogels van Antarctische Stormvogels langer de tijd nemen om te foerageren kan zowel betekenen dat ze meer tijd besteden aan voedsel zoeken, als ook dat ze verder weg vliegen naar hun voedselgebieden dan Zuidelijke Stormvogels. Eerder onderzoek had aangetoond dat beide soorten vrijwel hetzelfde

dieet hebben. Daarom werd in het seizoen 1998-99 een klein onderzoek gestart naar de foerageerstrategieën van deze vogels. Hiervoor werd een aantal oudervogels dat op dat moment een kuiken grootbracht van een satellietzender voorzien om hun bewegingen te kunnen volgen op zee.

In **Box 2** tonen we aan dat Zuidelijke Stormvogels binnen een cirkel van 100 km rondom het eiland en dus relatief dicht bij de kolonie bleven. Er waren slechts een paar incidentele uitzonderingen van vogels die een ongebruikelijk lange foerageertocht maakten van twee dagen of langer. Daarentegen vlogen Antarctische Stormvogels aanmerkelijk verder weg en in een aantal gevallen zelfs meer dan 300 km. De meeste individuen werden echter aangetroffen in de buurt van de rand van het continentale plat, waar koud en voedselrijk water van de zeebodem naar boven komt en waar vooral krill en vissen en dus hun roofdieren van profiteren. Dit gebied is in de winter bedekt met ijs en in de zomer vrij van zee-ijs. Dergelijke 'marginale seizoens-ijszones' staan bekend om hun grote voedselrijkdom en grote concentraties prooidieren en dieren hoger in de voedselketen.

De reden waarom Antarctische Stormvogels verder vliegen is niet helemaal duidelijk. Het kan zijn dat ze dit doen om voedselconcurrentie met Zuidelijke Stormvogels te vermijden, maar er zijn ook andere verklaringen mogelijk. Langer wegblijven kan ook een strategie zijn om het voedsel beter te verwerken en te concentreren in de maag. Op deze wijze worden de kosten om het voedsel te transporteren geminimaliseerd en de kosten om het voedsel verderop te halen gecompenseerd. Daarnaast is het ook mogelijk dat de soort gewend is om lange vluchten te maken, omdat de meeste Antarctische Stormvogels in de binnenlanden van Antarctica broeden en ver moeten vliegen naar open zee.

Onverwachte verklaring voor afgenomen broedsucces van Antarctisch Stormvogels.

Tijdens het eerste veldwerkseizoen (1996-97) bleek dat er een onverwachte factor in het spel was die het afnemende broedsucces van de afgelopen jaren goed leek te kunnen verklaren. Het onderzoek in dit seizoen startte veel vroeger dan in voorgaande jaren en in **hoofdstuk 4** worden met name de gebeurtenissen in de eerste helft van dit seizoen beschreven. Het viel op dat er nog veel sneeuw lag die zich in de wintermaanden op beschutte plaatsen op het eiland had opgehoopt. Bovendien had zich in het studiegebied van de Antarctische Stormvogels een grote sneeuwbank gevormd die tot in december aanwezig bleef.

Zuidelijke Reuzenstormvogels bleken regelmatig te landen in de kolonies. Ook werden tussen 15 en 25 oktober in en rondom het studiegebied tien dode Antarctische Stormvogels, die door reuzenstormvogels waren gedood, aangetroffen. Het exacte aantal slachtoffers konden wij niet bepalen omdat in de tijd dat wij niet

in het studiegebied aanwezig waren, een onbekend aantal stormvogellijken kan zijn verdwenen (door wind weggeblazen of meegenomen door Zuidpooljagers).

Zuidelijke Reuzenstormvogels hebben door hun gewicht en stijve vleugels veel problemen met landen op een steile rotsachtige bodem. De meeste kleinere fulmariene stormvogels broeden op klifhellingen die bezaaid zijn met rotsblokken en ze zijn zodoende veilig voor Zuidelijke Reuzenstormvogels. Door de opgehoopte sneeuw was de studiekolonie wel toegankelijk voor reuzenstormvogels. Zij lieten zich als een kamikazepiloot in de zachte sneeuw vallen en liepen vervolgens de kolonie in. In eerste instantie vlogen de Antarctische Stormvogels wel op, maar na een aantal minuten keerden ze terug en wijdden ze zich aan dagelijkse werkzaamheden, zoals het nest op orde brengen voor de komende zomer en het copuleren met hun partner. Meestal besteedden ze dan nauwelijks meer aandacht aan de grote indringer, die zich na zich een tijdje (soms wel uren) gedeisd te hebben gehouden plotseling oprichtte en in snelle pas op een aantal dieren in de kolonie afstootte. Bij zulke plotselinge verrassingsaanvallen wisten ze af en toe een volwassen Antarctische Stormvogel te verschalken. Dergelijk opmerkelijk predatiegedrag door Zuidelijke Reuzenstormvogels was niet eerder bekend.

Van de in het seizoen 1996-97 geringde populatie volwassen Antarctische Stormvogels werd meer dan 15% slachtoffer van predatie door reuzenstormvogels. Uit de literatuur is bekend dat normaal gesproken elk jaar 4% van de volwassen stormvogels overlijdt. In het seizoen 1984-85 werden broedende dieren geringd en twee jaar later bleek het jaarlijkse overlevingspercentage inderdaad 96% te zijn. Daarna nam dat percentage snel af en bedroeg het 89% tussen 1990-91 en 1996-97. Ook bij een nieuwe groep vogels die geringd was in 1996 was dit percentage laag: maximaal 90% van de volwassen dieren overleefde gedurende dit veldseizoen.

Niet-broedende vogels die ook in latere seizoenen geen broedpogingen deden, bleken veel beter te overleven. De in 1984-85 geringde vogels van deze groep hadden een overlevingspercentage dat niet significant afweek van 96%.

Analyse van de weersgegevens van 1980-1995 leerde dat er lokale verschillen waren opgetreden in windrichting en sneeuwval. De sneeuwval was toegenomen met name in de winter en het voorjaar. Het broedsucces was dramatisch slecht in 1996-97 met slechts één kuiken dat uitvloog uit de 29 eieren die geteld werden. Dit exceptioneel slechte broedsucces kwam doordat een aantal eieren faalde in de sneeuw, maar vooral ook door de verstoring wanneer er een Zuidelijke Reuzenstormvogel in de broedkolonie aanwezig was. Antarctische Stormvogels verlieten dan enige tijd hun nest en alerte Zuidpooljagers waren er snel bij om deze onbewaakte eieren op te pakken en mee te nemen naar een veilige plek buiten de kolonie. Zuidelijke Reuzenstormvogels bleken geen eieren te eten.

Broedsucces bij de predator van de Antarctische Stormvogel

Door de onverwachte verklaring van het afnemende broedsucces van Antarctische Stormvogels rees de vraag hoe de sneeuwval het broedsucces van de predator zelf zou beïnvloeden. En tevens of dit een verklaring zou kunnen zijn voor de toegenomen predatie op fulmariene stormvogels, zoals hierboven beschreven. In de omgeving van het eiland Ardery broeden Zuidelijke Reuzenstormvogels alleen op de Frazier eilanden, een eilandengroep met drie kleine eilanden Nelly, Dewart en Charlton (zie hoofdstuk 5 voor een overzicht van de ligging van deze drie eilanden) zo'n 20 kilometer naar het noordwesten. Elk seizoen werden er tellingen verricht om schattingen te maken hoeveel vogels er broedden. Zuidelijke Reuzenstormvogels zijn uiterst gevoelig voor menselijke verstoring en vliegen snel op wanneer mensen in de buurt komen. Tellingen moeten daarom in principe altijd van een afstand gebeuren. In **hoofdstuk 5** beschrijven wij de tellingen van het aantal waarschijnlijk broedende reuzenstormvogels, en later in het seizoen, het aantal aanwezige kuikens. Het seizoen 1996-97 bleek dramatisch slecht te zijn voor reuzenstormvogels, maar de daarop volgende seizoenen waren zeer productief.

We probeerden daarom aan de hand van historische gegevens populatietrends op de drie Frazier eilanden vast te stellen. Dit bleek echter niet eenvoudig omdat er veel variatie was in de manier waarop de vogels werden geteld in het verleden: vroeg of laat in het seizoen, kuikens of broedende vogels, op grote afstand met een verrekijker of dichtbij door onderzoekers die telden terwijl zij door de kolonies liepen (bijvoorbeeld om kuikens te ringen). We creëerden nieuwe categorieën voor type tellingen en analyseerden deze per eiland. De uitkomsten bleken eerdere populatietrends niet helemaal te bevestigen. Gebaseerd op kuikenaantallen leek er inderdaad sprake van een toename in de laatste jaren. Echter op het eiland Nelly, waarvoor we de langste tijdreeks (1959-1999) met kuikentellingen hadden, bleek de broedpopulatie periodiek te fluctueren en was er geen eenduidige positieve of negatieve trend te bespeuren. Wel werd duidelijk dat het seizoen 1996-97 een seizoen was met een extreem laag aantal kuikens. In het hoofdstuk stellen we voor om in de toekomst, indien mogelijk, dit soort tellingen zoveel mogelijk te standaardiseren.

Overvloedige sneeuwval kan ook nadelig zijn voor Zuidelijke Reuzenstormvogels

De overvloedige sneeuwval leverde ook negatieve effecten op voor de Zuidelijke Reuzenstormvogels. In **hoofdstuk 6** bespreken we gevallen van individuen die tijdens het broeden overvallen werden door sneeuw. Tijdens de tellingen van het aantal broedende Zuidelijke Reuzenstormvogels in december 1998 werd een tweetal dode exemplaren aangetroffen op het eiland Dewart, één van de Frazier eilanden. We beschrijven deze vondsten samen met een derde geval dat in 1994 op dit eiland

gevonden werd. Alle drie bleken geruime tijd geleden geringd (12-21 jaar geleden): twee op hetzelfde eiland waar ze gevonden waren en de derde als kuiken in een kolonie ongeveer 1400 km verderop bij het Franse onderzoeksstation Dumont d'Urville, Adélie Land. Niet alleen de relatieve ouderdom van deze dieren maakte deze vondsten uniek, maar ook het feit dat ze alle drie aangetroffen waren met restanten van een ei op de broedplek van de buik. Deze dieren waren dus gestorven terwijl ze een ei aan het uitbroeden waren. Behalve vermageringsverschijnselen vertoonden de vogels geen duidelijke aanwijzingen voor hun doodsoorzaak zoals een bepaalde ziekte of gebroken ledematen.

Het is ongebruikelijk dat soorten die lang leven (zoals verschillende soorten stormvogels die ouder dan 50 jaar kunnen worden) vrijwillig hun leven in de waagschaal leggen als tijdens het broeden de omstandigheden drastisch verslechteren. Voor deze soorten zal het vaak veel aantrekkelijker zijn om het ei te verlaten en een nieuwe broedpoging te wagen in één van de volgende seizoenen. We kunnen slechts speculeren wat precies de doodsoorzaak is geweest, maar het vermoeden is dat door overvloedige sneeuwval de reuzenstormvogels onder een laag sneeuw zijn bedolven, waarna door verijzing van het sneeuwoppervlak ontsnapping onmogelijk werd of dat de verminderde zuurstoftoevoer de vogels uiteindelijk fataal is geworden. Opgemerkt moet worden dat volwassen reuzenstormvogels geregeld bedolven worden onder een laag sneeuw zonder nadelige gevolgen. Dit werd ook waargenomen op het eiland Ardery bij kleinere fulmariene stormvogels, waar broedende oudervogels geregeld enige tijd verdwenen onder de sneeuw en al broedend rustig dagen bleven wachten tot de sneeuw was weggeblazen of gesmolten.

Verspreiding van aantallen van Zuidelijke Stormvogels

Op het eiland Ardery broeden Antarctische en Zuidelijke Stormvogels gezamenlijk, maar dit is vrij ongebruikelijk. Beide soorten zijn talrijk in de Antarctische wateren, al komen ze niet overal in dezelfde mate voor. Stormvogels komen in de zomer veel voor in de buurt van hun broedkolonies en daarom is het belangrijk om een overzicht te hebben van alle locaties waar deze soorten broeden. Voor Antarctische Stormvogels bestond al zo'n overzicht, maar voor Zuidelijke Stormvogels ontbrak deze nog. Voor **Hoofdstuk 7** werd informatie over het voorkomen en de aantallen van broedende Zuidelijke Stormvogels uit zoveel mogelijk bronnen verzameld, inclusief niet-gepubliceerde rapporten en verslagen en oorspronkelijke veldnotities van biologen.

In totaal bleken er 83 locaties te zijn waar Zuidelijke Stormvogels broeden, en op basis van 73 locaties met gegevens over het aantal broedparen werd de wereldpopulatie op minimaal 400.000 broedparen geschat. Ongeveer 72% van de geschatte wereldpopulatie werd gevonden op eilanden van de zogenaamde Scotia-boog, tussen Antarctica en Zuid Amerika (de Zuid-Shetland, Zuid-Orkney en Zuid-

Sandwich eilanden) en het eiland Bouvet. Ook bleek circa 97% van de populatie te broeden op locaties waar geen kolonies van Antarctische Stormvogels zijn.

Het is onbekend hoe groot het deel van de populatie is dat jaarlijks niet broedt en dus buiten deze schattingen van broedende vogels valt. Ook is het aantal van 400.000 broedparen waarschijnlijk een grove onderschatting en wij vermoeden dat er op zijn minst 1 miljoen broedparen zijn. We illustreren dit aan de hand van uitkomsten van verschillende telmethoden die wij tijdens onze veldseizoenen in het studiegebied op het eiland Ardery gebruikten. We vonden dat aanmerkelijk meer eieren waren gelegd dan het aantal nesten dat werd waargenomen met broedende of waarschijnlijk broedende vogels. Doordat gedurende het seizoen steeds meer nesten falen, neemt dit verschil toe in de loop van de tijd. Aangezien de meeste kolonies zich op kliffen bevinden die alleen van grote afstand geschat kunnen worden, en ook omdat de tijdstippen van de tellingen zeer sterk verschilden, is de nauwkeurigheid van de schatting voor de wereldpopulatie broedende Zuidelijke Stormvogels gering.

Antarctische Stormvogels als graadmeter voor het Antarctisch ecosysteem

Deze studie toonde aan dat verwante stormvogelsoorten met een ogenschijnlijk vergelijkbare levenswijze toch op verschillende manieren aangepast kunnen zijn aan de Antarctische omgeving en de korte zomerperiode waarin zeevogels hier kunnen broeden. Ondanks een duidelijk verschil in het tijdstip van broeden bereikten de Antarctische Stormvogel en de Zuidelijke Stormvogel vrijwel hetzelfde broedsucces. Hoe de eventuele gevolgen van veranderingen in het klimaat, zee-ijs of voedselaanbod in het algemeen voor beide soorten zullen uitpakken, is moeilijk te voorspellen. Op het eiland Ardery bleken lokale weersveranderingen een onverwachte keten van gebeurtenissen te veroorzaken, met een drastisch effect op de plaatselijke stormvogelpopulatie als gevolg. Indien natuurlijke factoren een dergelijk groot effect kunnen hebben, zal het moeilijk zijn om de invloed te meten van specifiek menselijk handelen in het Antarctische ecosysteem, zoals bijvoorbeeld visserij. Het internationale krillverdrag heeft de Antarctische Stormvogel als indicatorsoort aangewezen, maar op dit moment lijkt het nog te vroeg voor eenduidige verklaringen van veranderingen in de broedbiologie en populatiegrootte van stormvogels. Meer gedetailleerd en vooral ook langduriger onderzoek, ook aan foerageerstrategieën van stormvogels op zee, zal nodig zijn om de toestand van het Antarctische ecosysteem te kunnen meten en de gevolgen van menselijke invloeden goed te kunnen voorspellen.





EPILOGUE

When I applied in 1996 for a job as seabird researcher in Antarctica I could not imagine that this would keep me busy for so long. It began with three long field seasons in a row on a small island, just off the coast of Antarctica. Living on Ardery Island with so much abundant and approachable wildlife was a unique experience, which I will not easily forget. It is really an awesome place. From time to time I still miss it. Back in Holland, working on my own and producing papers was not always easy. It felt again like being on a small island, but now with fewer birds and more people around. This island was more lonely, and I am happy that it is done. It would have been impossible without the help of many people who contributed to the project.

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Since my childhood my parents encouraged me to explore the natural environment and to broaden my horizon. This has influenced me throughout my life a lot and has led me to distant places like Antarctica. I am my parents very thankful for that. I deeply regret that my mother is not able to see the final result of my Antarctic expeditions.

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Jeroen
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