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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

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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 16 days earlier than Southern Fulmars. During the pre-laying exodus, all Antarctic Petrels deserted the colony, whereas some Southern Fulmars *Fulmarus glacialoides* 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.

**Keywords:** Antarctica, ecology, Fulmarine petrels, *Fulmarus glacioloides*, seabirds, timing of breeding, *Thalassoica antarctica*.

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 1990, 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 & LeResche 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

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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 with other procellarids (Warham 1990, Hodum 2002). The smaller Antarctic fulmarines (Southern Fulmar *Fulmarus glacialoides*, 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 2 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 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

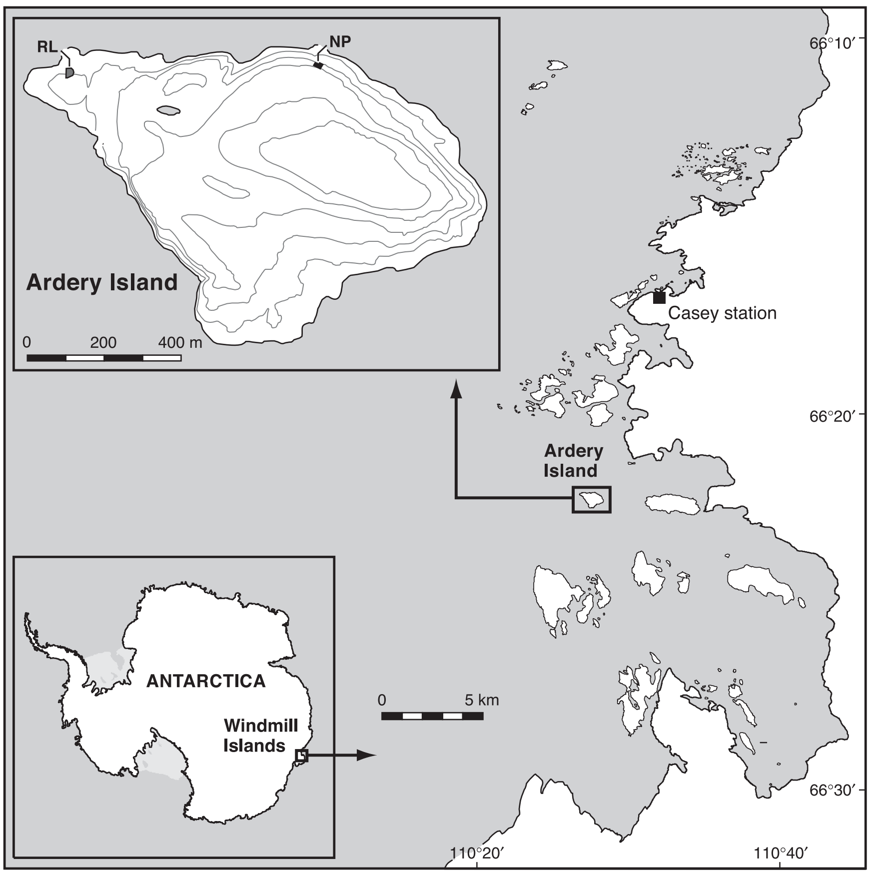


**Figure 1.** Ardery Island, Windmill Islands, Wilkes Land, Antarctica. On the detailed map of Ardery Island, 20-m height contours are shown, and study colonies are denoted by RL for Robertson Landing (Southern Fulmars), and NP for Northern Plateau (Antarctic Petrels).

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-$m^2$ 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 $m^2$ 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 occurring 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.

## 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 1 day (Weimerskirch 1990, van Franeker 2001, J. C. S. Creuwels & J. A. van Franeker unpubl. data).

The sex of adult birds was determined with a generalized 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.

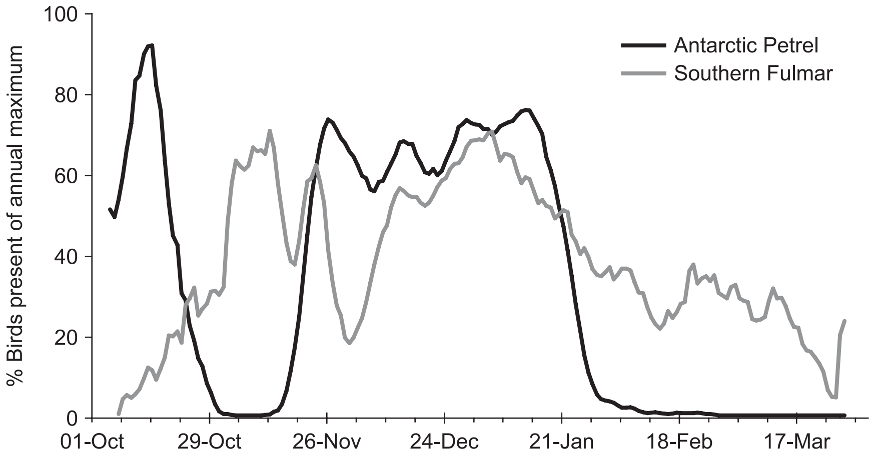


**Figure 2.** Relative colony attendance. Seven-day running means of the number of counted birds expressed as a percentage of the yearly maximum, and averaged over the three seasons.

Dates of breeding events and breeding periods were not normally distributed, but as the variance between the subgroups 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 1995). When comparing more than two groups, multiple comparisons were performed with Hochberg's GT2 test, due to unequal sample sizes (Sokal & Rohlf 1995). However, when variances between the groups differed significantly, the Games–Howell multiple comparisons test was used (Sokal & Rohlf 1995).

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, days 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 with 1997 and 1998, in 1996 egg-laying was later by about 3–4 days

**Table 1.** Timing of breeding events. Mean dates (± sd) are given with sample sizes in parentheses. Where there were significant differences between seasons, pairs of seasons sharing a superscript letter did not differ significantly*.

| | Mean 1996–98 | 1996 | 1997 | 1998 |
|---|---|---|---|---|
| *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 Jan. ± 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) |

*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.

**Table 2.** Duration of different phases of the breeding period. Mean durations (± sd) 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 significantly*.

| | Mean 1996–98 | 1996 | 1997 | 1998 |
|---|---|---|---|---|
| *Antarctic Petrel* | | | | |
| Incubation | 47.7 ± 1.0 (73) | 47.0 ± 2.1 (2) | 48.0 ± 0.9 (26) | 47.5 ± 1.1 (45) |
| Guarding | 14.3 ± 2.7 (57) | 16.0 ± 2.1 (2)[ab] | 16.8 ± 2.3 (19)[b] | 12.9 ± 1.7 (36)[a] |
| Chick period | 48.7 ± 1.7 (50) | 48.5 (1) | 48.1 ± 1.6 (18)[a] | 49.1 ± 1.6 (31)[b] |
| Total breeding | 96.6 ± 1.9 (50) | 97.0 (1) | 96.3 ± 1.8(18) | 96.7 ± 2.0 (31) |
| *Southern Fulmar* | | | | |
| Incubation | 46.5 ± 1.1 (117) | 46.1 ± 1.2 (22)[a] | 46.8 ± 1.0 (33)[b] | 46.5 ± 1.0 (62)[ab] |
| Guarding | 20.1 ± 6.5 (101) | 14.8 ± 2.9 (20)[a] | 23.8 ± 7.9 (31)[c] | 19.9 ± 5.2 (60)[b] |
| Chick period | 50.1 ± 1.6 (77) | 51.1 ± 1.4 (12)[b] | 50.8 ± 1.5 (27)[b] | 49.3 ± 1.4 (38)[a] |
| Total breeding | 96.6 ± 2.0 (77) | 97.2 ± 1.8 (12)[b] | 97.6 ± 1.6 (27)[b] | 95.6 ± 1.8 (38)[a] |

*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.

(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 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 days 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; $t_{125} = 0.01$, $P = 0.996$).

All breeding events were highly synchronized in both species (Table 3). Over 80% of records of each breeding event occurred within a 7-day period, except for the end of the guarding period in Southern Fulmars (56% in a 7-day period). The end of the guarding

**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 1996–98 are combined* and sample sizes shown in parentheses.

| | Antarctic Petrel | Southern Fulmar | Difference | |
|---|---|---|---|---|
| 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) | $G = 0.48$ | $P = 0.488$ |

*Differences 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 ($G = 6.83$, $P = 0.009$).

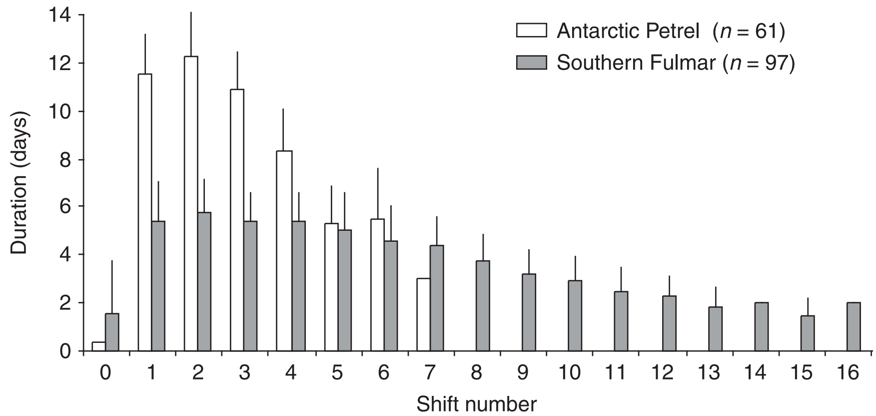


**Figure 3.** Incubation shifts. Means ± sd are given for the duration of shifts from egg-laying (shift number 0) until the last shift before hatching. Odd numbers are male shifts; even numbers are female shifts. Hatching occurred on average at shift number 4–5 for Antarctic Petrels, and at shift number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

period was significantly less synchronized 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 ($F_{1,94} = 7.39$, $P < 0.008$).

## 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-$t_{72} = 6.14$, $P < 0.001$).

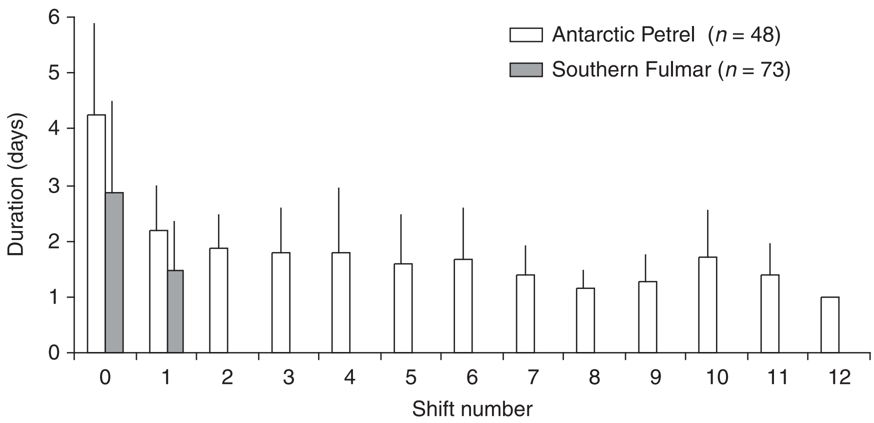


**Figure 4.** Guarding shifts. Means ± sd of the duration of hatching shifts (shift number 0) and guarding shifts are given. Shift numbers were irrespective of sex, and for Southern Fulmars only the first guarding shift could be reliably estimated. Data of three seasons were combined and the initial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

**Table 4.** Breeding success. Percentages of success are given with sample sizes in parentheses. Test statistics are given for interseasonal differences in success rate. Differences between species for the mean values of 1996–98 were not significant.

| | Mean 1996–98 | 1996* | 1997* | 1998* | 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* |
| 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* |
| Breeding success | 35.0 (78/223) | 17.9 (12/67) | 36.0 (27/75) | 48.1 (39/81) | $G = 14.54$ | $P < 0.001$ |

*Differences 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 ($G = 4.46$, $P = 0.035$).

## 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 of 22 chick failures occurred (46.3% of all breeding failures of that year).

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 laid during a period of 14–17 days, in which time 39 out of 220 (17.7%) the 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

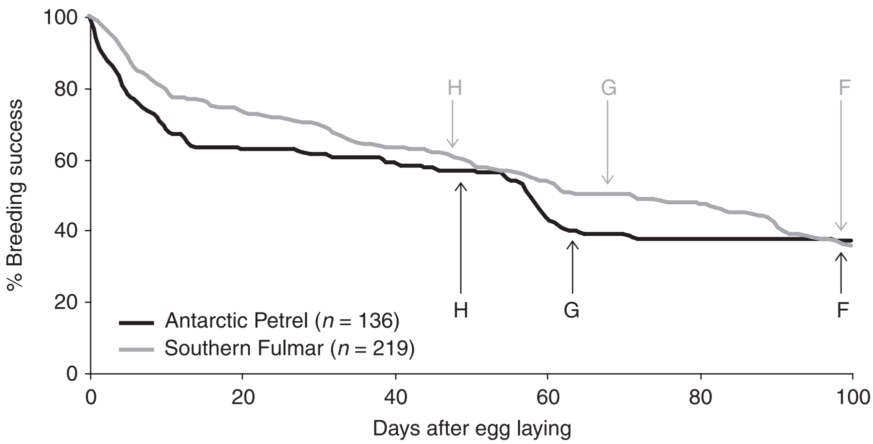


**Figure 5.** General trends in breeding success. Each nest started at the day the egg was laid (day 0). Data of three seasons were combined and totals are given in parentheses. Mean dates of main breeding events are indicated with arrows, grey arrows for Antarctic Petrels, and black arrows for Southern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

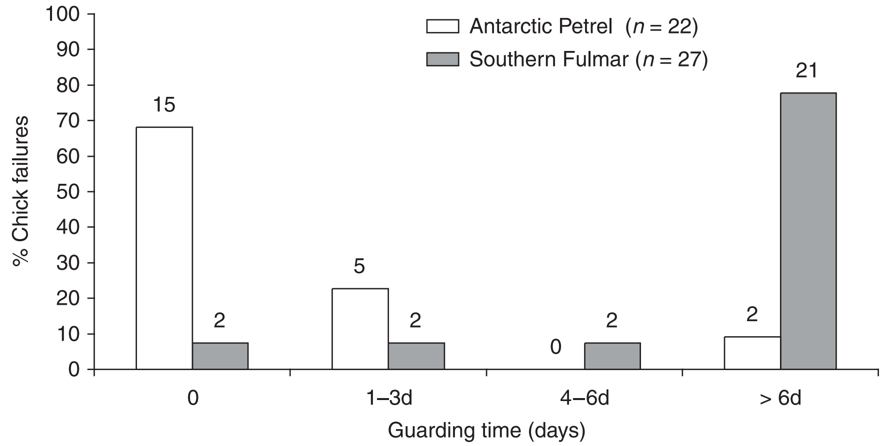


**Figure 6.** Chick failure in relation to guarding. All chick failures, categorized in the number of days a chick had been unattended. Data of all seasons are combined, and sample sizes of chick failures are indicated above the bars.

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.

## 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 and 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 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

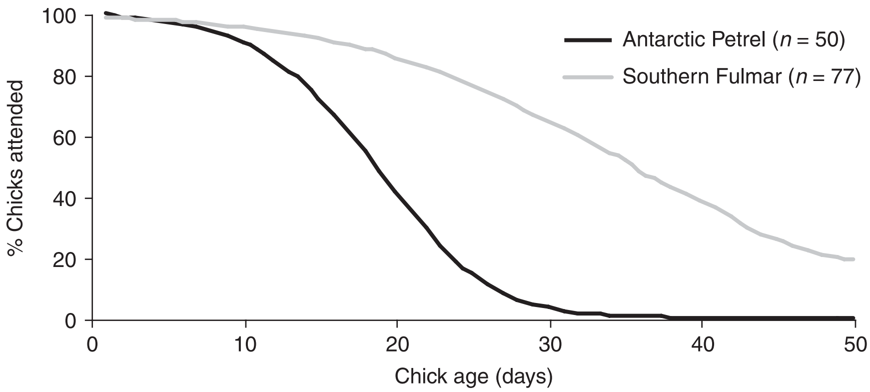


**Figure 7.** Chick attendance. Predictions, averaged over three seasons, are plotted from the logistic regression model (see text for details) on percentage of attended chicks. Sample sizes of total number of chicks are indicated in parentheses.

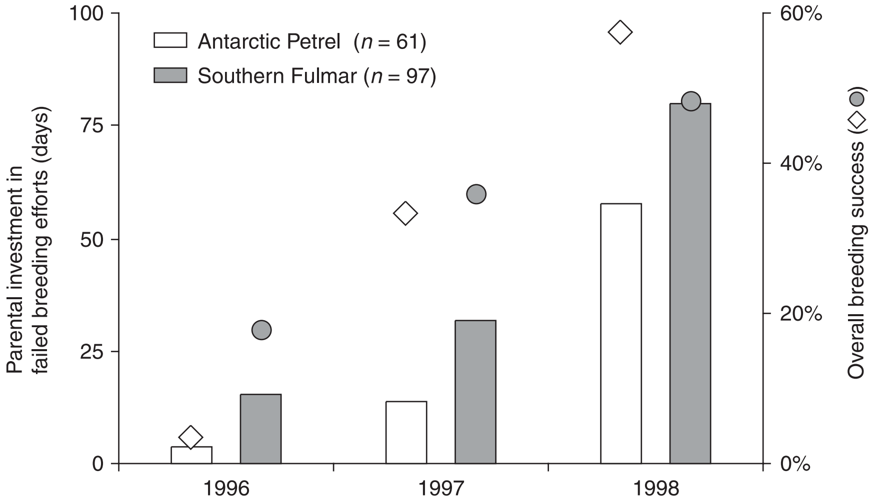


**Figure 8.** Investments in failed breeding attempts. Parental investment is expressed as the average number of days until nest failure, in different years with variable overall breeding success.

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 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 Petrels and 32.0 days ($n = 141$) for Southern Fulmars (Mann–Whitney, $Z = -3.19$, $P < 0.001$).

## 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 adult 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 2 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 the analyses, the consequences of early or late breeding were still apparent in the data.

### Implications of breeding strategies

Breeding requires a considerable energetic investment by the 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 for 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.

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