

FORAGING STRATEGIES OF ANTARCTIC FULMARINE PETRELS

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SUMMARY

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During breeding, procellariiform seabirds are typical central-place foragers, depending on distant pelagic resources. Especially in polar environments, where there is only a short time window to complete the breeding season, high chick provisioning rates are needed to allow chicks to fledge successfully. The duration of the chick period and of chick growth are linked to provisioning parameters such as the frequency and quantity of the chick meals, but probably also to the quality of the food delivered. We studied the provisioning and growth of chicks of Southern Fulmars *Fulmarus glacialisoides* and Antarctic Petrels *Thalassoica antarctica* on Ardery Island (66°S, 110°E) near the Australian Antarctic station Casey. During two seasons (1998, 1999) we deployed artificial nests to collect data on chick provisioning. Southern Fulmars delivered meals more frequently (one per 14 hours) than did Antarctic Petrels (one every 25–26 hours). In 1998, the mass of meals brought to chicks of both species was not significantly different and averaged around 128 g. In 1999, the meal mass of Southern Fulmars remained the same, but that of the Antarctic Petrel was 28 g heavier. Chick provisioning rates calculated from meal frequencies and masses were significantly different between Southern Fulmars (254 g/day) and Antarctic Petrels (151 g/day), even after correction for body size. Because growth rates for the two species were not significantly different we suggest that Antarctic Petrels deliver meals of higher nutritional value, probably related to food reaching a higher density in the parents' stomach during their longer foraging trips.

Key words: Antarctica, foraging strategies, chick provisioning, chick growth, automatic weighing system, Procellariiformes, *Fulmarus glacialisoides*, *Thalassoica antarctica*

INTRODUCTION

During their breeding season, procellariiform seabirds are typical central-place foragers, dependant on distant, unpredictable, and patchy food resources. Procellariiformes have developed different strategies to overcome such constraints when provisioning chicks (Baduini & Hyrenbach, 2003). First, by over-feeding their young, parents may give their offspring a buffer for periods with low food supply (Lack 1968, Ashmole 1971) or give chicks better survival chances just after fledging (Phillips & Hamer 2000b). Second, various species are able to process (part of) their prey into energy-rich stomach oil during the time they are foraging (Roby *et al.* 1997). Third, many species have developed a dual foraging strategy, where parents alternate short foraging trips with long trips (Weimerskirch *et al.* 1994, Baduini & Hyrenbach, 2003, but see Phillips *et al.* 2009). Parents may use short foraging trips to increase the feeding rate, which is beneficial for the chick but could deplete the parents' reserves, whereas long trips may be used by parents to recuperate.

The chick-provisioning rate depends on the frequency of the meals and quantity of food brought to the chick. When the food resources are located far away, parents may try to minimize the travel costs by reducing the number of foraging trips, but not the amount of food. This is probably why, in many procellariiform studies, feeding frequency rather than meal size was found to influence the total amount of food that a chick received per day (Huyn *et al.*

2000, Pinaud *et al.* 2005). Although the amount of food that a chick receives is supposed to affect chick growth, this relationship is not fully clear. Internal constraints, such as limited nutrient availability or the developmental stage of digestive capacities of the gut of the chick, may influence chick growth (Ricklefs *et al.* 1998). Overall, variations in chick growth appear smaller than variations in the provisioning rate (Gray *et al.* 2005). When comparing chick growth between species or between seasons, the growth rates may not only be affected by provisioning rates but also by differences in food quality (Prince & Ricketts 1981, Ricklefs *et al.* 1987, Huyn *et al.* 2000, Pinaud *et al.* 2005).

We investigated the chick provisioning and growth in two closely related procellariiforms: the Southern Fulmar *Fulmarus glacialisoides* and the Antarctic Petrel *Thalassoica antarctica*. Both species breed sympatrically along the continental coast of Antarctica, and they have a strong similarity in the composition of the food that they deliver to their chicks (Van Franeker 2001, Fig. 1). However, both species differ strongly in the frequency of the meals and the timing of breeding, although not in the length of the breeding season (Norman & Ward 1992, Van Franeker 2001, Creuwels *et al.* 2008). This is not what we expected, because the general assumption is that time is limited for chicks to fledge successfully in Antarctica. Hence, the chicks need to grow as fast as physiologically possible in order to allow fledging prior to the onset of poor weather and reforming sea ice late in the season.

In spite of the differences in both timing of breeding and foraging strategies, breeding success was similar for the two species (Creuwels *et al.* 2008). In this study, we investigated how these different provisioning strategies affected chick growth. During two summer seasons we used an automatic weighing system to assess meal frequencies, meal sizes and growth rates of Southern Fulmars and Antarctic Petrels.

METHODS

Study areas in colonies of Southern Fulmars and Antarctic Petrels were established during the 1980s on Ardery Island ($66^{\circ}22'S$, $110^{\circ}30'E$), Vincennes Bay, Wilkes Land, Antarctica, 11 km south of the Australian station Casey (Van Franeker *et al.* 1990). The Southern Fulmar study plot holds about 130 potential nest sites and that of the Antarctic Petrel about 100 potential nest sites, but in both species less than half of these sites are actively used for breeding in any given season. In this paper, we present data from fieldwork during chick rearing in the austral summers of 1997/98 and 1998/99 (hereafter referred to as seasons 1998 and 1999).

Within both study areas, about 80% of breeding adults were individually marked with leg bands and electronic tags (TIRIS transponder; injected subcutaneously along the tibia). For our study, we developed an automatic weighing and identification nest-system (AWIN; see Creuwels *et al.* 2000) which simultaneously weighed birds and read their unique transponder number. Every 5–7 minutes, each individual nest unit recorded the mass and identity of the bird on the nest.

To avoid disturbance, artificial nest units were installed as early in the season as possible. In the fulmar colony we placed up to 25 nest units and in the petrel colony up to 17 nest units. The number of pairs that bred successfully on these nests fluctuated because not all nests became occupied, and because of breeding failures. In the fulmar colony, eight chicks fledged from artificial nests in 1998 and nine in 1999, and in the petrel colony four and nine, respectively. Due to increasing snowfall, measurements in March were unreliable for both seasons and were not used.

For accurate estimates of meal sizes, chicks had to be alone on the nest. We therefore restricted our data to the period after the

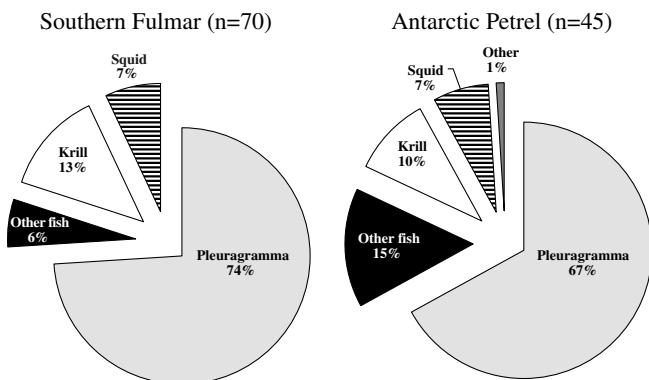


Fig. 1. Composition of food brought to chicks of Southern Fulmars and Antarctic Petrels on Ardery Island, in 1987 and 1991. Percentages denote reconstructed mass proportions of major prey groups in the original meals. Fish, mainly *Pleuragramma antarcticum*, dominated the diet of both species. For details see Van Franeker (2001).

parents continuously guard their chick. A mass increment of 25 g or more between two weighings was considered to represent a meal. Because there is always a time lag between consecutive reliable data points (from five minutes to several hours), we accounted for digestion when estimating a meal size using a mass loss rate of 10.13 g/h for fulmar and 5.37 g/h for petrel chicks (J.C.S. Creuwels unpubl. data). We omitted data on meal sizes when the gap between reliable measurements was six hours or more.

We expressed the feeding frequency by the time interval in hours between meals. The chick provisioning rate was defined as the total amount of food in grams brought to the nest per day. Chick growth was calculated from the difference in chick mass from midnight to midnight next day. Calculation of growth rate was only possible after the guarding period and only for the 1999 season due to the high incidence of data gaps in 1998. When comparing the daily food delivery, or growth between species, we corrected for differences in body size. This was done by dividing the measured values by the maximum mass of each individual chick. To avoid extreme values when chicks just had been fed, we only used the average mass of a chick between two meals.

In both study areas, we also weighed a subset of chicks manually, which allowed us to study chick growth in the early and late chick period. In 1999, we weighed fulmar chicks, on average, every 2 ± 0.5 days and petrel chicks every 2 ± 0.4 days. To avoid problems with common initial mass loss of chicks in the first 1–2 days, we used the projected mass of the egg at hatching (each egg was weighed 4–5 times during incubation). Procellariiform chicks typically grow to a maximum weight of 130–150% of the adult body mass, and after reaching peak mass they lose mass until fledging (Warham 1990). We used mass data of chicks up to 35 days old (average age when chicks attained peak mass) to construct a logistic growth model for each individual chick. For comparisons of the growth rates between species, we divided the mass difference of each chick by its asymptotic mass, as obtained from the logistic growth model.

We reduced variation in data on chick provisioning and growth by aggregating data in five-day periods. When data were missing, or could not be reliably estimated in a particular five-day period, we omitted that period. To calculate chick mass at the end of a five-day period, we assumed linear growth between two consecutive weighings. Some chicks could have consistently received more food, or had longer time intervals between the meals than others. We therefore checked for pseudoreplication, and found only small differences in grand means (per nest) in relation to population means. This was confirmed by the more sophisticated linear mixed models (fitted using Restricted Maximum Likelihood) that we used to account for the individual variation of repeated measurements of meal sizes and time intervals. Chicks were treated as a random effect, and model selection was based on the Akaike Information Criterion (Crawley 2007). We analysed other parameters with standard statistical techniques (Sokal & Rohlf, 1995). We present data as means \pm standard deviations, unless stated otherwise, and used a significance level of $P < 0.05$.

RESULTS

Chick provisioning

Meal sizes of Southern Fulmar chicks averaged at 127 ± 45 g in 1998 and 122 ± 44 g in 1999 (Fig. 2). In Antarctic Petrels meal sizes averaged at 113 ± 43 g in 1998 and 152 ± 47 g in 1999. A linear

mixed model indicates that meals of fulmars of both seasons and meals of petrels in 1998 were of similar size (i.e. 127 g; both factors $P > 0.2$), but that petrels delivered significantly larger meals in 1999 (on average 28 g more, interaction species*season $P = 0.01$).

Frequency distribution of the time intervals between meals shows that distributions are skewed to the left (Fig. 3). The median interval between meals for fulmars was 13.6 h in 1998 and 13.5 h in 1999. For petrels, the medians of these time intervals were almost twice as long: 25.0 h in 1998 and 26.4 h in 1999. A linear mixed model

with square root transformed values confirmed that Southern Fulmars had a much higher meal delivery rate than Antarctic Petrels ($P < 0.001$) and that a year-effect was not significant nor was the interaction year*species (both $P > 0.5$).

Southern Fulmars delivered about 40% more food (g/d) to their chicks than did Antarctic Petrels. In 1999, Fulmars delivered 254 ± 36 g ($n = 20$) and petrels 151 ± 45 g ($n = 44$) food per day. These differences were highly significant for all periods that we could test (t-tests, four 5-d periods between 15–35 d, all $P < 0.001$). Because fulmar chicks studied were larger (maximum mass: 1128 ± 125 g, $n = 5$) than were petrel chicks (992 ± 96 g, $n = 9$), we needed to correct for differences in chick size. After these corrections the differences between the species were smaller but still significant (Fig. 4; t-tests, four 5-d periods between 15–35 d with $P \leq 0.02$). In the period that chicks were between 15–35 days of age, fulmars delivered per day an amount of food that equalled 23 % (± 3.3) of the maximum chick mass, whereas petrels delivered 15% (± 4.9) of the maximum chick mass.

Within each species, we tested whether the rate of food delivery varied over the season (Fig. 4). In fulmars, between chick ages 15–35 days, there was no significant trend ($F = 0.9$, $P = 0.5$). Similarly, no significant trend in food delivery ($F = 1.3$, $P = 0.3$) was detected in petrels between 10–40 d, but in chicks older than 40 d the food delivery was drastically reduced ($F = 6.7$, $P < 0.001$).

Chick growth

We used the individual chick mass data from the artificial nest system to calculate the growth rates of chicks in the post-guarding period in 1999 (Fig. 5). Fulmar chicks achieved highest growth rates between 15–25 d. At about 35 days of age, their growth rates approached zero but we were not able to collect reliable data after 35 d. For petrel chicks, data collected over a longer period showed a similar pattern, with chicks starting to lose mass on average after 40 d. The differences in growth rate between species were similar between 15–25 d (t-tests for both 5-d periods, $P > 0.6$). Between 25–35 d fulmar chicks grew faster than petrel chicks, but these differences were not significant (t-tests: 25–30 d $P = 0.053$, 30–35 d, $P = 0.12$). Figure 5 and the statistical results were virtually

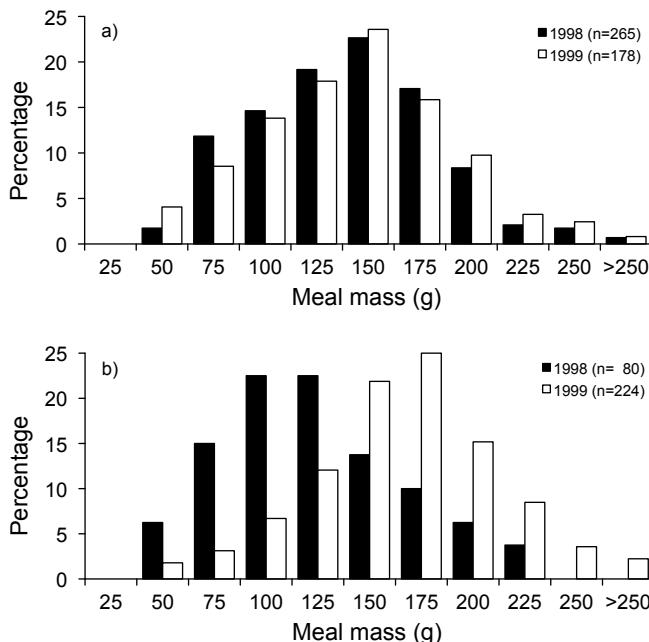


Fig. 2. Distribution of meal sizes of (a) Southern Fulmars and (b) Antarctic Petrels. Numbers of meals per season are given within parentheses.

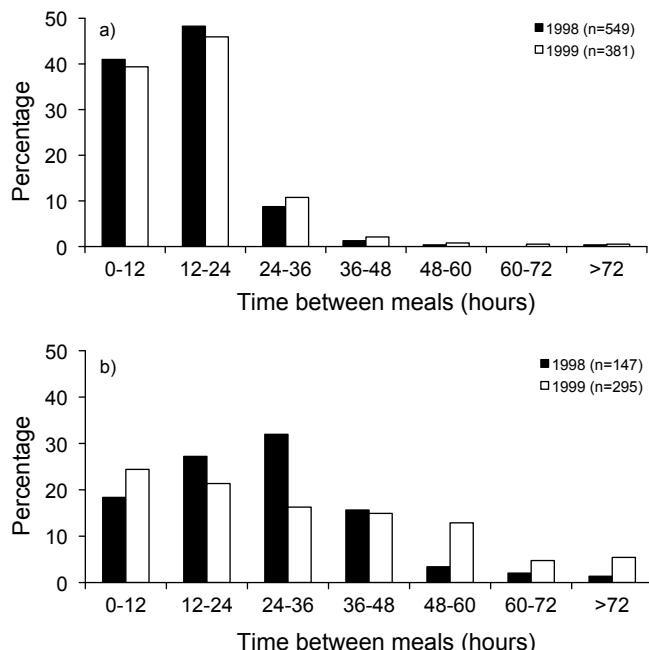


Fig. 3. Distribution of time intervals between the meals of (a) Southern Fulmars and (b) Antarctic Petrels. Numbers of intervals per season are given within parentheses.

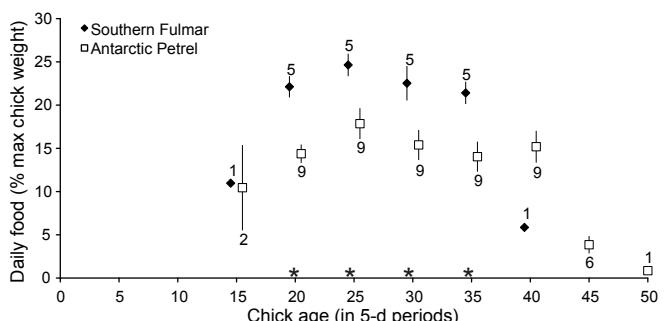


Fig. 4. Daily food delivery of Southern Fulmars and Antarctic Petrels. For each individual chick the average amount of food received per day was calculated over five-day periods in the 1999 season. This amount was divided by the maximum mass that each chick attained. Mean values with standard errors are given with the numbers of chicks of each period below or above the bars. On the x-axis, the end of each period is denoted (e.g. '20' means the period between 15–20 days) and asterisks show significant differences (t-tests) between species.

unaffected by correction for chick size (*t*-tests: between 25–35 d both $P > 0.6$, 25–30 d $P = 0.08$, 30–35 d $P = 0.2$).

We found a large individual variation in the proportion of delivered food that was converted to chick mass. For both species, the efficiency of food conversion was highest between 15–25 d. Due to small sample sizes, we could only find a significant difference between species in the period between 15–20 d. During this period, fulmar chicks converted on average 14% of delivered food to body mass, whereas petrels converted 23% (Mann-Whitney test, $P = 0.04$). The mean food conversions for the other periods were as follows: between 20–25 d 15% for fulmars and 24% for petrels (MW test, $P = 0.2$); between 25–30 d: 10% and 3%, respectively (MW test, $P = 0.2$); and between 30–35 d: 3% and 1%, respectively (MW test, $P = 0.2$). After 35 d, most chicks started to lose mass, resulting in negative values of the efficiency of converting food.

Manual weighing data for 1999 provided further information on chick growth especially in the early and late chick periods. Manual masses indicated that fulmar chicks had highest growth rates at an age of 15–20 d and petrels at 20–25 d. Logistic growth models for individual chicks up to 35 d suggest that average maximal chick growth rate was higher for fulmars ($k = 0.159$, $n = 22$) than for Antarctic Petrels ($k = 0.150$, $n = 12$) but that the difference was not significant (*t*-test, $P = 0.8$). As expected, fulmar chicks reached much higher asymptotic weights (average 1225 g) than did petrel chicks (1047 g, *t*-test, $P = 0.01$).

After correcting for body size, most periods showed no significant differences in relative growth rate between the two species (Fig. 6; *t*-tests, eight periods with $P > 0.1$). Only the growth rates of fulmar chicks of 20–25 d were significantly lower than those of petrels (*t*-test, $P = 0.03$), whereas chicks of 40–45 d lost significantly less mass than did petrel chicks (*t*-test, $P < 0.001$).

DISCUSSION

Chick provisioning

We found no differences in the average meal size that Southern Fulmar parents delivered to their chicks between the two seasons (122 to 127 g). Meal sizes on Ardery Island were considerably larger than that of 94 g reported for fulmars at Terre Adélie (Weimerskirch 1990a). In Antarctic Petrels, the difference in

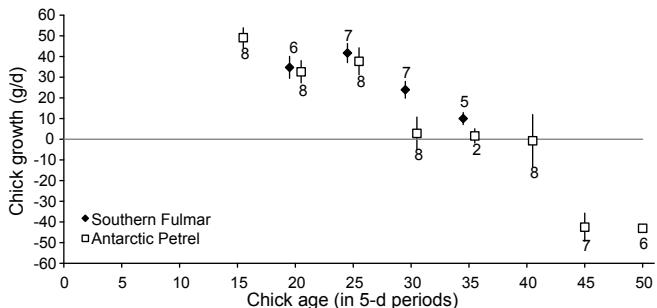


Fig. 5. Daily chick growth of Southern Fulmars and Antarctic Petrels. Growth rates for each individual chick are calculated over five-day periods in 1999. Mean values with standard errors are mentioned with the numbers of chicks of each period below or above the bars. On the x-axis, the end of each five-day period is denoted and asterisks show significant differences (*t*-tests) between species for each period.

average meal size between the two breeding seasons was 42 g, a difference of more than 25%. The smaller meals in 1998 correlated with the lower number of chicks and reduced fledging success for petrels in that season. In the better season of 1999, the average meal size on Ardery Island (152 g) was comparable with that recorded in the continental Antarctic colony of Svarthamaren, located 200 km inland (146 g; Lorentsen 1996).

Overall, fulmars on Ardery Island delivered meals of 15–16% of adult body mass, whereas petrels provisioned their chicks with meals of 16–22% of adult body mass. These values are somewhat higher than those for other fulmarine petrels, but within the range of other procellariiforms (Phillips & Hamer 2000a). Why Southern Fulmars deliver relatively lighter meals than do Antarctic Petrels is not fully clear. Most studies suggested that the wing loading of both species is similar (Warham 1996, Dijkstra 2003, but see Spear & Ainley 1998), although wing loading may fluctuate with seasonal variations in body mass (Weimerskirch 1990b, Huin *et al.* 2000). These seasonal fluctuations may differ between species and consequently the capacity to carry food. Furthermore, fulmars started moulting their flight feathers during the chick phase, which could have reduced their actual wing loading.

At Terre Adélie, Southern Fulmar chicks had to fast for an average of about 18 h between meals (Weimerskirch 1990a), which was substantially longer than on Ardery, even if arithmetic means are used instead of medians (1998: 14.6 h, 1999: 15.5 h). Because of a lower meal frequency and smaller meal mass, fulmars from Terre Adélie had a much lower daily food delivery rate (125 g/d) than on Ardery Island (254 g/d). Antarctic Petrel chicks at Svarthamaren, as expected from the remote location of the colony, fasted much longer between subsequent meals (1.6 day) than did the petrels on Ardery Island (1.1 d in 1998 to 1.3 d in 1999). As a consequence, the daily food delivery rate to chicks on Svarthamaren (91 g/d) was about 40% lower than on Ardery Island.

Southern Fulmars fed their chicks almost twice as frequently as do Antarctic Petrels. Such a large difference in the feeding rate cannot be explained by differences in diet, because they bring similar prey to their chicks. Both meal sizes and feeding intervals were highly variable, which indicates that both species were flexible in their foraging strategy or that they had mixed success in obtaining food.

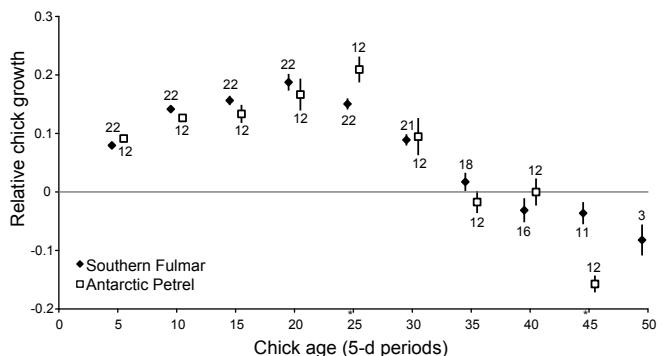


Fig. 6. Relative chick growth of Southern Fulmars and Antarctic Petrels in 1999. The average growth rates of individual chicks were calculated for each five-day periods and corrected for body size (see methods). Mean values with standard errors and the numbers of chicks of each period are mentioned below or above the bars. On the x-axis, the end of each five-day period is denoted and asterisks show significant differences (*t*-tests) between species for each period.

Both species may not always maximize their flight loads, as has also been suggested for the Arctic or Northern Fulmar *F. glacialis* (Phillips & Hamer 2000a). However, we found no evidence for a bimodal distribution in the meal intervals as observed in several procellariiform seabirds (Weimerskirch *et al.* 1994).

Chick growth

The high provisioning rates we found in this study indicate that the chicks were supplied with sufficient food to enable rapid chick growth. Food supply is probably not the constraining factor for chick growth in Antarctic fulmarine petrels (Weimerskirch 1990a, Hodum & Weathers 2003). Data of chicks on artificial nests suggest that Southern Fulmars tended to grow faster, but not significantly so. Data of manually weighed chicks enabled us to study growth during the whole chick period. For both our species, the values of the growth constant *k* that we calculated in the logistic growth model are among the highest values within the order Procellariiformes (Warham 1990). Such a fast chick growth might be not surprising, since the duration of the chick phase among smaller fulmarine petrels is half as long as expected on the basis of size (Warham 1990, Hodum 2002).

We found no significant differences in interspecific chick growth rates for most 5-d periods. The significantly higher chick growth of Antarctic Petrels between 20–25 d seemed to compensate for a somewhat reduced growth between 5–20 d. This may have been linked to unfavourable foraging conditions in this period, caused by a temporarily heavy sea ice cover in Vincennes Bay in late January/early February 1999 (Michael & Hill 2003). Data from AWIN showed that Antarctic Petrel chicks of 5–20 days old waited longer for meals in 1999 than in 1998, but not in other age groups. Because fulmar chicks hatched c. 15 d later, they were probably mostly unaffected, and we found only for the age group of 0–5 d longer fasting time intervals in 1999.

Southern Fulmar chicks between 40–45 d lost mass less rapidly than did Antarctic Petrel chicks of that age, probably because the fulmars attend and feed their chicks for longer (Creuwels *et al.* 2008). Our last visual observations of fulmar chicks being fed were made on 19 and 20 March 1999, two and three days after the mean fledging date. AWIN data showed that, on average, petrel chicks received their last meals on 20 February ($SD = 1.8$, $n = 9$), 10 days before the mean fledging date. The very last meal observed was delivered on 25 February 1999.

Efficiency of using food for chick growth

This study shows contrasting foraging strategies between Southern Fulmars and Antarctic Petrels, yet resulting in similar overall chick growth. Remarkably, fulmars brought 40% more food to their chicks, whereas their chicks were only 10–20% heavier than petrel chicks. Thus Antarctic Petrel chicks appeared to convert their food more efficiently into body mass. How can this be explained?

Firstly, the chick provision rates are given in gram food per time unit but not in the energetic value. Meals consisting of similar proportions of prey items could be still different in energetic density. Due to their longer foraging trips, Antarctic Petrels may extract more water from the food or partially digest their stomach contents and thus produce more energy-rich stomach oil (Van Franeker 2001, Norman & Ward 1992). In this way, petrel chicks may receive meals

of a higher nutritional value per unit mass than do fulmar chicks. Secondly, according to Weathers *et al.* (2000), Southern Fulmar chicks are less well insulated than are Antarctic Petrel chicks, and may therefore need to allocate a higher proportion of food energy to thermoregulation instead of to growth.

The coast of continental Antarctica, where we conducted this study, is the southern limit of the breeding distribution of Southern Fulmars and the northern limit of Antarctic Petrels (Van Franeker *et al.* 1999, Creuwels *et al.* 2007). This suggests that fulmars mostly breed in warmer conditions with easy access to open water and where wind conditions are more suitable for their gliding flight style (Creuwels *et al.* 2008). We suggest that due to physical and physiological limitations, Southern Fulmars in coastal Antarctica live on the edge of their capabilities.

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