

Development of homeothermy in chicks of sub-Antarctic burrowing petrels

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The development of homeothermy was studied in chicks of five species of sub-Antarctic burrowing petrels. Chicks of white-chinned and blue petrels were capable of maintaining body temperatures of 37° to 40°C at ambient temperatures between 5° and 30°C within one day of hatching. On average, chicks of grey petrels, great-winged petrels and Salvin's prions attained homeothermy within five days of hatching, but some individuals exhibited well-developed homeothermy within 24 h of hatching. Chicks demonstrated a high capacity for heat production and maximum cold-induced oxygen consumptions ranged from 2,57 ml O₂ g⁻¹ h⁻¹ in white-chinned petrel chicks to 4,94 ml O₂ g⁻¹ h⁻¹ in the much smaller blue petrel chicks. The rapid development of homeothermy in burrowing petrel chicks is regarded as an adaptation in pelagic seabirds, in that it frees the adults both to replace energy reserves used during incubation and to forage for the chicks as soon as possible after hatching. In burrowing petrels it is reportedly facilitated by the chicks' thick down and a favourable burrow microclimate. This hypothesis was investigated by analysing cooling rates of dead chicks at wind speeds of 0,0 m s⁻¹ and 7,5 m s⁻¹, which simulated conditions within and outside burrows. Chicks exposed to windspeeds of 7,5 m s⁻¹ lost heat at a rate 2,5 times greater than those not exposed to wind. However, this increase was substantially less than predicted for 'model' chicks and this difference is attributed to the efficiency of the chicks' down.

Die ontwikkeling van homeotermie is in kuikens van vyf soorte sub-Antarktiese grawende stormvoëls bestudeer. Kuikens van witkenstormvoëls en bloustormvoëls kon binne een dag na uitbroei liggaamstemperatuur van 37° tot 40°C handhaaf by omringende temperatuur van 5° – 30°C. Kuikens van pediunkers, langvlerkstormvoëls en mediumbekwalvisvoëls het homeotermie binne vyf dae na uitbroei bereik, maar sommige individue se homeotermie was alreeds goed ontwikkel binne 24 h nadat hulle uitgebroei het. Kuikens het 'n hoë kapasiteit vir hitteproduksie getoon en die hoogste koue-geïnduseerde suurstofverbruik was tussen 2,57 ml O₂ g⁻¹ h⁻¹ in witkenstormvoëlkuikens tot by 4,94 ml O₂ g⁻¹ h⁻¹ in die kleiner bloustormvoëlkuikens. Die vinnige ontwikkeling van homeotermie in grawende stormvoëlkuikens word as 'n aanpassing in pelagiese seevoëls beskou om die ouers vry te stel om energiereserwes wat gedurende broei gebruik is te herstel en dit laat hulle ook toe om so gou moontlik na uitbroei kos vir hulle kuikens te soek. In grawende stormvoëls word dit na bewering moontlik gemaak deur die kuiken se digte dons en die gunstige mikroklimaat binne die nes. Hierdie bewering is ondersoek deur die afkoelingstempo's van dooie kuikens by windsnelhede van 0,0 en 7,5 m s⁻¹, wat toestande binne en buite die nes simuleer, te analiseer. Kuikens wat aan 'n windsnelheid van 7,5 m s⁻¹ blootgestel was het hitte 2,5 maal so gou verloor as kuikens wat nie aan wind blootgestel was nie. Hierdie toename in hitteverlies was nogtans aansienlik minder as wat vir 'model'-kuikens voorspel is en die verskil is aan die doeltreffendheid van die dons toegeskryf.

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The development of homeothermy in birds is related to the length of the nestling period and growth rate, with homeothermy developing more rapidly in precocial than in altricial species (Ricklefs 1968; Dunn 1975). Procellariiform seabirds (albatrosses and petrels) rear only single chicks which are characterized by slow growth rates and long nestling periods but they hatch with a thick covering of down. Consequently, they are regarded as being semi-altricial or semi-precocial (Nice 1962). They are frequently left unattended by their parents soon after hatching, and have been shown to attain homeothermy more rapidly than other altricial species with similar growth rates (Wheelwright & Boersma 1979; Bech, Brent, Pedersen, Rasmussen & Johansen 1982). Although it is now well established that petrel chicks are able to maintain high body temperatures at low ambient temperatures soon after hatching (Farner & Serventy 1959; Mougin 1969, 1970a; Wheelwright & Boersma 1979), the metabolic responses of petrel chicks to cold stress are less well reported

(Ricklefs, White & Cullen 1980; Bech *et al.* 1982; Ricklefs & Roby 1983). The few relevant studies all indicate that petrel chicks have a high capacity for heat production from an early age.

In this paper we report on the development of homeothermy in chicks of five species of sub-Antarctic burrowing petrels: white-chinned petrels *Procellaria aequinoctialis*, grey petrels *P. cinerea*, great-winged petrels *Pterodroma macroptera*, Salvin's prions *Pachyptila vittata salvini* and blue petrels *Halobaena caerulea*. In addition, we attempted to quantify the effect of chick down and burrow microclimate on the thermoregulatory ability of the chicks. Grey petrels and great-winged petrels are winter breeders, with hatching at Marion Island beginning in mid-May and early July respectively. Blue petrels, Salvin's prions and white-chinned petrels are summer breeders, and hatching at Marion Island starts at the beginning of December, the beginning of January and in early January respectively.

Materials and methods

The study was carried out at Marion Island (46°52'S, 37°51'E). Burrows containing eggs were checked daily until hatching was completed. Chicks aged 1, 3, 5, and 7 days (day of hatching equals day 0) were collected from their burrows, taken to the laboratory (a trip of 35 min for Blue petrels but usually less than 10 min for the other species) and placed on a layer of cotton wool in a 5 l, airtight, translucent, metabolic chamber. Their oxygen consumption was measured using an open flow-through system coupled to a Taylor Servomex OA 570 paramagnetic oxygen analyser. Air from outside the laboratory was dried and passed through a regulating flowmeter and a Rotameter flowmeter before entering the chamber. Air exiting the chamber was passed through a Carbosorb/silica gel tube to remove water vapour and CO₂ before entering the analyser. Flow rates were set to produce a drop in oxygen content of 1–2% below that of ambient air, and ranged from 85 to 550 ml min⁻¹ depending on the age and size of the chicks. Ambient air was assumed to have an oxygen content of 20,94% and calibration of the oxygen analyser was checked at regular intervals during the experiment.

Chamber temperature was maintained by placing the chamber in a water bath connected to a refrigerated circulating bath, and oxygen consumption was measured between 5°C (the lower temperature limit of the apparatus) and 30°C in younger chicks (less than 7 days) and between 5°C and 25°C in older chicks. Chamber temperature was measured by inserting a thermocouple into the chamber through a rubber bung, and chick body temperature was measured by inserting a thermocouple 30–70 mm (depending on the size of the chick) into the proventriculus and taping it to the lower bill. Temperatures were measured with an accuracy of 0,1°C on a Model BAT-12 digital telethermometer (Bailey Instruments Inc.).

A period of at least 60 min was allowed for a chick to settle and the chamber air to equilibrate before commencing an experiment. Thereafter readings of flow rate, chamber and body temperature, and percentage oxygen in the effluent air were taken at 5-min intervals over a period of 30 min at each temperature. A period of 30 min was allowed for chamber air to equilibrate after each temperature change. The chicks were returned to their burrows at the end of an experiment.

Oxygen consumption was calculated using the equation of Hill (1972) for dry, CO₂-free air and was corrected to standard temperature and pressure of dry air.

Body temperatures of white-chinned, great-winged and blue petrel chicks were recorded in the field for comparison with measurements made in the laboratory. Chicks were removed from their burrows and body temperature measured by inserting a thermocouple several centimetres into the proventriculus. Body temperatures were read within 1 min of removing the chicks from their burrows. Burrow temperatures were measured by placing a thermocouple in the burrow nest chamber about 10 cm from the chick.

To attempt to quantify the effects of the down and burrow microclimate on the thermoregulatory abilities of the chicks, cooling curve analyses were carried out on dead white-chinned, great-winged and blue petrel chicks between one and three days old. The chicks were heated to about 40°C in an oven and then placed in a wind tunnel. The rate of heat loss (measured with a thermocouple placed several centimetres into the proventriculus) was then measured at wind speeds of 0,0 m s⁻¹ (to simulate a chick in the burrow) and 7,5 m s⁻¹ (the average monthly wind speed at Marion Island; Schulze, 1971). A cooling curve analysis was performed and the total resistances to forced and free convection were calculated from the resulting time constants. Measured values were compared with predicted values for 'model' chicks. These were assumed to be spheres with the density of water and weighing the same as the live chicks. Total resistances to heat loss by free convection at a wind speed of 0,0 m s⁻¹ were calculated from standard heat transfer equations and compared to the calculated total resistances to heat loss by forced convection at a wind speed of 7,5 m s⁻¹.

Results

Burrow and body temperatures

Burrow temperatures measured ranged from 2,1–12,8°C and were generally 1,0–2,5°C above ambient temperature (Table 1). The coolest burrows were those of the winter-breeding grey and great-winged petrels.

White-chinned and blue petrel chicks were able to maintain almost constant body temperatures ($\pm 0,3$ and $0,1^\circ\text{C}$ standard deviation, respectively) between 5 and 25°C within one day of hatching (Figure 1, Table 2). On average, Salvin's prion, great-winged and grey petrel chicks only attained homeothermy at 5°C between 3 and 5 days of age (Figure 1, Table 2). Body temperatures prior to this were erratic ($\pm 0,6$, $1,2$ and $0,8^\circ\text{C}$ standard deviations, respectively). Individual grey petrel chicks, in particular, exhibited different body temperature responses. For example, a one-day-old, 90 g grey petrel chick increased its body temperature from 32,7 to 39,1°C between ambient temperatures of 5 and 30°C,

Table 1 Mean burrow temperatures (± 1 standard deviation) of burrowing petrels at Marion Island (figures in parentheses are the number of burrows measured)

Species	Ambient temperature (°C)	Burrow temperature (°C)
White-chinned petrel	8,0	9,0 \pm 1,2 (6)
	8,6	11,5 \pm 1,1 (6)
Great-winged petrel	-0,1	2,1 (1)
Grey petrel	3,3	4,9 (1)
	3,8	6,4 \pm 1,3 (5)
Blue petrel	10,5	12,8 \pm 2,6 (8)

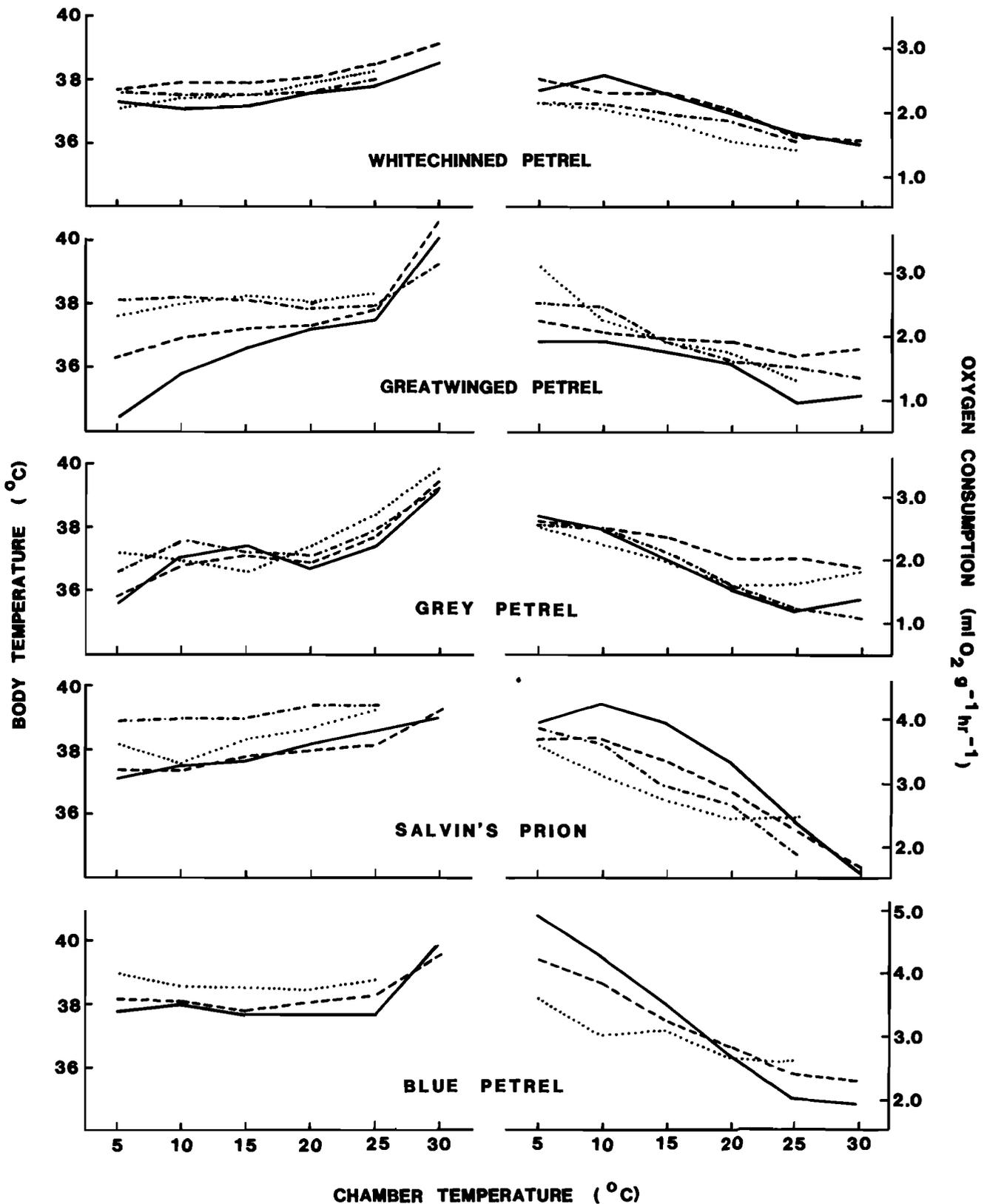


Figure 1 Mean body temperatures and rates of oxygen consumption of five species of burrowing petrel chicks in relation to chamber temperature. — = 1 day old, -- = 3 days old, - . - . = 5 days old, = 7 days old. Mean masses of chicks used in the experiments and sample sizes are provided in Table 2.

whereas a 108 g chick was essentially homeothermic at the same age and could maintain its body temperature above 38,0°C over the same temperature range. Similar differences in body temperature response were evident

in individual great-winged petrel and Salvin's prion chicks but were not as marked as in the grey petrels. All species had individuals which exhibited well-developed homeothermy within one day of hatching and all chicks

Table 2 Mean mass ($g \pm 1$ standard deviation) of chicks in each age class used in the experiments (figures in parentheses are sample size and asterisks denote a significant positive relationship ($P < 0,05$) between ambient and body temperatures over the temperature range 0–25°C)

Species	Age (days)			
	1	3	5	7
White-chinned petrel	114 \pm 16 (4)	169 \pm 33 (4)	242 \pm 45 (4)	296 \pm 34 (4)
Great-winged petrel	87 \pm 10 (3)*	88 \pm 13 (3)*	90 (2)	130 (2)
Grey petrel	99 (2)	155 (2)*	180 (2)	204 \pm 44 (3)
Salvin's prion	32 \pm 7 (4)*	40 \pm 8 (4)*	58 \pm 5 (4)	72 \pm 6 (4)*
Blue petrel	35 \pm 4 (4)	43 \pm 10 (4)	----	99 (2)

measured were able to maintain body temperatures above 30°C from one day of age. The lowest body temperature recorded was 31,0°C for a one-day-old great-winged petrel chick weighing 95 g. Great-winged, grey and blue petrel chicks showed marked increases in body temperature between 25 and 30°C, suggesting that they were thermally stressed at temperatures greater than about 25°C. This increase in body temperature was not as marked in white-chinned petrel and Salvin's prion chicks.

Body temperatures of known age white-chinned, great-winged and blue petrel chicks, measured in the field (Table 3) at typical burrow temperatures (see Table 1), were similar to those measured for homeothermic chicks in the laboratory and there was no consistent increase in body temperature with age in any of these species.

Oxygen consumption and thermal conductance

Oxygen consumption of burrowing petrel chicks of all five species investigated increased with decreasing temperature at all ages measured (Figure 1), suggesting that they have the capacity to regulate body temperature to some extent from at least one day of hatching. Mass-specific oxygen consumption was lower in the larger white-chinned, great-winged and grey petrel chicks than in the smaller blue petrel and Salvin's prion chicks. Oxygen consumption of one-day-old white-chinned petrel chicks increased between 25 and 5°C by 1,4 times from 1,65 to 2,37 ml O₂ g⁻¹ h⁻¹. Oxygen consumption of greatwinged and grey petrel chicks doubled between 25 and 5°C from 0,97 to 1,9 and from 1,35 to 2,69 ml O₂ g⁻¹ h⁻¹ respectively. Oxygen consumption of blue petrel

Table 3 Mean (± 1 standard deviation) and range of body temperatures measured for three species of burrowing petrel chicks within one minute of removal from their burrows at Marion Island (figures in parentheses are sample sizes)

Age (days)	White-chinned petrel	Great-winged petrel	Blue petrel
1 – 5	37,5	37,8 \pm 0,4 37,2 – 38,4 (8)	38,0 \pm 0,6 37,3 – 38,4 (3)
6 – 10	37,9	37,7 \pm 1,0 36,6 – 38,8 (8)	37,6 \pm 0,4 37,3 – 38,0 (3)
11 – 15	37,9 \pm 0,3 37,8 – 38,2 (5)	37,5 \pm 1,1 36,2 – 38,3 (3)	---
16 – 20	38,0 37,7, 38,2 (2)	37,7 \pm 0,4 37,3 – 38,4 (7)	---
21 – 25	38,1 \pm 0,2 37,9 – 38,3 (3)	---	39,0 \pm 0,5 38,3 – 39,6 (6)
>25	37,7 \pm 0,5 37,0 – 38,2 (5)	---	---
Overall	37,9 \pm 0,4 37,0 – 38,3 (17)	37,9 \pm 0,5 36,2 – 38,8 (26)	38,4 \pm 0,8 37,3 – 39,6 (12)

chicks rose from 2,00 to 4,94 ml O₂ g⁻¹ h⁻¹ between 25 and 5°C, a 2,5 times increase and that of Salvin's prion chicks increased from 2,38 to 3,93 ml O₂ g⁻¹ h⁻¹, a 1,7 times increase.

With the exception of Salvin's prion chicks, rate of oxygen consumption of burrowing petrel chicks was reduced or oxygen consumption actually increased between 25 and 30°C, consistent with the evidence from body temperatures that the chicks were thermally stressed above 25°C. Maximum cold-induced oxygen consumptions measured were 2,57, 3,09 and 2,69 ml O₂ g⁻¹ h⁻¹ in white-chinned, great-winged and grey petrels respectively. The smaller Salvin's prion and blue petrel chicks had peak levels of 4,24 and 4,94 ml O₂ g⁻¹ h⁻¹ respectively.

Thermal conductances of burrowing petrel chicks, calculated from the equation presented by Ricklefs and Roby (1983), were relatively high in the smaller Salvin's prion and blue petrel chicks (Figure 2), ranging from 0,11 to 0,16 ml O₂ g⁻¹ h⁻¹ °C⁻¹ (2,13 – 3,03 J g⁻¹ h⁻¹ °C⁻¹). Conductances in the larger white-chinned, great-winged and grey petrels ranged from 0,06 to 0,09 ml

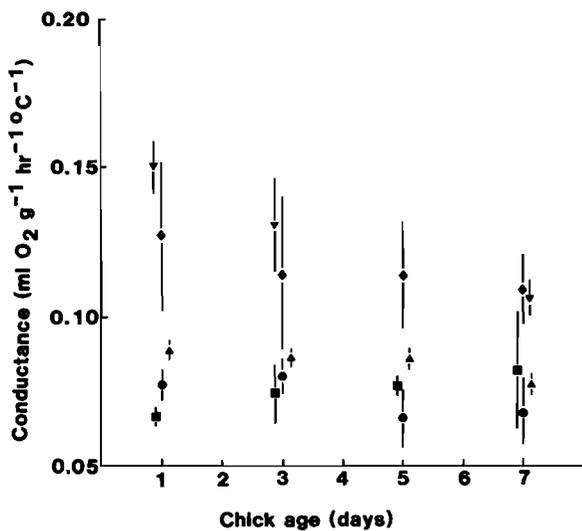


Figure 2 Thermal conductances of burrowing petrel chicks at 5°C in relation to age. Points are means \pm standard deviation. White-chinned petrel (●), greatwinged petrel (■), grey petrel (▲), Salvin's prion (◆) and blue petrel (▼).

$\text{O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ($1,33 - 1,79 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$). In general, conductance decreased with age (Figure 2) with the exception of the greatwinged petrel chicks which showed a slight, but not significant increase in thermal conductance between 1 and 7 days ($t = 1,24; P > 0,2$).

Measured ratios of the resistance to heat loss by forced convection ($7,5 \text{ m s}^{-1}$ wind speed), to resistance to heat loss by free convection ($0,0 \text{ m s}^{-1}$ wind speed) were 2,48 for white-chinned and great-winged petrel chicks and 2,23 for blue petrel chicks. The predicted ratios were 12,9, 14,0 and 15,0 for white-chinned, great-winged and blue petrel chicks respectively.

Discussion

Burrow and body temperatures

Burrow temperatures of white-chinned petrels, blue petrels and Salvin's prions at the Crozet Islands (47°C) ranged from $5,3 - 11,9^\circ\text{C}$ (Mougin 1975) and those of diving petrels *Pelecanoides* spp. at South Georgia (54°S) were between 5 and 10°C (Ricklefs & Roby 1983), all similar to those measured at Marion Island. Even temperatures in the burrows of Wilson's stormpetrels *Oceanites oceanicus* at the Argentine Islands (65°S) are remarkably constant, seldom dropping below 0°C during the chick-rearing period (Roberts 1940). It appears that burrowing petrel chicks in the sub-Antarctic, with the occasional exception of grey and great-winged petrel chicks, are seldom exposed to temperatures below 5°C .

Individual chicks of all species measured had the ability to maintain relatively constant body temperatures from one day after hatching. On average, however, whitechinned and blue petrels had a more precocial development of homeothermy than did Salvin's prion and grey and great-winged petrel chicks. The development of homeothermy in the Antarctic prion *Pachyptila desolata* is more rapid than that observed for

the closely related Salvin's prion in the present study. Antarctic prion chicks could maintain a constant body temperature from hatching of about 35°C at an ambient temperature of 5°C (Ricklefs & Roby 1983). The diving petrels *Pelecanoides georgicus* and *P. urinatrix*, however, only attained homeothermy at 5–6 days and 9 days respectively (Ricklefs & Roby 1983). Chicks of the Manx shearwater *Puffinus puffinus* are able to maintain body temperatures between 36 and 30°C from 3–5 days but homeothermy is only fully developed at 12 days (Bech *et al.* 1982). Early development of homeothermy in burrowing petrel chicks is similar to that of other semi-precocial seabirds such as the puffins and auks (Alcidae) (see Barrett 1984 and references therein).

Despite their ability to regulate body temperature from an early age, whitechinned and great-winged petrel chicks had body temperatures significantly lower than those measured for adults (Table 4), even after 20 days of age ($P < 0,001$). Body temperatures of adult great-winged petrels were, however, measured at night, when they are generally higher than during daylight hours (pers. obs). Grey petrel chick body temperatures were not significantly different from those of incubating adults ($P > 0,2$), but body temperatures during incubation may be lower than at other times (see Warham 1971). Blue petrel and Salvin's prion chicks attained adult body temperatures at 3 and 5 days of age respectively.

Oxygen consumption and thermal conductance

Burrowing petrel chicks were able to maintain high body temperatures by metabolic adjustments soon after hatching and could increase their heat production by as much as 2,5 times in response to a decreasing temperature gradient, Bech *et al.* (1982) measured a 2,7 fold increase in metabolic rates in small Manx shearwater chicks. Maximum cold-induced metabolic rates measured ($2,57 - 4,94 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) are similar to those measured for Manx shearwaters (Bech *et al.* 1982), South Georgian and common divingpetrels and Antarctic prions (Ricklefs & Roby 1983).

Thermal conductances of chicks were also similar to

Table 4 Mean body temperatures (± 1 standard deviation) of adult burrowing petrels at Marion Island

Species	Body temperature	
	($^\circ\text{C}$)	N
White-chinned petrel	$39,1 \pm 0,7$	9 Day-time, resting
Great-winged petrel	$40,8 \pm 0,6$	9 Night-time after flight
Grey petrel	$37,5 \pm 0,5$ 38,1	5 Incubating 2*
Blue petrel	$38,4 \pm 0,6$	23 Day-time, resting
Salvin's prion	$38,9 \pm 0,5$	22 Day-time, resting

*From Warham (1971)

those previously measured; in particular, thermal conductances of Salvin's prion chicks were very close to those measured for Antarctic prions (Ricklefs & Roby 1983).

The development of homeothermy has previously been found to correlate with the length of the brooding period (Ricklefs *et al.* 1980; Bech *et al.* 1982; Ricklefs & Roby 1983). Blue petrel chicks are brooded for 1 – 3 days (pers. obs) and white-chinned petrel chicks for 1 – 2 days (Mougin 1970a), although adult white-chinned petrels may be present in the burrow with the chick for up to 7 days (pers. obs). Jouventin, Mougin, Stahl & Weimerskirch (1985) report that grey petrel adults remain with the chicks in the burrow for 1 – 3 days although the chicks are only brooded for a few hours. Greatwinged petrel chicks are brooded for 2 – 3 days (Warham 1956) and prions for an average of 3 – 4 days with a normal range of 1 – 5 days (Tickell 1962; Ricklefs & Roby 1983). On average, all the species in the present study were capable of maintaining constant body temperatures by the time brooding normally ceases, although the body temperature control of some individuals was still erratic.

Erratic control of body temperatures in individual chicks of the same age has been reported for several petrel species. Farner & Serventy (1959) noted that individual slender-billed shearwater *Puffinus tenuirostris* chicks had their own characteristic body temperatures, and Ricklefs *et al.* (1980) noted erratic control of body temperature in Leach's stormpetrel *Oceanodroma leucorhoa* chicks in the first week after hatching. Wheelwright & Boersma (1979) found that body temperatures in homeothermic forktailed stormpetrel *O. furcata* chicks were independent of age but correlated with the amount of food that the chicks had been fed the previous night. Similarly, Simons & Whittow (1984) reported that changing food reserves in dark-rumped petrels *Pterodroma phaeopygia sandwichensis* resulted in body temperature fluctuations of several degrees, whereas well fed chicks maintained near adult body temperatures. Chicks which remain unfed for long periods may enter a state of partial torpor and their body temperatures may drop markedly, but they recover rapidly when warmed and fed by the adults (Ricklefs *et al.* 1980; Bech *et al.* 1982; Simons & Whittow, 1984; Boersma 1986). Clearly, feeding has an important consequence for thermoregulation and is of particular importance in the chicks of these highly pelagic seabirds where food availability and adverse conditions may affect food delivery rates to the chicks. Although the relative nutritional statuses of the chicks in the present study were not known, their effects may well have accounted for some of the variation in body temperatures and temperature responses observed.

The early development of homeothermy in burrowing petrel chicks has been regarded as an adaptation in species which feed at great distances from their breeding grounds, in that it frees the adults both to replace energy reserves used during incubation and to forage for the chicks as soon as possible after hatching (Ricklefs 1979; Wheelwright & Boersma 1979). However, the

maintenance of a high body temperature by metabolic adjustment is energetically expensive to the chicks. In contrast to petrels, puffin chicks do not utilize their full metabolic scope to maintain a high body temperature, but rather allow their body temperatures to fall to a lower level (Bech, Aarvik & Vongraven 1987). Such behaviour is energy conserving, but is only advantageous if chicks are subsequently passively rewarmed by their parents and do not have to expend energy rewarmed themselves. Presumably, it is energetically less costly for petrel chicks to maintain a high body temperature when they have the energy reserves to do so (see above), especially as energy expended for thermoregulation may be balanced by that saved as a result of their inactivity in the burrow.

In addition to their capacity for heat production, the ability of burrowing petrel chicks to thermoregulate from an early age has been attributed to their thick down (Bech *et al.* 1982) and is reportedly facilitated by the favourable microclimate within the burrow (Mougin 1969, 1970a, 1975). Mougin (1970a) reports that a 1- to 2-day old white-chinned petrel chick, able to maintain a constant body temperature of 37,2°C within the burrow, showed a rapid drop in body temperature when removed and exposed to low ambient temperatures, and that its body temperature increased when ambient temperature and insolation were high. Similar changes in body temperatures of Kerguelen petrel *Lugensa* (= *Pterodroma*) *brevirostris* chicks were observed when they were removed from their burrows under similar conditions (Mougin 1969).

Measured ratios of resistance to heat loss by forced and free convection suggest that chicks lose heat about 2,5 times faster when exposed to wind speeds of 7,5 m s⁻¹ than they would in a burrow where wind speed is negligible. Under the same conditions, the predicted ratios from the 'model' chicks suggest a 12,9, 14,0 and 15,0 times increase in heat loss for white-chinned, great-winged and blue petrel chicks respectively. This is about five times greater than measured for the dead chicks, and is an indication of the effectiveness of the chicks' down. Nevertheless, a 2,5-fold increase in heat loss would necessitate a similar increase in heat production if chicks were still to maintain a constant body temperature when exposed to average wind speeds outside the burrow. This figure is conservative since it considers only heat loss across the body surface and does not include heat lost through respiration.

Many petrel species, probably constrained either by body size or availability of sites suitable for burrowing, nest in crevices or on the surface. Despite the generally more favourable surface area to volume ratios of the larger surface-nesting species, the development of homeothermy in their chicks, and in the crevice-nesting species, is relatively slow. The chicks of crevice-nesting snow petrels *Pagodroma nivea* attain homeothermy at about eight days of age and those of crevice-nesting Cape petrels *Daption capense* at 12 days of age (Mougin 1968). Chicks of the surface-nesting southern giant petrels *Macronectes giganteus* and the sooty albatrosses *Phoebetria palpebrata* and *P. fusca* do not exhibit well-

developed homeothermy until about 17 days of age (Mougin 1968, 1970b) and homeothermy in the surface-nesting wandering albatross *Diomedea exulans* is complete only at about 30 days of age (Mougin 1970c).

It is evident that the burrow-nesting behaviour of burrowing petrels allows early thermoregulatory independence in chicks at a relatively low metabolic cost compared to that which they would incur if they were exposed to the harsher conditions on the surface. The chicks themselves have efficient insulation and a high capacity for heat production which they are able to maintain provided they have the energy reserves to do so.

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