The food demand in the nest of Wilson's storm petrel

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ABSTRACT: Energy delivered to the nests of Wilson's storm petrel, *Oceanites oceanicus* (Kuhl, 1820), was evaluated by measurement of the oxygen consumption of brooding adult birds and nestlings of different ages. During the brooding period adult birds have to deliver more than 180 kJ per visit to the nest vs. less than 170 kJ during the rest of the nesting period. It seems likely that the parental ability to deliver large quantities of food per visit affects the duration of the brooding period and therefore also affects growth rates of Wilson's storm petrel chicks and the duration of their nesting period.

Key words: Antarctic, birds, Wilson's storm petrel.

Introduction

Ricklefs (1983) developed a model that calculates the energy requirements of reproduction (i.e. of the eggs, chicks, and adults at the nest site) and includes the ability of parents to transport energy from the feeding area to the breeding colony. The greatest energy requirement relative to the ability of parents to provide food occurs during the chick brooding period. During this time the energetic demands of the nestling are increasing with chick growth, while adult foraging is still constrained by the requirement of one parent to remain at the nest site. This consideration suggests that shorter brooding periods should occur in species that hatch larger chicks with higher energy requirements, and in smaller species.

The greater thermogenic capacity of precocial chicks is associated with slower growth. Many authors (Choi *et al.* 1993, Shea *et al.* 1995, Dietz and Ricklefs 1997, Ricklefs *et al.* 1998) have pointed out that there is a trade-off between tissue growth rate and their mature function (e.g. efficiency of muscle activity or thermoregulatory capacity). Shortness of the brooding period is possible when maturation of chick muscles, which are responsible for thermoregulatory heat production (Hohtola and Visser 1998), is rapid. On the other hand, growth of fully ma-

tured tissues is slower and chicks leave their nests later (Ricklefs *et al.* 1994). However, prolongation of the nesting period is difficult or impossible in environments where summer season is short. The trade-off between early thermoregulation and a short nesting period is especially important in Antarctic birds, which spend much energy for thermoregulation and require that their chicks should leave their nest as early as possible, before frosts and snowstorms.

Chicks of Wilson's storm petrel (*Oceanites oceanicus*), the smallest Antarctic bird, are already homeothermic on the 5th day after hatching (Gębczyński 1995). Moreover, their hatchlings weigh 7 g, i.e. about 20% of adult body mass and stay in the nest about 60 day after 45-day incubation of eggs. Late summer snowstorms strongly increase chick mortality in the nest, thus natural selection should prefer a higher growth rate of nestlings and earlier departure. There remains the question: why do the chicks not leave their nest earlier? One of constraints may be the necessity of early homeothermia. But why can't the parents brood their chicks longer? I wanted to test the hypothesis that parental ability to deliver food to the nest can affect the length of brooding and nesting period in Wilson's storm petrel. I wanted to estimate amount of food which should be delivered to the nest by an adult during one visit in different periods of the breeding season.

Material and methods

In the summer of 1990/1991 thirty eight nests (colony located near Polish Antarctic Station, King George Island, South Shetlands) with chicks younger than 5 days were observed continuously for 24 hours (6 days, 5–8 nests daily, 1 day of observation every 4 days) in order to obtain feeding rates. Feeding rate data are reported as means ± standard error.

I measured body temperatures (Tb) and resting metabolic rate (RMR) of chicks and adults of Wilson's storm petrels. Body temperature was measured in the esophagus using a thermistore thermometer. Resting metabolic rates were measured in a closed system, constant pressure respirometer (Górecki 1975). Measurements of 1–4 day-old chicks' (n = 9) RMR were performed at 30°C – the temperature at which nestlings' Tb were as high as in the nest during brooding. The resting metabolic rate of homeothermic chicks was measured when the chick energy demand was highest (35–50 days after hatching, Obst and Nagy 1993). I measured RMR of chicks (n = 26) and parents (n = 24) at 0–3°C, the temperature corresponding to ambient temperature in nests.

Adult birds deliver energy to the nest as food in their stomachs. Their stomachs contain both fresh food and partly digested fraction – stomach oil (Wasilewski 1986, Croxall and North 1988, Croxall *et al.* 1988, Quillefeldt 2002). I assumed that all energy used at the nest derived solely from parental stomach oil. This assumption may underestimate differences in food demand in the nest between dif-

ferent periods of the nesting season (because of differences in assimilation rates of stomach oil and fresh food), but it does not change my general conclusions. I used an assimilation ratio of the stomach oil of 0.9 (Obst and Nagy 1993). I did not include changes in energy contents in the lean dry mass of chicks. During the first five days of chick life and during the second part of nesting period chick lean dry mass did not increase significantly (Obst and Nagy 1993). I calculated energy needed in the nest using following equation:

Energy needed in the nest (kJ per visit) = (chick RMR + chick deposition of fat + adult RMR) $*$ (assimilation ratio)$^{-1}$ $*$ (feeding rate)$^{-1}$.

In this article the energy demand in nests is reported as a range of minimum and maximum values.

Results

I estimated energy requirements in the Wilson's storm petrel nests, i.e. metabolic rate of chicks, energy deposited as their fat, and the metabolism of brooding adult. Costs of deposition of fat and growth were included in the metabolic rate of chicks. The feeding rate during the brooding period equaled 0.78 ± 0.31 day^{-1}. It increased up to 1.12 ± 0.23 day^{-1} during the highest growth rate period and next decreased to 0.83 ± 0.42 day^{-1}.

If the parents feed ectothermic chicks at a rate of 0.78 day^{-1}, then they should deliver 201 kJ (range 181–223 kJ) of food to the nest per one visit (Table 1). During the feeding of homeothermic chicks, when chick fat deposition is maximum, food demand in the nest significantly decreases to 150 kJ visit^{-1} (range 138–168 kJ visit^{-1}, ANOVA, P < 0,001, Tukey post-hoc test) and next to 94 kJ visit^{-1}, just before fledging (range 38–143 kJ visit^{-1}, ANOVA, P < 0,001, Tukey post-hoc test).

Table 1

Chick and adult energy requirements at the nest during breeding period (for high variations of data I present their ranges).

	Chick requirement (kJ day^{-1})		Adult RMR at the nest (kJ day^{-1})	Feeding rate (feeding day^{-1})[b]	Requirement at the nest	
	RMR	deposition of fat[a]			(kJ day^{-1})	(kJ visit^{-1})
Brooding period	13	21–42	93–102	0.78	141–174	181–223
Maximum fat accumulation	103	34–63	0	1.1	152–184	138–168
Just before fledging	103	–76[c]–0	0	0.8	30–114	38–143

[a] Obst and Nagy 1993, Gębczyński and Jadwiszczak 2000
[b] Beck and Brown 1972, Obst and Nagy 1993, this work
[c] decreasing of fat reserve

Discussion

With respect to temperature regulation, chicks of Wilson's storm petrel develop precocially. They are homeothermic on the 5th day after hatching (Gębczyński 1995). Water content in their muscles significantly decreases at that time (Jadwiszczak pers. comm.). This suggests a fast rate of muscle maturation, which is necessary in order to obtain the high thermogenic capacity needed in early homeothermia. Chick ability to produce heat metabolically is consistent with slower growth and a longer nesting period (Beck and Brown 1972, Wasilewski 1986, Gębczyński and Jadwiszczak 2000). The long breeding season in Wilson's storm petrel lasts through late April-early May. At that time ambient temperatures in nests fall below 0°C and snow covers the breeding colony (Gębczyński 1995). High chick mortality (Beck and Brown 1972) may increase with each day of the nesting period. Thus, earlier fledging (faster growth) should be adaptive. Fast growth is possible when chick tissues would not be fully matured (Ricklefs *et al.* 1998), but then their thermogenic capacity would be low and nestlings, especially living in low ambient temperatures, should be brooded.

The Ricklefs' (1983) model of energy requirement, supported with my calculations (Table 1), suggests that the maximum demands upon parents occur during the brooding period. At this time, the parent must support not only itself but also the increasing energy requirements of the chick. If at any time during the nesting cycle parents must tolerate a negative energy balance, it is during the brooding period. Parental ability to deliver large quantities of food per visit might be a factor shortening the rate of thermoregulation development in the youngest chicks. Quillfeldt and Peter (2000) found that the meal size delivered to the Wilson's storm petrel nest averaged 8.5 g per feed. Energy density of typical chick feed is 16.1 kJ g^{-1} (Obst and Nagy 1993), or about 137 kJ per averaged feed. Food demand in the Wilson's storm petrel nest exceeds 180 kJ per feed during the brooding period. Thus, neither parent delivers as much food as needed in the nest at that time.

Feeding frequencies found in my studies correspond to the data reported by other authors for the same parts of the nesting period. Beck and Brown (1972) and Obst and Nagy (1993) found feeding frequency in Wilson's storm petrel on 1.1 day^{-1} (1–5 day after hatching) and 0.8 day^{-1} (35–50 day of life). During first five days after hatching a chick is brooded and only one parent feeds it. However, adult birds can leave the nest just after feeding, before the second parent returns. This behaviour enables the bird to reduce the food demand in the nest, but it also reduces growth rate of nestling. In ambient temperatures of 0–5°C the body temperatures of ectothermic chicks and their metabolism quickly decrease (Gębczyński 1995).

In summary, it seems likely that the parental ability to deliver food to the nest per visit, and in consequence the duration of the brooding period, plays an important role in the growth rates of Wilson's storm petrel chicks and therefore the duration of their nesting period.

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