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Importance of fat reserves in Wilson's storm petrel chicks

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All petrels store large quantities of fat during nesting period. Several hypotheses have offered explanations for the exceptional accumulation of fat by petrels and that stored in smaller amounts by other birds. Fat reserves of Wilson's storm petrel chicks attain 80% of dry mass. Lipid index increases up to value of 2.0 during nesting period. The aim of our study was to explain the role of fat stores in the nestlings. Stable growth of chicks during first three weeks of life suggests that stochastic variation of chick food provisioning arises from unpredictable snow storms rather than fluctuating food availability at the sea. The lack of correlation between body mass and head, tarsal or wing length rejects hypotheses that chicks accumulate lipid in order to increase their rate of intake of a limiting nutrients. Accumulation of excessive lipid reserves may be a consequence of overfeeding of the chicks by their parents. This strategy protects offspring from death during periods of starvation, when nest entrances are covered by snow.

1. Introduction

Unlike most other birds, all petrels store large quantities of fat during nestling period (Warham 1990). For example, by the time nestlings of Wilson's storm-petrel (*Oceanites oceanicus*) have reached their peak mass, they have accumulated 2–3 time as much lipid as lipid free dry mass. Much of the fat is metabolized prior to fledging and mass drops to a level at which the fully developed chick can fly (Obst & Nagy 1993).

Several hypotheses have offered explanations for the exceptional accumulation of fat by petrels and that stored in smaller amounts by other birds:

1. Since Lack's studies (1968) it is widely believed that many seabirds species exploit highly variable and unpredictable food resources, unevenly distributed at sea and of fluctuating availability. Lack (1968) suggested that fat deposits provide insurance against periods of poor feeding conditions, during which time delivery of meals to the chick might decrease or stop altogether.
2. In contrast, Ricklefs (1976) suggested that fat depots in many seabirds' chicks are not primarily adaptation to prolonged and unpredicted fast, and that they may be a by-product of utilization of fat-rich but nutrient-poor food (Ricklefs 1979).
3. Chicks may accumulate fat early in the growth period, when energy requirement is low, to subsidize increased demands later in the growth period (Ricklefs & Schew 1994).
4. Accumulation of excessive lipid reserves is a consequence of the tendency of parents to overfeed their offspring, on average, to reduce the probability of poor nutrition resulting from stochastic variation in food provisioning (Ricklefs & Schew 1994).

Wilson's storm petrel is the smallest (39 g) Antarctic bird laying a single egg. The growth rate of Wilson's storm-petrel nestling is one of the fastest in Procellariforms (Warham 1990). Breeding period (from laying to fledging) lasts 3.5 months. Chicks are already homeothermic on 5th day of life, when metabolic rate and body temperature of non brooded nestling does not change. Last chicks leave their nests at the end of April or at the beginning of May, when air temperatures in the nests are very low and the breeding colony is covered by snow (Gębczyński 1995). Thus it could be predicted that Wilson's storm petrel chicks have to rely very often on their fat reserves. The aim of our study was to explain the role of fat stores in the nestlings.

2. Material and methods

2.1. Animal and body measurements

Growth of Wilson's storm petrel (*Oceanites oceanicus*) chicks was studied at the breeding colony located near Polish Antarctic Station "Arctowski" (62°10′S, 58°28′W), King George Island (South Shetlands), in summer 1990/91, during 15th Polish Antarctic Expedition of Polish Academy of Sciences. Nests with chicks (n = 86) were marked individually. All nests were inspected daily (between 9.00 and 14.00) up to the end of the second week of chick's life, and later, every 2–3 days. Hatchlings found for the first time were assigned the age of day 1. Nestlings were weighed with Pesola spring scales (± 0.5 g), and length of their heads (from the tip of a bill to the projection of occipital bone), tarsus, and wings were measured with accuracy 0.1 mm, 0.1 mm and 1 mm, respectively.

2.2. Carcass analysis

Chicks for carcass analysis were collected in summer 1994/1995 (during 19th Polish Antarctic Expedition of PAS) at the same colony in six age categories: on days 1 (n = 6), 7 (n = 6), 14 (n = 6), 35 (n = 7), 49 (n = 5) and 56 (n = 5) after hatching.

The chicks were sacrificed with ether and weighed to the nearest 0.1 g. Stomach contents were removed by dissection, weighed, and fresh weights of birds were corrected by subtracting the weight of food. Chicks were then dried to constant weight in an oven at 70°C (about 2–4 days); water content was calculated from the difference in body weight before and after drying.

The dried material was ground and homogenized in an electric mill. Aliquots of 3 to 4.5 g of this material were extracted in petroleum ether in Soxhlet extractors, re-dried, and the lipid content calculated from the weight lost during extraction. The mass of the remaining material was lean dry mass. The extractions were made in duplicate for each chick and additional extraction was taken when the first two values were not in agreement.

All dead chicks found were also collected and treated with the same procedure. Water index of those chicks was not considered.

We estimated the maximum interval that each chick could survive when using only its lipid stores as an energy source. We calculated the energy available in lipid stores of each chick using 38 kJ/g as the energy density of lipid (Ricklefs 1974, Taylor & Konarzewski 1989, Obst & Nagy 1993) and assuming that the part of extracted fat being equivalent to lipid index of 0.1 is not available as energy source. The fasting capability of each chick was calculated from its energy reserves, from metabolic rates of the Wilson's storm petrel chicks (Obst & Nagy 1993, Gębczyński 1995), and body masses of analysed chicks.

One of the values assumed in the calculation of fasting capability is the amount of fat not available for metabolic needs. Body composition analysis of adult birds starved to death showed in different species the presence of the petroleum ether-extractable material equal to 0.5–2 % of wet body weight which gives lipid indices (fat mass/lean dry mass) lower than 0.1 (Evans 1969, Chaplin 1974, Wishart 1979, Jenni & Jenni-Eiermann 1987). We do not know of any similar data on growing chicks. However, such a drastic emaciation resulting from starvation is perhaps not compatible with recovery, even if environmental conditions are improved before the death of the birds. It is unknown at what level of emaciation recovery would be possible. Therefore we used the fat mass equal to lipid index of 0.1, being the lower limit of variability of this index in nestlings in which both the level and variability of fat reserves

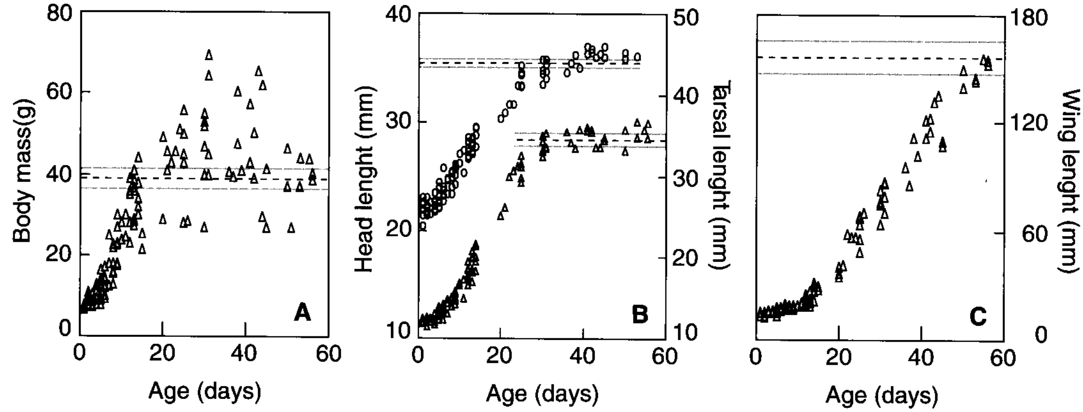

Fig. 1. Changes of body mass (A), head length (B, circles), tarsal length (B, triangles), and wing length (C) of Wilson's storm petrel chicks during nesting period. Broken lines and areas show average values of adult birds with standard error, respectively.

are high during development (Bryant & Gardiner 1979; Bryant & Hails 1983; Tatner 1984).

3. Results

3.1. Chick's growth

Chicks grew at the similar rate during first 10 days. Thereafter their body mass varied widely (Fig. 1A). Body mass of chicks declined to approach the value typical of adult birds just before fledging.

In contrast to the high variability of body mass, the lengths of tarsus, head (Fig. 1B), and wing (Fig. 1C) were similar in all chicks during the whole nesting period. The lengths of tarsus and head attained values characteristic for adult birds already in the middle (about of 30th day of life) of the nesting period. Wing length increased up to fledging. There were no correlation between body mass and lengths of tarsus ($r = -0.37$, $p = 0.11$), head ($r = 0.05$, $P = 0.84$) or wing ($r = 0.01$, $p = 0.96$) in 30 days old and older offspring.

3.2. Body composition

The changes of body composition with age can be considered in terms of three main components: water, lipid and lean dry fraction (the third being principally protein plus ash). The changes of these components throughout whole nest period can be followed in collected chicks.

Water index (water content/lean dry mass) was 4.95 in 1 day old nestlings, and declined to approach the value typical of adult birds just before fledging (Fig. 2).

The lipid index (fat content/lean dry mass) was 0.482 on the first day after hatching (Fig. 3). The index of homeothermic chicks increase and stabilize at the level approximately 1.5. On day 50 the index attained its maximum value of about 2.0. Decrease of lipid index prior to fledging (day 60th) was consistent with the lowering of body mass of chicks by 30 g (Fig. 1A, 3). The lipid index in found dead chicks was not lower than 0.1 (Fig. 3).

Lean dry mass increased from value 1.12 g at hatching up to about 35 day of life, and stabilized on value of about 9.5 g (Fig. 4).

Estimated fasting capability, i.e. the maximum time that the chick could be sustained by its reserves was on average 5.6 days.

4. Discussion

The changes of body mass of Wilson's storm petrel chicks during second half of nesting period mainly depend on variable fat stores accumulated in nestling bodies (Fig. 3) rather than on water content (Fig. 2). Chick lean dry body mass does not change with time (Fig. 4). Nestling body mass is affected mainly by feeding rate in that time.

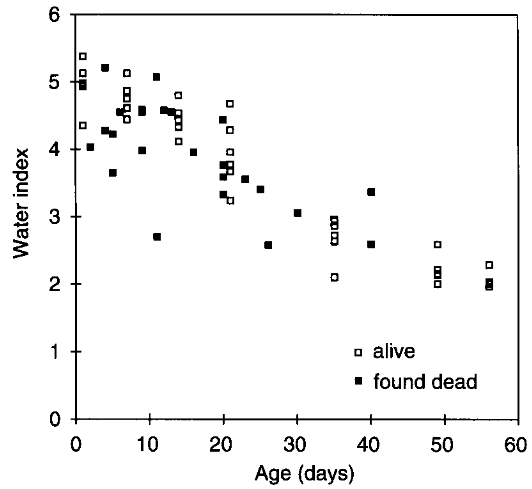

Fig. 2. Variation in water index (grams water/grams lean dry) as a function of age in Wilson's storm petrel in 1995.

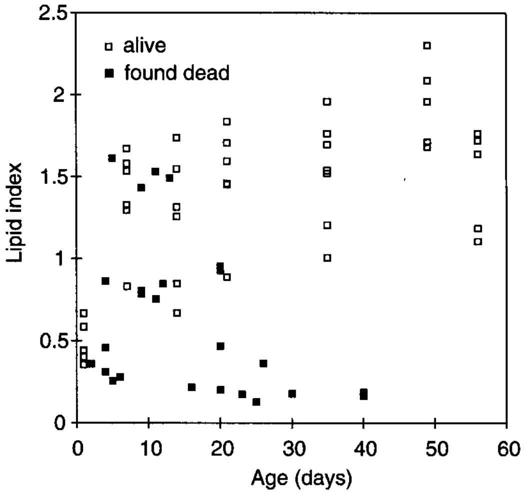

Fig. 3. Variation in lipid index (grams fat/grams lean dry) as a function of age in Wilson's storm petrel in 1995.

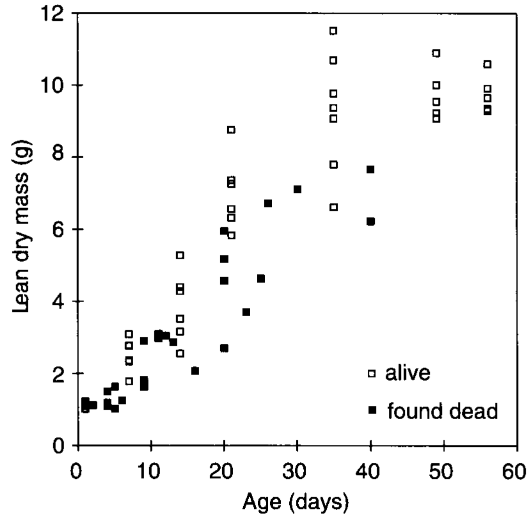

Fig. 4. Variation of lean dry mass (LDM) as a function of age in Wilson's storm petrel in 1995.

The stable lean dry mass and the lack of correlation between body mass and head, tarsal or wing length suggest that the diet of Wilson's storm petrel chicks, which consists primarily of planctonic crustaceans and stomach oil (Beck & Brown 1972, Warham 1977, Croxall et al. 1988, Obst & Nagy 1993), provides an excess of nutrients for skeleton and feathers growth. Accordingly, it seems possible that chicks do not accumulate lipid in order to increase their rate of intake of limiting nutrients. That conclusion is similar with results of Ricklefs et al. (1987) experiences with Leach's storm petrel.

If the main purpose of lipid reserves is to supply energy to the chick during food shortage, we need to compare fasting capability with which chicks receive meals. Obst and Nagy (1993) found the mean feeding rate equal to 1.1 feed per chick per 24 hours and that weather conditions play important role in Wilson's storm petrel chick foraging. Wasilewski (1986) reported few days periods of chick fasting after snow falls, when nests were covered by snow and adult birds could not feed their chicks up to one week. Starving chicks stay at the nest at ambient temperature of – 5°C to 2°C (Gębczyński 1995). In this situation the high value of fasting capability seems to be crucial for nestling survival. Decrease of chick body mass (fat content) during nesting period mainly depends on blocking nest entrances by snow (Wasilewski 1986). The chicks which starve too long or have not sufficient fat storage die of starvation after strong snow fall (Wasilewski 1986, Fig. 3). It was possible that Wilson's storm petrel chicks use also protein as an energy source, but differences in nonlipid matter content between sacrificed and starving to death (found dead) chicks were no more than 3 g (Fig. 4) or 60 kJ (1 g of nonlipid matter = 20 kJ; Ricklefs 1974). This value changes fasting capability by no more than 0.5 day. Moreover, Wilson's storm petrels are good flyers and feed about 2–10 km off the nearest shorelines (Alerstam et al. 1993). This suggests that stochastic variation of chick food provisioning arises mainly from unpredictable snow storms rather than fluctuating food availability at the sea or bad weather (strong wind).

Stable and high lipid index in homeothermic chicks illustrates that fat content in non-starved chick body may increase regularly up to 50th day of life (Fig. 3); and this is opposite to hypothesis about accumulation of fat early in growth period. It is possible that accumulation of excessive lipid reserves is a consequence of overfeeding the chicks by their parents. This strategy protects offspring from death during periods of starvation. Overfed chicks are not handicapped because surplus energy can be removed by dissipation or starvation. The lipid index declines during few last days of nesting period when fledglings attain body mass needed for departure. Measurements of chick metabolic rate during the breeding season (Obst & Nagy 1993, Gębczyński 1995) show that oxygen consumption just before fledging and after few days of starvation decreases, but body temperature is stable. Therefore thermal conductance of obese chick is higher than of lean one (Gębczyński 1995). High level of thermal conductance of overfed chicks probably plays important role in decreasing body mass in obese chicks before departure from their nests. On the other hand, slow rate of chick provisioning can be followed by chick loss. Most of found dead homeothermic chicks died in consequence of undernutrition — their lipid index was very low (Fig. 3).

Our studies show that proximate reason for fat reserves in Wilson's storm petrel chicks may be overfeeding offspring by their parents. The ultimate reason for this phenomenon is ensuing resistance to unpredictable food supply rather than intaking nutrients from nutrient poor diet.

Selostus: **Rasvavarastojen merkitys etelänkeijun poikasille**

Useimmista muista linnuista poiketen keijutlajit varastoivat runsaasti rasvaa pesäpoikasaikana. Ilmiölle on esitetty useita syitä: 1) merilintulajien varautuminen huonoihin ravinnonhankinta olosuhteisiin, 2) rasvan kertyminen linnunpoikasiin runsaasti rasvaa sisältävän, mutta ravinneköyhän ravinnon vuoksi, 3) poikasten rasvan keruu energiatarpeeltaan vähäisemmän varhaisen kasvuvaiheen aikana myöhempää tarvetta varten ja 4) rasvojen kertyminen yliruokinnan seurauksena. Emojen ruokintakäyttäytyminen voisi parantaan poikasten ravitsemuksellista tilaa huonojen ravinnonhankinta olosuhteiden aikana. Kirjoittajien tavoitteena oli selvittää pesäpoikasten rasvavarastojen merkitystä Antarktiksen Etelänkeijulla. Etelänkeijun poikasten tasainen kasvunopeus kolmen ensimmäisen viikon aikana viittasi siihen, että meressä tarjolla olevan ravinnon määrän vaihtelulla ei ollut juurikaan merkitystä poikasten ruokintaan, kun taas yllättävillä lumimyrskyillä oli merkitystä. Poikasten paino ei korreloinut morfologisten mittojen kanssa. Poikaset eivät oletettavasti keränneet rasvoja lisätäkseen kasvua rajoittavien ravinteiden määrää. Kirjoittajat päättelevät, että etelänkeijun poikasten suuret rasvamäärät ovat seurausta yliruokinnasta. Yliruokinta-strategian avulla etelänkeijun poikaset voivat selviytyä hengissä huonojen ravinnonhankinta olosuhteiden aikana.

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