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Is there a hypothermia in Wilson's storm petrel chicks?

ABSTRACT: Thermoregulation is fully developed in 5 day old Wilson's storm petrels *Oceanites oceanicus* (Kuhl). Resting metabolic rate (RMR) and body temperature (Tb) of unattended 1- and 3-day old chicks continuously decrease at ambient temperature (Ta) of 5°C. After being heated the chicks return to normothermia. Ability to survive temporal deep hypothermia seems to be an adaptation to absence of parents and low temperatures in the nest during first days of life. After snow storm, during two days of starvation, chick RMR decreases by 40% at Ta of 0°C, but chick Tb is stable. This suggest decrease of thermal conductance (Ct). Fall of Ct may suggest beginning of hypohermia.

K e y w o r d s: Antarctic, Wilson's storm petrel, hypothermia, metabolic rate, starvation.

Introduction

A characteristic feature of birds and mammals is their ability to adjust their metabolism and thereby maintain relatively high and constant body temperatures over a wide range of thermal conditions. Endothermy confers a large advantage with respect to independence from environmental conditions, but it requires high and sustained expenditures of energy. Because of these energetic costs, it is not surprising that neither birds nor mammals are precise homeotherms. Virtually all individuals reduce body temperature, and hence metabolic rate, during inactive portions of the daily cycle, and many species are able to decrease their body temperature well below this normothermic range (French 1993). Short-term facultative torpor is used in a wide variety of avian species spanning eight orders (Dawson and Hudson 1970, Reinersten 1983). Moreover, majority of endotherms is ectothermic during their first few days of life, when thermoregulatory mechanisms are not fully developed. Hypothermia in those offsprings cannot be classified as hibernation because of incomplete thermoregulation at low body temperatures.

Hypothermia can be both a response to immediate energetic emergencies and a means for preservation of energy supplies, as observed during food deprivation and/or bad weather conditions (Prinzinger and Siedle 1988). It seems certain that small birds, breeding at high latitudes are most likely to have such adaptation. I tried to follow hypothermia in chicks of the Wilson's storm petrel *Oceanites oceanicus* (Kuhl), the smallest known Antarctic endotherm. Weather (storms and low temperature) affects chick's growth rate, energy expenditure and feeding frequency (Beck and Brown 1972; Obst, Nagy and Ricklefs 1987). During strong storms snow covers nest entrances and adult birds cannot feed their offsprings for several days. The periods of brooding, when chicks are ectothermic, and starvation seem to be crucial in chick's life. It was interesting to find is ability to hypothermia one of adaptation to environment conditions at that time.

Material and methods

The study was carried out at the Wilson's storm petrel colony located on Rakusa Point, King George Island, South Shetland Islands (Wasilewski 1986), in summer 1990/91, during the 15th Polish Antarctic Expedition to H. Arctowski Station. All nests were marked with numbers and inspected daily. Hatchlings found for the first time were assigned an age of one day. To record thermal conditions in the nests air temperature was daily registered in five occupied nests. Chicks retrieved at the colony were carried to the laboratory in cotton bags. Before and after measurements of resting metabolic rate (RMR) chicks were weighed with Sartorius balance (± 0.1 g), and their body temperatures (Tb) were measured with thermistor probe ($\pm 0.2°C$) inserted 3 cm into oesophagus (near stomach). The temperature corresponded to deep body temperature. All measurements of oxygen consumption were made with closed-system, constant-pressure respirometer (Górecki 1975) and converted to standard conditons (STP), and then to energy expediture assuming 1 cm^3 $O_2 = 20.1$ J (Nagy, Siegfried and Wilson 1984). Oxygen consumption was registered in consecutive 3-minute periods. Means are reported throughout the text with one standard error.

I carried out two experiments: first with youngest, still ectothermic chicks up to five day of life; second, with $45-55$ days old chicks during period of starvation after snow storm and covering nest entrances.

Development of homeothermy: Eighteen chicks were studied on 1st (n = 6), 3rd (n = 6) and 5th (n = 6) day after hatching. RMR was measured at ambient temperature (Ta) of 5°C, which prevails at the nest. This simulated a situation devoid of both parents. Measurements lasted $150-180$ minutes, depending on the rate of RMR decrease. I calculated oxygen consumption in $12-15$ minute periods. Chicks were returned to their nest after each measurement.

I compared RMR depression of chicks from three age groups in the linear phase of decrease/stability. To find this time interval, results from first 30 minutes of measurement, when RMR was not stabilized, were rejected. I fitted straight line to changes of RMR in each group by least-squares method. I compared slopes of regression lines between group using ANCOVA and Tukey test (Zar 1984).

Metabolic rates in starving chicks: Eight starving chicks were studied, when nest entrances were covered by snow, and adult birds could not feed their offsprings. After taking the chicks from the nests I shut the entrances to parents, as a protection against abandoning of empty nests by the birds. The chicks were put into a closed box located outside the laboratory, where air temperature was the same as nest temperature $(0-3°C)$. The box protected the chicks against rains and strong winds. Each box contained only one bird. Resting metabolic rates of chicks were obtained at Ta of $0°C$ (similar to nest temperatures at that time), just after isolation, and every day during next two days. Before measurement chicks were acclimated to metabolic chamber for 30 minutes. Measurement lasted $45-60$ minutes. Metabolic rate was evaluated only when oxygen consumption was stable for at least 15 minutes. Chicks were returned to their nest after three measurements (about 2 days). Thermal conductivity (Ct) of chicks was counted using equation described by Obst, Nagy and Ricklefs (1987):

$$Ct = RMR/(Tb - Ta)$$

where: RMR — resting metabolic rate ($J\ h^{-1}\ chick^{-1}$), Tb — body temperature ($°C$), Ta — ambient temperature ($°C$).

Results

Development of homeothermy

Ambient temperatures during measurement of resting metabolic rate (RMR) correspond to air temperatures in nests (Fig. 1). There were no significances of RMR between age groups during the first 30 minutes of exposure to temperature $5°C$ (ANOVA, $174 \pm 9.2\ j\ g^{-1}\ h^{-1}$, $p = 0.44$). Mean RMR of each group was stable in that time (paired t test, $p > 0.05$ — for each group). Prolongation of exposure of chicks to this low temperature resulted in significant decrease of RMR in nestlings one and three day old (Fig. 2). Chick body temperature (Tb) significantly decreased together with changes of metabolic rate, from average $37.1 \pm 0.7°C$, and $38.0 \pm 0.8°C$ to $13.6 \pm 1.8°C$ and $18.0 \pm 1.6°C$ for 1- and 3-days old nestlings, respectively (paired t test, $p < 0.001$ — for both age classes). Mean RMR (Fig. 2) and Tb ($38.9 \pm 0.4°C$ before and $38.5 \pm 0.8°C$ after exposure) of 5-days old chicks were stable throughout measurement (paired t test, $p > 0.1$). Slopes of regression lines of RMR vs. time, differed significantly between chicks of 5 days old and another chicks, but did
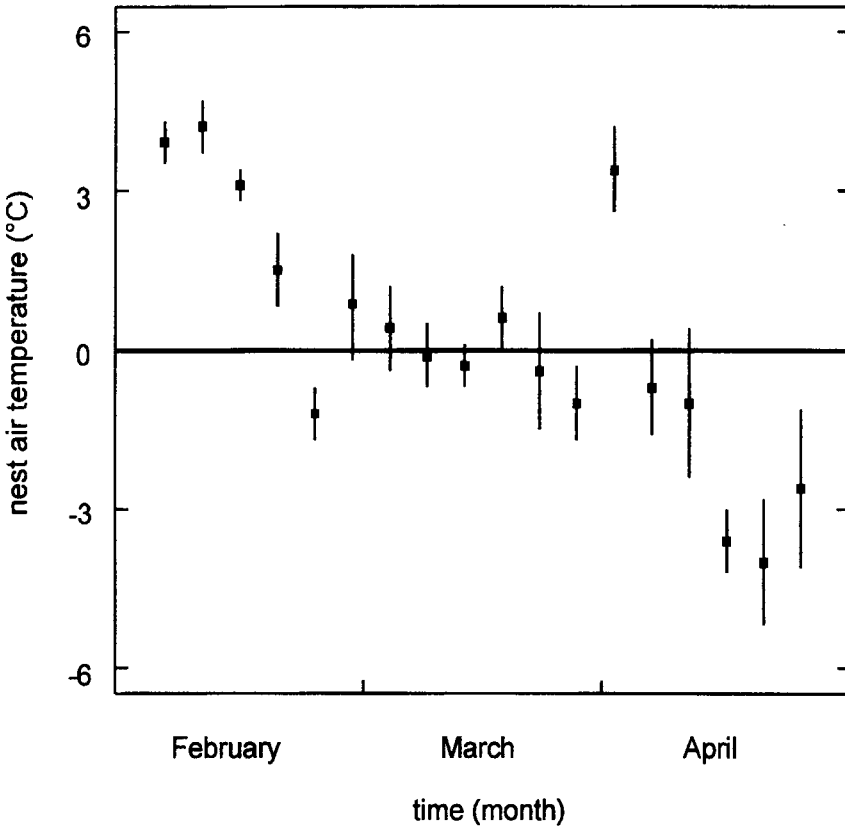
Fig. 1. Changes of air temperatures in five occupated Wilson storm petrels' nests during breeding season 1991 (mean for five days period ±SE).

not differ between chicks of 1 and 3 days old (ANCOVA: $F_{2,146} = 110.2$, $p < 0.001$; Tukey test). After cooling no chick could increased Tb itself, but after being heated chick Tb increased to $39.0 \pm 0.9°C$.

I found three 1-, 2-, 2-days old cold chicks (Tb = 12.4, 15.2, 18.0°C) in the nests devoid of parents. Despite much lowered Tb the chicks survived and grew normally.

Metabolic rates in starving chicks

There was considerable variability in chick RMR values at the beginning of starvation, i.e. just after nest entrances were covered by snow. In spite of the variability the mean chick's RMR then was significantly higher than on next days of experiment (Fig. 3; paired t test, $p < 0.01$), but chick body temperature was stable all the time ($37.7 \pm 1.0°C$ at the beginning, $38.5 \pm 0.06°C$ on the first day, $38.4 \pm 0.8°C$ on the second day; paired t test, $p > 0.1$). The thermal
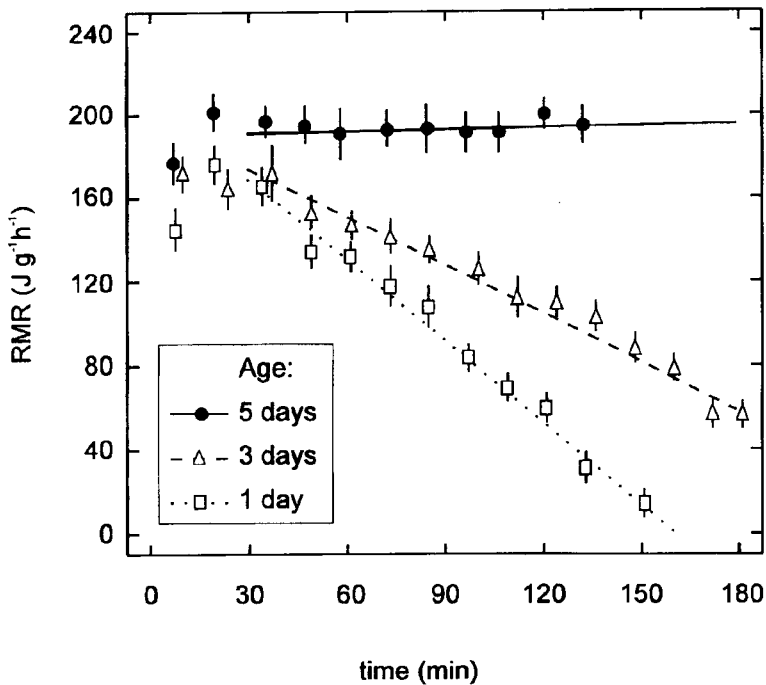
Fig. 2. Regression lines of Wilson's storm petrel chick resting metabolic rate (RMR) vs. time in five days old chicks (RMR $= 199.8 - 0.06t$, $r^2 = 0.02$, ANOVA, $p < 0.5$), three days old chicks (RMR $= 194.2 - 0.75t$, $r^2 = 0.97$, ANOVA, $p < 0.001$), and one day old chick (RMR $= 202.4 - 1.25t$, $r^2 = 0.99$, ANOVA, $p < 0.001$). Vertical lines illustrated standard errors
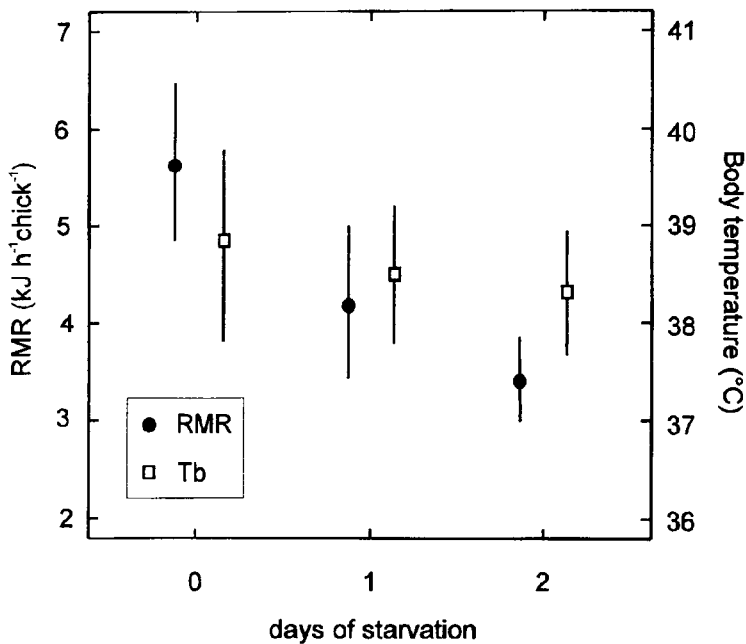

Fig. 3. Changes of chick resting metabolic rate (RMR) and body temperature (Tb) before (0 day) and during starvation (after 1 and 2 days). Vertical lines illustrated standard errors

conductivity (Ct) of nestlings decreased from $0.149 \pm 0.007n$ kJ h^{-1} $°C^{-1}$ chick^{-1} at the beginning to 0.088 ± 0.004 kJ h^{-1} $°C^{-1}$ chick^{-1} on second day of starvation. The values differed significantly (paired t test, $p < 0.001$). Chick RMR during starvation was correlated with body mass (ANCOVA, $F_{1,23} = 127.8$; $p < 0.001$).

Discussion

Development of homeothermy

As shown by Beck and Brown (1972) egg incubation in Wilson's storm petrel is shared equally by both adults in alternating spells of approximately 60 hours (range $36-96$ hours). At some sites incubation was not continuous, being marked by the absence of the incubating bird during the day. This day-time absence was particularly noticeable when one parent did not return from feeding and the incubation spell of another one continued for longer than the average 60 hrs. This suggests that those departures were probably made for feeding (Beck and Brown 1972). It is likely that the same may happen during brooding of a chick, when adult bring the greatest amount of food to the nest (Ricklefs 1983), and brooding spells might be shorter or/and feeding time longer than during incubation (Ricklefs and Roby 1983). Day-time absence of brooding parents in their nest, especially during bad weather conditions (storms, strong wind, low temperature) seemed to occur frequently. After the departure of parents from the nest the chick was exposed to low temperatures for several hours. This suggests that both early development of thermoregulation (during $4-5$ days of life) in youngest chick, and its ability to survive temporal hypothermia were preferred by natural selection in Wilson's storm petrel.

Bad weather conditions affected growth of those chicks, by affecting changes of thermal conductivity (wet down) and chick's daily intake of food (Wasilewski 1986). In my view the influence of the latter on chick's growth was crucial, because the chick is well protected against most of weather factors in the nest, and only melting snow or rain water would likely increase chick thermal conductivity. During observations all nests were dry. On the other hand field metabolic rate (FMR) of adult birds in offshore feeders might be affected by weather, e.g. wind (Gabrielsen et al. 1990). Therefore the FMR of adult would be altered sufficiently to change the amount of food brought to the nest daily. This diminished food might then be insufficient to feed a chick and brood it longer, forcing the adult bird to leave the nest for food before arrival of the second parent. During long parental absence the ability of a chick to survive temporal hypothermia and subsequently to recover normal body temperature (Tb) when attended, may increase chick's chances of successful development and fledging.

Metabolic rate in starving chicks

During breeding season, especially in March and April, snow storms and low temperatures affected conditions in Wilson's petrel nests. In result of storms snow covers breeding colony and most of nest is not accessible for several days. At the time chicks in these nests are not fed at all (Wasilewski 1986). Air temperature in the nest decrease up to $-3°C$ (Fig. 1) and affects mortality of chicks (Wasilewski 1986). In many birds low temperature and suspension of feeding of chick by their parents result in decreasing metabolic rate and body temperature of the chick (Prinzinger *et al.* 1981, Krüger, Prinzinger and Schuchmann 1982, Boersma 1986, Prinzinger and Siedle 1988). Whereas Wilson's storm petrel chicks starved for few days their resting metabolic rate (RMR) decreased by about 40%. For explanation of the decreasing on basis of Tb differences, body temperature should decrease by $4.6°C$ (for Q_{10} of 3). Any decrease of Tb was not observed. Thus, changes of RMR could be explained only on basis of thermal conductivity (Ct) changes, which fall by 41%. Snyder and Nestler (1990) suggest the mechanism causing the low metabolic rates in torpid endotherms is reductions of thermal conductance and $Tb-Ta$ differences. After two days starvation Ct decreased significantly without change of $Tb-Ta$ difference. This is possible that Wilson's storm petrel chicks could decrease Tb, after longer starvation. Wasilewski (*pers. commun.*) found at nests several torpid chicks, older than 5 days (unfortunately he did not measure chick's Tb). Boersma (1986) noted that chicks of fork-tailed storm petrel (*Oceanodroma furcata*) reduced Tb to as low as $10.6°C$ in result of food deprivation.

Table 1.

Comparison of chick resting metabolic rates (RMR) in Wilson's storm petrel and other birds with similar body mass

Species	Body mass (g)	RMR (kJ h^{-1} chick^{-1})
Oceanites oceanicus		
before starvation	38.5	5.6
on 1st day	34.2	4.2
on 2nd day	32.2	3.4
Oceanodroma leucorhoa[a]	67	3.3
Oceanodroma furcata[b]	49	2.3
Oceanodroma furcata[c]	45	1.6
Oceanodroma leucorhoa[b]	42	2.3
Delichon urbica[d]	17	1.1
predicted from equation[e]	35	2.4
predicted from scaling equation for hummingbird[f]	38	6.16

[a] Ricklefs, White and Cullen 1980, [b] Iverson and Krog 1972, [c] Vleck and Kenagy 1980, [d] Bryant and Gardiner 1979, [e] Weathers 1991, [f] Krüger, Prinzinger and Schuchmann 1982

I found that Wilson's storm petrel chicks' RMR before starvation was significantly higher than RMR of other birds with similar body mass and two times higher than value predicted from Weathers' (1991) scaling equation for relationship of body mass and average daily metabolic rate (Tab. 1). Unfortunately all species used to comparison breed in temperate zone. There are no data of chick's RMR of birds such small as Wilson's storm petrel which breed in polar zone. Because I studied the smallest Antarctic bird I compared its RMR with RMR of hummingbirds, the smallest birds in temperate and tropical zones (Tab. 1). I found that differences between RMR of Wilson's storm petrel chicks before starvation and value predicted from scaling equation for active hummingbirds (Krüger, Prinzinger and Schuchmann 1982) were not significant (t test: $p = 0.09$).

During breeding season some chicks store large amount of fat. Fat reserves can be used when chick is not fed, but they always have to be removed before fledging. Obst and Nagy (1993) observed significant decrease of chick RMR on last days of nesting period, and it was similar to reduction of metabolic rate during starvation. The decrease equal respectively 0.53 and 0.55 kJ h^{-1} chick^{-1}. The RMR decreased after reduction of fat reserves. On the other hand, after analyzing of Wasilewski's (1986) results of chick's body mass I found that after long starvation body mass of not extremely obese chicks decreased in smaller rate than one expected on pre-starvation RMR base (with assumptions: 1 g of body mass decrease $= 38$ kJ, fat utilize yield $= 75\%$). This corresponds to my results. However, during shorter starvation heaviest chicks fasted in predicted rate. In my view chick's RMR decreases only when fat reserves are utilized both before fledging or in result of starvation.

I did not find hypothermia in endotherm chicks (older than 5 days), but the results did not reject it. If Snyder's and Nestler's (1990) hypothesis about entering to hypothermia is true, decrease of chick's RMR (and decrease of Ct as result) seems to be the beginning of hypothermia. If food deprivation will be prolonged, fall of Tb may be present.

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Streszczenie

Pisklęta nawałnika Wilsona [*Oceanites oceanicus* (Kuhl)] badane były latem 1990/91 na wyspie Króla Jerzego (Szetlandy Południowe). Przez cały sezon rejestrowana była temperatura powietrza w zajętych przez ptaki pięciu gniazdach (Rys. 1).

Przeprowadzono dwa rodzaje eksperymentów:

1. Rejestrowano zmiany spoczynkowego metabolizmu (RMR) i temperatury ciała (Tb) u piskląt w wieku 1 − 5 dni, eksponowanych na temperaturę otoczenia (Ta) równą 5°C. Zarówno RMR, jak i Tb piskląt 1- i 3-dniowych obniżały się podczas trwania pomiaru (Rys. 2) i były istotnie różne od RMR i Tb piskląt 5-dniowych. Niska temperatura ciała piskląt wracała do normalnej po ogrzaniu zwierzęcia. Zdolność do przeżycia okresowej hipotermii wydaje się być adaptacją zmiennocieplnych piskląt do niskiej temperatury powietrza po opuszczeniu gniazda przez rodziców.

2. Rejestrowano RMR i Tb piskląt głodujących po tym, jak śnieg zasypał na kilka dni wejście do gniazd. RMR piskląt przed głodówką było bardzo wysokie (Tab. 1). Spadek RMR w czasie głodówki był podobny do spadku RMR w ostatnich dniach przed wylotem piskląt z gniazd. Podczas gdy RMR piskląt spadło o ok. 40%, ich Tb pozostawała nie zmieniona (Rys. 2). Wynika stąd, że zmianę RMR można wyjaśnić jedynie spadkiem przewodnictwa cieplnego (Ct) piskląt, co z kolei może być pierwszym krokiem do zapadania w stan hipotermii.