TEMPERATURE REGULATION OF YOUNG JACKASS PENGUINS, *SPHENISCUS DEMERSUS*

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ABSTRACT

Data from five jackass penguin chicks (mean mass 201 g) showed that even young chicks can increase their oxygen consumption from 0.76 ± 0.16 ml O_2/gxhr at 35°C to 2.09 ± 0.21 ml O_2 at 20 °C. Close parental attendance may therefore be interpreted not only as protection against aerial predators but also as creating a microclimate which could favour a decrease in maintenance requirements and thus channel a substantial part of the available energy into growth. A decrease in rectal temperature, despite the increase in heat production, is interpreted as indicative of poor insulative properties of the down. Preliminary data on the ontogeny of thermoregulation indicate that penguin chicks may attain mature thermoregulatory abilities at a mass of approximately 400g.

Observations on breeding jackass penguins *Spheniscus demersus* on St. Croix Island, 33° 47′ S 25° 37′ E, off the south-east African coast, revealed that these birds never leave their young chicks unattended. The question arises whether this behaviour may be attributed only to the need to protect young from everpresent, predatory southern black-backed gulls, *Larus dominicanus*, or whether it may also be concerned with the thermoregulatory requirements of the young. The rocky island precludes burrowing and the majority of nesting sites are in the open and are exposed to high solar radiation and cold wet winds. No information is available on the ontogeny of thermoregulation in the jackass penguin.

The only data on thermoregulation of penguin chicks are those reported for the Adelie penguin, *Pygoscelis adeliae*, and the emperor, *Apdenodates forsteri* (Sapin-Jaloustre 1955; Goldsmith & Sladen 1961). The existing literature precludes speculation on the need for close parental attendance in the jackass penguin living in a subtropical biogeographical zone (Stonehouse 1967). This paper reports on aspects of thermoregulatory responses of jackass penguin chicks to various ambient temperatures in the laboratory, as well as data on the rectal temperatures of nestlings in the field.

MATERIAL AND METHOD

The chicks (51) used in this study hatched on St. Croix Island and varied from 72 to 1 142 g.

Experiment 1: Oxygen consumption studies

To determine whether penguin chicks can thermoregulate in the absence of their parents, five chicks ranging from 93 to 206 g were transported to the laboratory and the oxygen consumption measured during exposure to various ambient temperatures. A thin-walled perspex closed circuit respirometer with a compensating chamber and soda lime as the CO_2 absorbant was used. The respirometer was immersed in a water-bath at various temperatures and the temperature of the air in the respirometer box was measured and taken as the ambient.

In an attempt to minimize the effect of starvation (no food was offered) on oxygen con-

sumption readings all readings for a chick were completed within nine hours of initial capture on the island. The chicks were captured on the first day (day 1), used and returned to their nests on the following day (day 2) when the last two chicks were caught and brought to the laboratory.

The three chicks captured on day 1 were weighed and then subjected to air temperatures of 25°C, 30°C, 20°C and 15°C in the respirometer. Oxygen consumption determinations were done at each temperature with a recovery period of at least 60 minutes at an ambient temperature of 28°C in a climatic chamber between oxygen consumption readings. The treatment regime for the two chicks of day 2 was 25°C, 30°C, 35°C, 20°C and 15°C with the same recovery period at 28°C between oxygen consumption determinations.

After lowering the respirometer into the water-bath, sufficient time was allowed for temperature and pressure to stabilize before oxygen consumption readings were started. At least four readings were taken at approximately three minute intervals and the mean of these readings corrected to STP was taken as the oxygen consumption of a chick at that specific temperature.

Rectal temperatures were recorded immediately after the chick was taken out of the respirometer to recover in a climatic chamber at 28°C.

Exposure time (equilibration plus measuring) attending the various temperatures varied from 30 minutes for temperature treatments near room temperature to 60 minutes for the lower (15°C) temperature treatment.

A chick from day 1 was known to be 30 hours old and weighed 94 g. The ages of the other chicks are unknown but were estimated from previous observations on the island to be less than five days.

Experiment 2: Laboratory body temperatures

Data from experiment 1 suggested that ambient temperatures (Ta) below body temperature (Tb), gave rise to a decrease in rectal temperatures. An attempt was therefore made to investigate the possible decrease in rectal temperatures of chicks during exposure to the prevailing climatic conditions on St. Croix Island. The handling and struggling associated with separation of chicks from their nests or parents, however, resulted in such an increase in rectal temperatures that the possible effect of climate on body temperatures was obscured.

Four chicks, ranging from 142 to 497 g at the time of capture, were therefore taken to the laboratory and kept individually in containers in a dimly lit climatic chamber. Their body temperatures were monitored with Fe-Co thermocouples inserted into their stomachs via the oesophagus. The thermocouples, accurate to 0,05°C, were connected to a multichannel recording potentiometer. The chicks were exposed for successive 30 minute periods to each of the following ambient temperatures in the following sequence, 28°C, 30°C, 35°C, 28°C, 25°C, 28°C, 20°C, 28°C, 16°C, 28°C, 13°C, 28°C, 35°C, 28°C, 20°C, 15°C and 13°C. Relative humidity was kept between 75 and 80 per cent. The chicks were not disturbed by handling and proved to be quiet and restful during the entire experiment except at temperatures below 20°C.

As these chicks were not handled, the stomach temperatures recorded were regarded as true core temperatures for the specific ambient temperature.

Experiment 3: Ontogeny of thermoregulation

Data from experiment 2 suggested that age could influence the reaction of chicks to changing

ambient temperatures. It was not possible to evaluate the ontogeny of thermoregulation in jackass penguin chicks by exposing chicks of various ages to the prevailing climate on the island, because the handling and the struggling of the chicks to find shelter when exposed, gave rise to a marked increase in rectal temperatures. Although this technique was used successfully by Sapin-Jaloustre (1955) when he exposed Adelie penguin chicks to the climatic conditions at Port Martin (66° 49′ S/141° 24′ E) the temperature of −1°C was so low that it masked any rise in body temperature associated with struggling. In the present experiment it was not regarded as advisable or practical to bring a relatively large number of chicks to the laboratory.

An alternative approach was taken where the rectal temperatures of 42 chicks were measured immediately upon being taken from their nests.

The postulate underlying this approach is that a chick with well-developed thermoregulatory abilities could be expected to have a Tb resembling the Tb of a mature bird (39°C) more closely than a chick with less-developed thermoregulatory abilities. The mean egg temperature, and therefore the most likely "nest" temperature of 31,5 ± 1,3°C (as measured on 10 eggs), is 7,5°C below adult Tb. The less developed the thermoregulation of a chick, the more its Tb will approach "nest" temperature and, therefore, the rectal temperatures of chicks of varying ages as measured immediately upon being taken from the nest might be indicative of the effect of age on thermoregulatory abilities of chicks.

To assess relative age, mass determination, accurate to 0,5 g, was done on each chick after rectal temperature determination. These chicks were then divided into two groups according to mass and the rectal temperatures of the lighter group were compared with those of the heavier group for statistically significant differences. The following comparisons were made using the same data but different mass groupings for different comparisons: rectal temperatures of chicks with a mass of less than 200 g were compared with those with a mass of more than 200 g and the procedure was repeated with the chicks divided into two groups at 300, 400, 500 and 600 g.

RESULTS

Experiment 1: Oxygen consumption
The effect of various ambient temperatures on the oxygen consumption and rectal temperatures of chicks ($\bar{x}$ = 201 g) is presented in Figure 1.

Oxygen consumption increased steadily (mean ± S.D.) from 0,76 ± 0,16 ml O_2/g × hr at 35°C to 2,09 ± 0,21 ml O_2/g × hr at 20°C and plateaued at a level of 1,90 ± 0,43 ml O_2/g × hr at 15°C. Shivering started between ambient temperatures of 20–22°C and was sporadically evident at temperatures down to 15°C.

Experiment 2: Laboratory body temperatures
The effect of a varying temperature on the body temperatures of the four chicks is illustrated in Figure 2.

From the results it was obvious that the three heavier chicks ranging from 414 to 497 g ($\bar{x}$ = 450 g) not only had a less-varying body temperature than the chick of 142 g but also maintained body temperature at a constantly higher level. Although only one lighter chick was
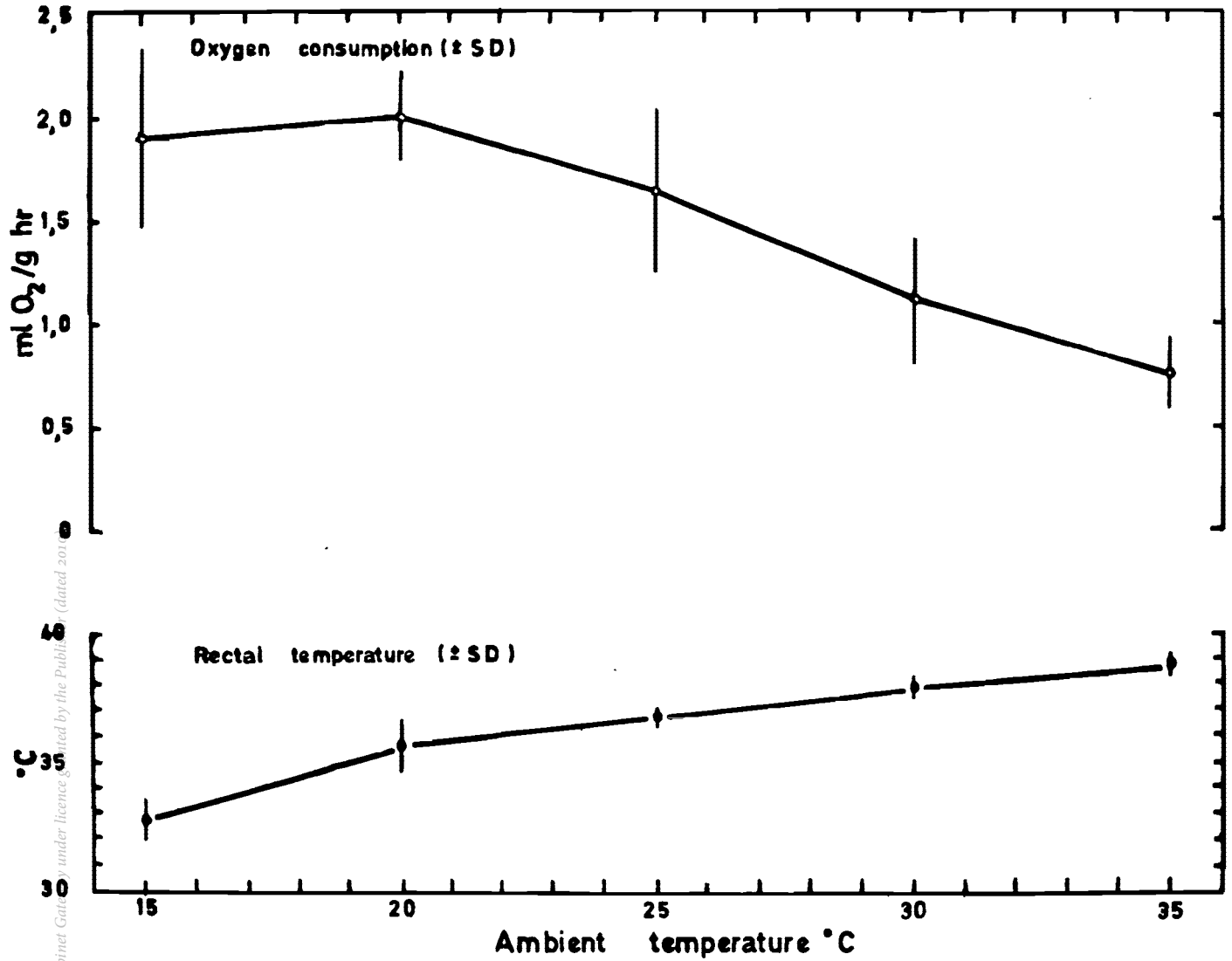
FIGURE 1

The effect of various ambient temperatures on the oxygen consumption and rectal temperatures of five
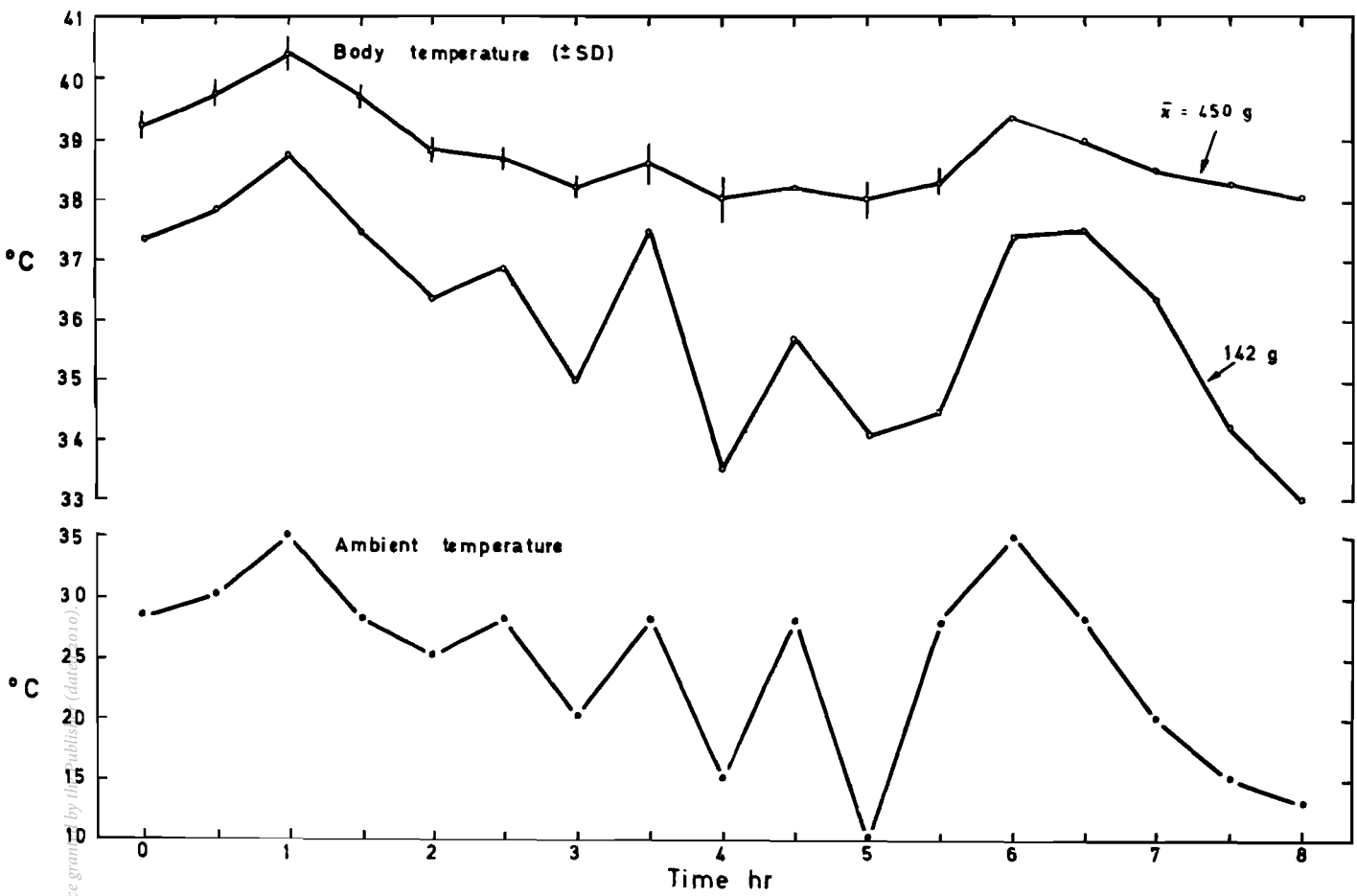
FIGURE 2

The effect of varying ambient temperatures on the body temperatures of three chicks with a mean mass of 450 g and one chick with a mass of 142 g.

available, the difference between chicks of different mass is regarded as significant because it agrees with observations on rectal temperatures in experiments 1 and 3.

Experiment 3: Ontogeny of thermoregulation

The mean rectal temperature of 42 chicks, ranging from 72 to 1 142 g, $(\bar{x} = 450\,g)$, measured immediately after capture during the day, was $39,4 \pm 0,8°C$.

The comparisons of the rectal temperatures of the various mass groups are presented in Table 1.

From Table 1 it appears that chicks lighter than 400 g have a statistically significantly lower rectal temperature (p = 0,05) than heavier chicks. This difference disappears beyond 400 g. The correlation between mass and rectal temperature over the entire weight range was +0,29 and was significant at p = 0,05.

TABLE 1

COMPARISONS OF RECTAL TEMPERATURES OF CHICKS OF VARIOUS MASS GROUPS

Comparison	Mass groups g	n per group	Mean rectal temperatures °C	t-value* per comparison
1	<200	11	38,9 ± 0,9	4,487*
	>200	31	39,7 ± 0,7	
2	<300	14	39,0 ± 0,9	3,030*
	>300	28	39,7 ± 0,6	
3	<400	18	39,2 ± 0,9	1,994*
	>400	24	39,6 ± 0,7	
4	<500	20	39,3 ± 0,9	1,541*
	>500	22	39,6 ± 0,7	
5	<600	25	39,4 ± 0,8	0,959*
	>600	17	39,5 ± 0,8	

* $t0,05 = 2,021$

DISCUSSION

The five chicks with a mean mass of 201 g did increase their oxygen consumption concomitant with a decrease in ambient temperature (Figure 1). Moreover, the one smaller chick (94 g),

known to be 30 hours old, showed the same general pattern as the older (5 days old) chicks. Also worth noting was the inability of these chicks to further increase their oxygen consumption at ambient temperatures below 20°C. Shivering was also used below 20°C presumably to augment heat production but this did not result in an increase in body temperature. This apparent inefficiency of shivering may be due to the increased rate of heat loss due to the increased peripheral circulation that accompanies shivering.

The 2,75-times increase in heat production from 35°C to 20°C compares favourably with the three-times increase that can be regarded as a maximum in most inactive homeotherms according to Scholander et al. (1950). Young jackass penguin chicks therefore do have the ability to increase their heat production to combat heat-loss. However, the lower rectal temperatures of younger chicks (see Figure 2 and Table 1) when exposed to Ta below Tb are an indication that heat-loss exceeds heat production.

There are no other oxygen consumption data available for penguin chicks and it is therefore difficult to evaluate the heat production of the five chicks in this experiment. The heat production of these chicks at 35°C (assuming this temperature to approach standard heat production conditions) is 37% of what may be expected from an adult bird of the same weight, calculated from the formula for non-passerine birds given by Lasiewski & Dawson (1967). This figure (37%) is considerably lower than the 70 to 80 per cent relative heat production reported by Koskimies & Lahti (1964) for duck chicks, *Melanitta fusca* and *Somateria mollisima*, with well-developed thermoregulatory abilities. The young penguin chicks would therefore appear to be less mature in terms of heat production ability.

The only oxygen consumption figures for penguins are those given by Drent & Stonehouse (1971) for three adult Peruvian penguins *Spheniscus humboldti*. Since the Peruvian penguin is to some extent comparable with the jackass penguin (Drent & Stonehouse 1971), it may be justified for purposes of discussion to compare the data for adult *humboldti* with those for *demersus* chicks.

The mean heat production (standard) of the *humboldti* birds in their thermoneutral range was 0,51 ml O_2/g × hr with lower critical temperatures of 1–3°C (Drent & Stonehouse 1971), (assuming the calorific value of 1 ml of oxygen as 4,8 calories in the recalculation of their data from kcal to ml O_2). Their basal metabolic rate was 0,46 ml O_2/g × hr. Although it was not possible in the present experiment to determine the thermoneutral range of the chicks, Figure 1 indicates that the lower critical temperature is higher than 30°C and probably at or higher than 35°C. The chick's oxygen consumption at 35°C was 0,76 ml O_2/g × hr which is approximately 50 per cent higher than the figure for adult *humboldti* in their thermoneutral zone.

This apparent discrepancy of a relatively higher metabolism (50 per cent) than adults coupled with the ability to increase heat production at lower Ta, but a more labile rectal temperature (Figure 2 and Table 1) may possibly be due to the fact that rectal temperature alone is not a valid criterion for evaluating the degree of thermoregulation attained by a chick at a certain age. Poor insulation may result in a labile temperature despite maximum increase in heat production.

The nature of the surface insulation may be assessed by calculating the thermal conductance of the chicks (O_2 – consumption/Tb–Ta). Conductance was constant at 0,14 ml O_2/g × hr × °C between 20°C and 30°C but at 35°C it increased to 0,20 ml O_2/g × hr × °C and at 15°C it

decreased to 0,11 ml O_2/g × hr × °C. Although these observed conductance figures are considerably lower than the calculated value of 0,24 ml O_2/g × hr × °C for birds of similar mass (see Herreid & Kessel 1967), it is not justified to interpret the results in terms of any superior properties of insulation which the chicks might have. On the contrary, the labile body temperature is more likely a result of poor insulation and a lower than required heat production. The apparently low conductance values may therefore be due to low oxygen consumptions and not to marked gradients between body and ambient temperatures. The unqualified calculation of the thermal conductance for these chicks would appear to give false information. In this connection, the reserved approach to thermal conductance calculations advocated by Drent & Stonehouse (1971) and Tracey (1972) is pertinent.

It can thus be concluded that young jackass penguin chicks have a lower rate of heat production than required to make them fully independant of environmental temperature changes, but that they do have the ability to increase heat production when required. This increase in heat production, however, is not sufficient to compensate for heat loss and rectal temperatures will therefore decline during exposure to cool ambient conditions.

In answering the question posed at the beginning as to the reason for close parental attendance of jackass penguins to their young chicks it may thus be stated that young chicks not only benefit from being protected from the gulls by the close attendance of their parents, but if the nest temperatures of 31,5°C are kept in mind it is obvious that parental attendance increases the ambient temperature of a chick to such an extent that this may save oxygen consumption by a factor of at least two, even when the air temperature is as high as 20°C. This potentially channels a substantial amount of the energy fed to young chicks from maintenance into production (growth).

From the present data it is not possible to give a final figure for the amount of energy saved by close parental attendance in older chicks for it was observed on the island that even large chicks (*ca* 1 kg) were still guarded by their parents. Data from Table 1 and Figure 2, despite their preliminary nature, do indicate that the importance of the micro-climate supplied by the adult birds decreases in significance as the chicks grow older. Oxygen consumption data for chicks of various ages may solve this problem.

ACKNOWLEDGEMENTS

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