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In situ Heart Rate and Activity of Incubating Adélie Penguins (*Pygoscelis adeliae*)

B. Culik[1], **D. Adelung**[1], **M. Heise**[1], **R.P. Wilson**[1], **N.R. Coria**[2] and **H.J. Spairani**[2]

[1] Institut für Meereskunde an der Universität Kiel, Düsternbrooker Weg 20, D-2300 Kiel 1, Federal Republic of Germany
[2] Instituto Antarctico Argentino, Cerrito 1248, Buenos Aires, Argentina

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Summary. Heart rates and activity were monitored over 24 h in unrestrained, incubating Adélie penguins (*Pygoscelis adeliae*) exposed to natural conditions in the colony. Heart rate (HR in bpm) increased linearly with wind speed (w; range 0–19 m/s): $HR = 85.8 + 1.35w$, but was unrelated ($P > 0.05$) to temperature (−2.5 °–6 °C), humidity (37% – 100%) cloud cover (0–8/8) and estimated solar radiation (0–12). Wind-induced heat loss was apparently compensated to a large degree by increased metabolic activity. Activity (A) measured as frequency of standing per hour, decreased linearly with temperature (t) and wind speed (w): $A = 1.651 - 0.033w - 0.090t$. After correcting for meteorological influences, heart rate and bird activity showed no diurnal periodicity. When incubating, metabolism and activity of Adélie penguins appear to be mainly governed by climatic variations.

Introduction

In addition to other morphological adaptations, homeotherms living in low temperature environments conserve heat by having substantial insulation. Heat loss can be regulated by pilo- or ptiloerection, vasoconstriction (especially in the extremities) and by postural changes (Goldstein 1983; Drent and Stonehouse 1971). Other than this, heat loss must be balanced by a concomittant increase in metabolic rate. Adélie penguins (*Pygoscelis adeliae*) breed on the Antarctic continent to latitudes of 77 °S. These birds weigh only 4–6 kg and conserve heat by having a very dense feather coat, countercurrent heat exchange system in flippers and feet, complex nasal passages and a unique extensive feathering of the base of the bill (Stonehouse 1970). Such an extensive suite of heat-conserving mechanisms might imply that differential metabolic activity may only play a very small part in regulating body temperature. However, massive seasonal variation in feather and fat insulative capacity, according to breeding and moulting cycles (Prévost and Sapin-Jaloustre 1965), would argue otherwise.

Several authors have reported a good linear correlation of heart rate (HR) with energy expenditure in birds (e.g., Owen 1969; Ferns et al. 1980; Gessaman 1980). Oxygen consumption in birds is affected mainly by HR, less so by the differential O_2 concentrations in arterial and venous blood, and avian heart stroke volume is relatively constant (Ferns et al. 1980). We assumed HR to be directly proportional to metabolic rate in adult Adélie penguins and found this to be the case in chicks (Culik et al., in preparation). By recording HR of incubating Adélie penguins in their colony over 24 h, while observing the birds from a blind, we examined the extent to which they had to compensate for heat loss with increases in metabolic rate when exposed to varying environmental conditions. We report here on the variation of HR and activity during the day and on the effect of meteorological conditions on these 2 parameters.

Materials and Methods

Nine incubating Adélie penguins in a small colony (approx. 50 pairs) located on Seal Point, Esperanza Bay (63.5 °S, 57 °W), Antarctic peninsula, were observed from a small, solid hide placed 3 m from the nearest nest. Between November 27 and December 16, 1987, we conducted 5 experiments, recording HR and activity of one incubating penguin at a time for periods of 24–27 h. Further data were acquired during 12 short term observations lasting from 2–6 h.

The Electrocardiogram (ECG) recorder described in Heise (1988, in press), was placed 0.5 m from the bird in an isolated and heated housing (20×20×20 cm). Two gold-plated safety pins were inserted into the penguin's skin a few cm posterior to each flipper. The safety pins were connected to the ECG recorder via crocodile clamps and a short (0.5 m) cable to avoid interference. ECG output was fed to a Linseis plotter and recorded by counting pen deflection for 60 s every 5 min. To check the validity of counts, the signal was plotted for 30 s every 15 min. Several experiments had to be ended because of a short circuit between the ECG electrodes due to rain.

The complete process of equipping the penguin with the electrodes and cables lasted approx. 10 min. Subsequently, the bird was released in the vicinity of its nest where incubation of the eggs was resumed within a few seconds. HR were high after manipulation of the bird, decreasing to a steady level within 60 to 90 min. After this time, behaviour of ECG-fitted penguins did not differ from that of surrounding birds. We never observed any penguin trying to remove the safety pins or the cables, or attempting to flee from the nest.

Although the Adélie penguins used in this study seemed to behave normally after termination of the experiments, their breeding success, i.e. hatching of the eggs, was very low. This may have been due to their nests lying at the edge of the colony (Davis and McCafrey 1986) but most likely our interference was the cause (cf., Lishman 1985).

The activity of the ECG-fitted penguins was recorded at all times. Rated activities were: rest (lying flat on the nest and incubating motionless), rest with head movement, standing (including standing still as well as short activity bursts such as rearranging eggs, preening, picking at stones) and disturbance (sheathbill-, penguin-, or man-induced disturbance). During four of the five 24-h sessions, we also recorded the activity of 8 penguins in the vicinity of the monitored bird. We noted the standing frequency per hour for each of the 9 observed birds, counting every time a bird stood up as a single standing-event, irrespective of duration.

Meteorological observations were made by the personnel of Esperanza station (Argentina) at approx. 500 m from the penguin colony. Every 3 h (starting at 00 h) wind speed (5 m above ground), temperature, cloud cover and humidity were recorded. Wind speeds during the experiments were in the range of 0–4 m/s for one day to 12–19 m/s for another day, with a wide variation of wind speeds and duration in between. Moczydlowski (1986) reports for another locality that wind speed at 2 m above ground was the same at the meteorological station and at the penguin colony. However, microclimatic conditions at the penguin colony possibly differ from the synoptic measurements. In particular, wind speed at 25 cm above the ground could only equal about 40% of the values measured at the meteorological station (Geiger 1961; Hüppop 1987). The data presented here come from the synoptic measurements, and were not corrected for height above the ground.

In order to obtain some value approximately proportional to solar radiation (cloudless sky), time of day was converted into hours before/after noon. Thus 12 h became 0, 11 h and 13 h became 1 and so on, while 00 h became 12. Variables hour (0–12), cloud cover (0–8/8), humidity (37%–100%), time of day (0–23), temperature (–2.5 °–6 °C) and wind speed (0–19 m/s) were regressed against the mean HR of the calm, resting penguin at that time (±30 min of the meteorological observation), and against mean standing frequency. Vertical bars or hatched areas in figures, and values preceded by a ± sign in the text are 95% confidence intervals. Statistical analyses were performed on a PC using "Statgraphics" by Statistical Analysis Systems. The 3-D plot shown in Fig. 1 was calculated with the inverse distance squared weighed average technique provided by the programme "Surf" by Golden Software. The lines shown are contour lines calculated by interpolation from the data, and do not correspond to the original data itself.

Results

Meteorological Influences on Heart Rate and Activity

Three-dimensional graphic analysis of the influence of temperature and wind speed on HR (Fig. 1) shows the increase of HR with wind velocity and with lower temperatures. The sheet shown was computed by interpolation of the data points (*n* = 51). In a multiple parameter regression, however, the only meteorological factor that significantly influenced HR was wind speed (Table 1). As also shown in Fig. 1, temperature accounted for some of the variance.

In a separate regression of wind speed (w in m/s) against HR (in beats per minute, bpm) we obtained the best first with a linear relationship (Fig. 2). Comparison of individual slopes showed that HR increased with wind speed even at the lower end of the wind speed range, and that differences between penguins were not significant. We therefore pooled the data obtained from all birds. In resting, incubating Adélie penguins, HR increased with wind speed, the relationship being best described by:

$$HR = 85.8 + 1.35\,w$$

$$(r^2 = 0.44,\ F = 39.3,\ P < 0.00001,\ n = 51).$$

Both wind speed and temperature had a significant negative influence on activity (Table 2). Adélie penguins stood more frequently when temperatures and wind speeds were low. The best fit, a linear relationship between activity (A, no. of times standing per hour), wind speed (w in m/s) and temperature (t in °C) was $A = 1.651 - 0.033w - 0.090t$ ($r^2 = 0.21$, $F = 5.14$, $P = 0.012$, $n = 31$).

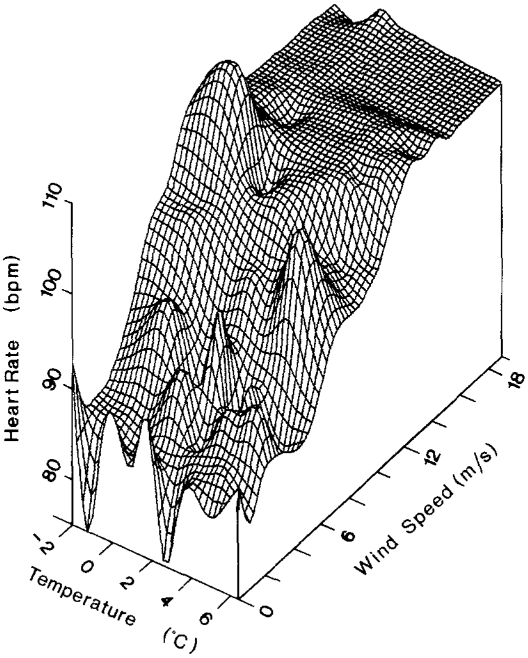

Fig. 1. In situ HR of incubating, resting Adélie penguins vs. ambient wind velocity and temperature. The sheet is a computer-interpolated presentation of the data set (*n* = 51). HR increases with wind speed and more at lower temperatures

Table 1. Regression of meteorological data on heart rate. The model fits the equation $HR = K + a \cdot cl + b \cdot h + c \cdot hu + d \cdot w + e \cdot t$, where HR = heart rate (bpm), K = constant, cl = cloud over (0–8/8), h = hour (0–12), hu = humidity (%), w = wind speed (m/s), t = temperature (°C). $F = 8.14$, $P < 0.0001$, $r^2 = 0.41$, $n = 51$. The only variable that significantly affects heart rate is wind speed ($P < 0.05$)

Independent variable	Coefficient	Significance level
Constant	92.2	0.00
Cloud cover	2.19	0.65
Hour	0.38	0.37
Humidity	–0.10	0.37
Wind speed	1.12	0.00
Temperature	–0.50	0.52

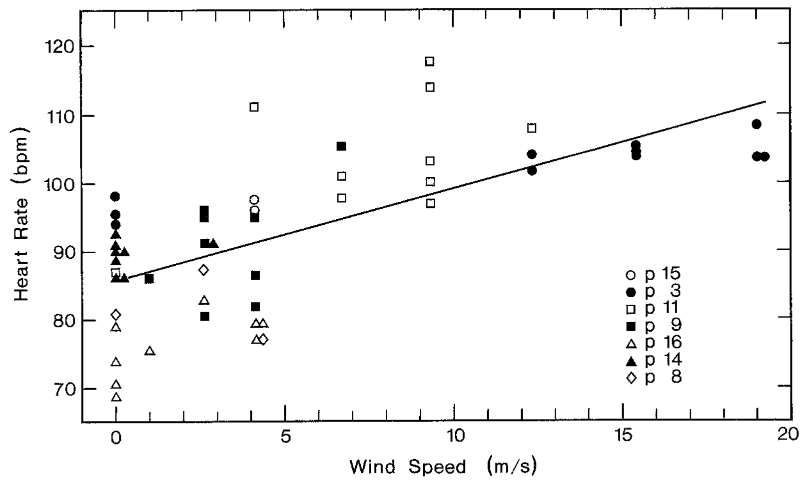

Fig. 2. Regression of synoptic wind speed (w) on heart rate (HR) of 7 individuals, in situ incubating, resting Adélie penguins. The relationship is best described by HR = 85.8 (±3.3)+1.35 (±0.44) w ($r^2 = 0.44$, F = 39.3, $P < 0.00001$, $n = 51$)

Table 2. Regression of meteorological data on mean standing frequency per hour (n = 9 birds). The model fits the same equation as in Table 1. F = 2.87, $P = 0.0339$, $r^2 = 0.23$, $n = 31$. Two variables significantly affect standing frequency: temperature and wind speed ($P < 0.05$)

Independent variable	Coefficient	Significance level
Constant	2.24	0.04
Cloud cover	0.205	0.42
Hour	−0.026	0.18
Humidity	−0.005	0.51
Wind speed	−0.050	0.01
Temperature	−0.127	0.02

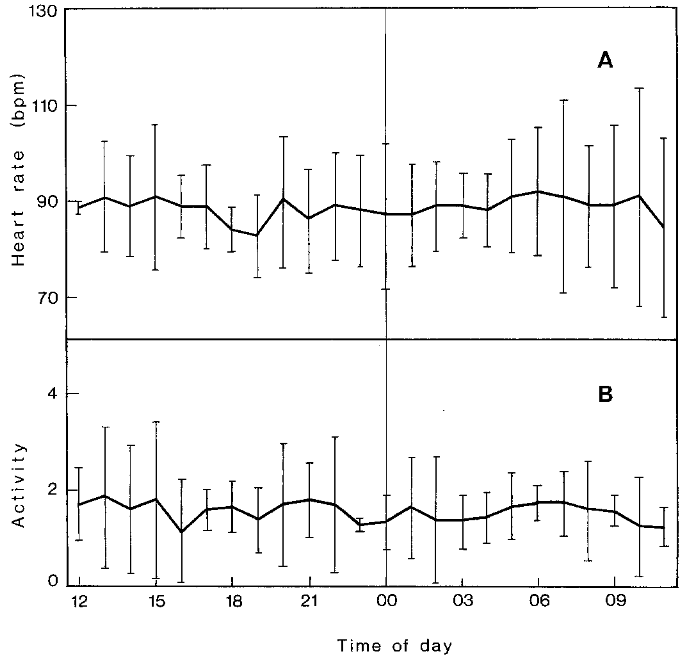

Fig. 3. A In situ mean hourly heart rates of 5 incubating Adélie penguins. Variation is due to activity. **B** Mean standing frequency of 9 incubating Adélie penguins monitored during 4 days. The values were corrected for the effects of wind speed and temperature

Heart Rates and Activity over 24 Hours

The mean hourly HR of 5 individual Adélie penguins incubating over 24 h were corrected for the effect of wind speed (Fig. 3 A). The remaining variation around the means is due to activity. Mean HR were in the range of 83−91 with no clear pattern of periodicity. This was confirmed by time series analysis of the data.

The mean hourly standing frequency of 9 individual Adélie penguins observed over 24 h on 4 days was corrected for the effects of wind speed and temperature (Fig. 3 B). There was no apparent diurnal periodicity, and this was confirmed by time series analysis.

Heart Rates During Activity

The mean resting HR of incubating Adélie penguins was 86±5 bpm (n = 16) at zero wind speed. Standing was the most important activity affecting HR. When the bird was rearranging the eggs, preening or adding stones to the nest, these activities (grouped as "standing") lasted 60±25 s (n = 11) and HR rose to 127±6 bpm (n = 11). Standing frequency per hour is shown in Fig. 3 B. Head movement in lying birds, i.e., increased attention, led to HR of 99±5 bpm (n = 11). Disturbance of incubating Adélie penguins by congeners or sheathbills led to HR of 118±14 (n = 6) and 110±8 (n = 7), respectively. Disturbance by humans approaching to within 3 m of the nest resulted in HR of 127±10 bpm (n = 9).

Discussion

Adélie penguins show some circadian rhythm in activity during the austral summer, particularly when they are foraging for chicks (Müller-Schwarze 1966; Derksen 1977; Paulin and Sagar 1977; Halpryn et al. 1982). These patterns are probably related to light-dependent foraging efficiency in combination with krill availability (Wilson et al., in preparation). We believe that in incubating birds, apparent circadian rhythms in physiological parameters are caused by climatic variations rather than by a diurnal rhythm per se (cf., Yeates 1971b).

Experiments on the influence of wind speed on pelt conductance or metabolic rate have been, thus far, carried out with restrained penguins or with penguin pelts in wind tunnels (Chappell and Holsclaw 1984; Taylor 1986; Stahel et al. 1987) at wind speeds below 5 m/s. We believe that our measurements of HR, conducted on Adélie penguins in situ exposed to wind speeds between 0 and 19 m/s and "normal" turbulence are more representative of the natural situation than previous studies.

The components responsible for insulation in Emperor penguins (*Aptenodytes forsteri*) are subcutaneous fat (1.5% – 2%), skin (12.5% – 17%) and feathers with their entrapped air (81% – 86%) (Jarman 1973). Drent and Stonehouse (1971) found that in the Peruvian penguin (*Spheniscus humboldtii*) 1/5 of the insulation was through body tissues and 4/5 through the feathers. In the Little penguin (*Eudyptula minor*) the major factor in insulation were the feathers (73%) (Stahel and Nicol 1982). Kooyman et al. (1976), finding no blubber layer in Adélie penguins during the summer, assumed feathers to be the main insulator, with fat contributing only 2% – 20% to total insulation.

Wind disrupts the plumage and the boundary layer around an animal, thereby shifting the thermoneutral zone towards higher temperatures (Goldstein 1983; Chappell and Holsclaw 1984). The thermal insulation afforded by an animals coat is highly dependent on the amount of air trapped, i.e., the width of the boundary layer determined by the length of the feathers, and its resistance to disturbance by wind, e.g. the density of the feathers. Published values for conductance in penguins are far greater than would be expected from their weight and aquatic life style. Stahel and Nicol (1982) found that insulation in the Little penguin does not differ significantly from that found in the Emperor penguin ($0.6\,\mathrm{w}^{-1} \cdot \mathrm{m}^2 \cdot {}^\circ\mathrm{C}$). They suggest that although very dense, penguins feathers are rather short (2.8 ± 0.5 cm) which leads to high heat loss on land.

According to Taylor (1986) the insulative properties of Gentoo *Pygoscelis papua* and Chinstrap *P. antarctica* penguin pelts increased at wind speeds above 5 m/s by compression and sealing of the feathers. This would lead to lower metabolic rates with increasing wind speeds. There was no evidence in our data to support this and we suggest that Taylor's results are artifacts created by using pelts where feathers are not orientated or maintained as in living birds, under conditions (air flow, turbulence) not representative of those found in nature (cf., Stahel et al. 1987).

The linear increase of pelt conductance or metabolic rate with wind speed (not the square root of wind speed) has been reported by several authors (Tregear 1965; Campbell et al. 1980; Chappell 1980; Goldstein 1983; Chappel and Holsclaw 1984). The fit between HR and wind speed presented here for the incubating Adélie penguin was best with a linear relationship. The apparent plateau of HR above wind speeds of 12 m/s may be due to variation between birds. However, incubating Adélie penguins might not be able to increase their metabolic rate above a certain value without becoming active, and this is not compatible with breeding. This point needs to be further investigated.

Temperatures during our experiments (−2.5° to 6 °C) represent a narrow range towards the lower end of the thermoneutral zone of Adélie penguins in still air (−10° to 20 °C; Chappell and Souza 1988) and therefore had no significant effect on metabolic rate. Adélie penguins nest in areas with high wind velocities, probably because these birds lay their eggs early in the season where the only available rocky substrate are wind-blown ridges (Trivelpiece et al. 1987). Adélie penguins normally appear to live within their thermoneutral zones and to compensate for changes in climatic conditions by altering their insulative capacity. However, facing the wind at high velocities (Yeates 1971 a), ptiloerection, vasoconstriction etc. are apparently insufficient to counter wind-induced heat loss.

Brown (1984) found in Macaroni (*Eudyptes chrysolophus*) and Rockhopper (*E. chrysocome*) penguins the energetic cost of incubation to be much lower than the resting metabolic rate and approaching basal metabolic rate. Croxall (1982) reports that in the Adélie penguin daily energy cost of incubation is 1.3 to 1.4 times the cost of basal metabolism. The resting heart rate for incubating Adélie penguins at zero wind speed (86 ± 5 bpm) compares well to values reported earlier for resting, non-incubating birds (92 bpm: Kooyman et al. 1976; 90 bpm: Millard et al. 1973), indicating that the energetic costs of incubation and rest are similar. Various figures for resting oxygen consumptions in Adélie penguins have been reported in the literature (Table 3). We calculated from these figures a mean oxygen consumption of 47.6 ml/min for a 4 kg resting Adélie penguin at zero wind speed. At wind speeds of 19 m/s (heart rate 112 bpm) this value would increase by about 30%. Rates of metabolic heat production in Adélie penguins resting at thermoneutrality in still air, are about 20% higher than predicted for non-passerines (Chappell and Souza 1988).

Although incubating Adélie penguins encounter temperatures above −10 °C (LCT in still air) most of the time, wind leads to a substantial increase in metabolic heat production. Weathers and Buttemer (1984) report that combined basal and thermoregulatory requirements typically represent 40% – 80% of total metabolic cost in

Table 3. Oxygen consumption of Adélie penguins at rest. The values given in the literature were used to calculate O_2 consumption of a 4 kg bird. The mean of these is 47.6 ml O_2/min

O_2 consumption (reported)	At w = 4 kg (calculated)	Source
0.0112 ml/g·min	44.8 ml/min	Chappell and Souza 1988
$13.55\ \mathrm{ml/kg}^{-0.72}\cdot\mathrm{min}$	36.8 ml/min	Kooyman et al. 1976
0.92 l/kg·h	61.3 ml/min	Ricklefs and Matthew 1983

birds. Increases in these requirements have therefore significant effects on the overall energy budget.

Increased metabolic rates in Emperor and King (*Aptenodytes patagonicus*) penguins have been reported for wind speeds above 4.5 and 5 m/s, respectively (LeMaho et al. 1976; Barré 1984). Stahel et al. (1987) report that winds up to 4.7 m/s have no influence on metabolic rates in the Little penguin at thermoneutrality. At low temperatures, however, metabolic rates increase linearly with wind speed. As opposed to these reports, Tregear (1965) and Goldstein (1983) maintain that there is no indication of a threshold wind velocity below which metabolic rate in homeotherms remains constant.

These apparently contradictory findings result from the fact that the thermoneutral zone of homeotherms cannot be described by temperature alone. Forced convection disrupts the boundary layer and leads to heat loss. The combined effect of low temperature and high wind speeds, presumably leads to larger heat loss and therefore higher metabolic rates than each factor by itself (Fig. 4). The lower critical temperature (LCT) of the thermoneutral zone is lowest in still air, and increases with wind speed. The resulting thermoneutral zone is a triangle. The shaded area in Fig. 4 schematically represents our data shown in Fig. 1. Accordingly, thermoregulatory cost remains constant until a certain threshold combination of both wind velocity and temperature is reached. Our data presented in Fig. 2 is a simplification, because the variance did not allow us to derive a threshold wind velocity for the temperature range encountered.

Observations from ships suggest that Adélie penguins spend most of the winter in the pack ice zone, rather than in the open ocean (W. Z. Trivelpiece, personal communication). L. S. Davis (personal communication) reports from radio-tracking data that Adélie penguins foraging at sea spend substantial amounts of time resting on ice floes. This supports the assumption of Kooyman et al. (1976) that Adélie penguins can cope with the cold temperatures of the Antarctic waters only as long as they are actively swimming and generating heat. It appears that resting birds prefer a dry environment, where thermal conductance is 25 times lower than in water. This allows them to conserve heat and maintain a low metabolic rate.

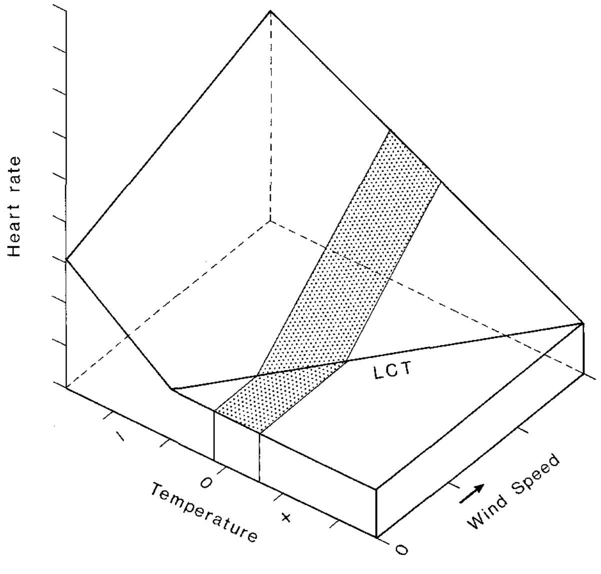

Fig. 4. Schematic representation of the combined effects of wind speed and temperature on metabolic rate in homeotherms. The thermoneutral zone is the flat area below the Lower Critical Temperature. The shaded area corresponds to Fig. 1

However, our study demonstrates than even under the most favourable natural meteorological conditions, on the nest, during the summer, these birds are not particularly well insulated. Although Adélie penguins adjust to climate by facing into the wind and standing less frequently, they have to compensate wind exacerbated heat loss by substantial (30%) increases in HR and therefore metabolic rate. At winter temperatures this effect will be even more pronounced. Living in an extreme environment is energetically costly for Adélie penguins.

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