

THERMAL INSULATION OF THE DOWN AND FEATHERS OF PYGOSCELID PENGUIN CHICKS AND THE UNIQUE PROPERTIES OF PENGUIN FEATHERS

JAN R. E. TAYLOR¹

*Department of Polar Research, Institute of Ecology, Polish Academy of Sciences,
Dziedkanów Leśny, 05-150 Łomianki, Poland*

ABSTRACT.—The thermal insulation of the down and feathers of Chinstrap (*Pygoscelis antarctica*) and Gentoo (*P. papua*) penguin chicks was measured throughout development in still air and in wind parallel and perpendicular to the plumage. Insulation increased with age. Whole-body insulation of chicks measured in still air (body core to environment) was significantly correlated with the insulation of their pelts at a given age. The insulation of the downy pelts of 10- and 15-day-old chicks was significantly lower than that of all older chicks, and explains the dependence of chicks of that age on continuous brooding by parents, despite their high thermogenic capacities. The down of older chicks provided good insulation in wind speeds of 3–5 m/s. With no wind, the down of Gentoos immediately before molting was a better insulator than feathers of preflledged chicks. The insulation of the feathers of preflledged chicks in parallel air flow up to 5 m/s was 87–112% of its value in still air. However, the insulation increased at higher wind speeds; in Gentoo pelts at winds of 15 m/s, it averaged 136% (maximum 179%) of the insulation in still air. Increasing insulative values of feathers or fur under increasing wind speeds have not been demonstrated previously in any bird or mammal. The insulation of down at various wind speeds and micrometeorological data from the Gentoo Penguin rookery on King George Island, Antarctica were compared. It follows that heat loss of older downy Gentoo chicks is not affected significantly by wind. These chicks can remain within their thermoneutral zones on windy days. *Received 6 March 1985, accepted 16 September 1985.*

ONE of the basic adaptations of homeothermic animals to cold is a thick, dense coat of fur or feathers that effectively diminishes heat loss (Scholander et al. 1950). There are few data on the insulative value of penguin feathers, but plumage provides most of their insulation (Le Maho 1977) and antarctic penguin species tend to have longer feathers than penguins in warmer climates (Stonehouse 1967).

Penguin chicks spend their preflledged development on land. They are covered with down during this time, but just before they leave land, feathers replace down. At least until chicks achieve homeothermy, they are brooded by their parents, and thereafter are frequently exposed directly to the prevailing climatic conditions. The chicks of antarctic penguins, in particular, are exposed to low temperatures and strong winds typical of that

region (Sapin-Jaloustre 1960, Goldsmith and Sladen 1961, Prévost 1961, Boyd and Sladen 1971). It is thus of interest to determine the extent to which the down protects penguin chicks from heat loss in these circumstances. Except for studies by McNabb and McNabb (1977) and Chappell (1980), no research has been done on the insulative value of the down of chicks of wild birds, or the influence of wind on the insulation of down.

One object of my work was to define the insulative properties of the down and feathers of Chinstrap (*Pygoscelis antarctica*) and Gentoo (*P. papua*) penguin chicks. Measurements of insulation were carried out on pelts of chicks when they were partially (at 10–15 days of age) or fully (when they were no longer brooded) exposed to climatic conditions.

The second object of the study was to estimate the extent to which wind affected the insulation of down and feathers of penguin chicks. I measured pelt insulation with a simulated wind. These measurements make the metabolic data of pygoscelid penguin chicks

¹ Present address: Department of Biology, University of Warsaw, Sosnowa 64, 15-887 Białystok, Poland.

more useful in extrapolations to natural conditions.

MATERIALS AND METHODS

All pelt samples were collected on King George Island, the South Shetlands, Antarctica in the vicinity of the Polish Academy of Sciences Henryk Arcowski Station, during the austral summer of 1979-1980. Pelts were obtained from 10-, 15-, and 25-day-old Chinstrap and Gentoos penguin chicks; from 40-day-old downy Gentoos young; and from fully feathered, prefledged chicks of both species (about 55-day-old Chinstraps and 70-day-old Gentoos). Because 40-day-old Chinstrap chicks were molting, I did not use their pelts.

Pelts were collected from two individuals in each age category. Two dorsal pelts were obtained from each 10-day-old chick, two dorsal and two ventral pelts from 15-day-old chicks, and three dorsal (one from the front, one from the middle, and one from the back region of the body) and three ventral pelts from each older chick. The positions of the pelts were thus fairly evenly distributed over the trunk of each chick. The whole collection comprised 84 pelts.

Fat and flesh were removed from skins, and 10 × 10-cm squares of skin were pinned flat and dried slowly at room temperature.

The thermal insulation of a sample of the coat (I_c , $\text{m}^2 \cdot ^\circ\text{C} \cdot \text{W}^{-1}$) of an animal was defined as

$$I_c = (T_s - T_a)/H,$$

where T_s is the temperature of the lower surface of the skin ($^\circ\text{C}$), T_a is the air temperature, and H is the heat flow through the coat (W/m^2). I_c is the sum of the thermal insulation of the skin, the thermal insulation of down or feathers, and the thermal insulation of the boundary layer of air above the coat. The reciprocal of I is thermal conductance.

For measurements of thermal insulation, pelts were mounted on a conventional heat-flow apparatus that consisted of a heat source and heat-flow meter (Fig. 1). A constant controllable temperature was provided by one face of a 9 × 9 × 2.5-cm steel chamber. Water at a constant temperature of 40°C ($\pm 0.1^\circ\text{C}$), monitored with a thermistor probe within the chamber, was circulated continuously from a temperature-controlled reservoir. The edges and bottom surface of this steel box were covered with a 2-cm layer of Styrofoam to minimize heat loss. A heat-flow meter 3 mm thick and 5 cm in diameter (WS 32, Dutch Office of Technical Physics) was attached centrally to the face of the chamber and was mounted within a sheet of plastic that formed the upper surface of the apparatus (Fig. 1). The plastic sheet had a thermal conductivity similar to that of the heat-flow disc. The meter consisted of thermopile embedded in a flexible material. The heat flow through the disc generated

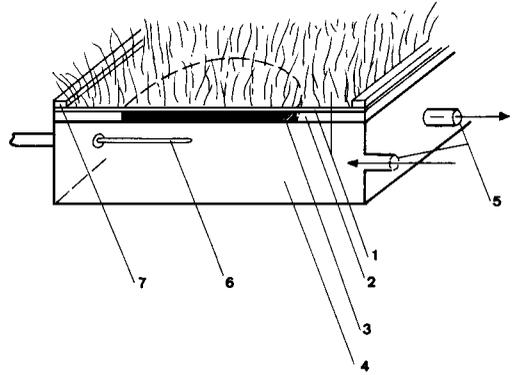


Fig. 1. Apparatus used in heat-flow measurements. 1 = skin with down or feathers, 2 = plastic sheet, 3 = heat-flow meter, 4 = steel box, 5 = inlet and outlet for temperature-controlled water, 6 = thermistor probe, 7 = clamp.

an electromotive force due to the temperature difference between the thermocouple junctions of the thermopile. The output was measured with a potentiometer. A sample of each pelt mounted on a wooden frame was placed over the upper surface of the apparatus. The bonding between the pelt and plate was achieved with a thin film of grease.

The entire complex (pelt, heat-flux transducer, hot plate) was placed in an open-ended wind tunnel, 40 cm in diameter. Air was drawn through the tunnel by a fan. Air turbulence was reduced by the presence of flutes at the inlet and outlet ends of the tunnel. For each pelt sample the insulation was determined in still air and at 1, 3, 5.5, 8, 10, and 15 m/s. Air speed was measured with a Prandtl tube. In these experiments air flow was parallel to the surface of the sample and, in the case of pelts from prefledged chicks, perpendicular to the shafts of the feathers. While the temperature of the air in the tunnel, measured with a mercury thermometer ($\pm 0.1^\circ\text{C}$) was constant during each experiment, it varied between 10 and 15°C in different experiments.

The same measurements were carried out with the heat-flow apparatus placed upright, with the wind flow perpendicular to the plumage. These measurements were performed without the wind tunnel, using a blower only, at wind velocities of 1, 3, 5.5, and 10 m/s.

The temperature gradient between the water in the metal chamber and the air above the pelt was divided by the measured value of heat flow (H) through the pelt, the meter, and the upper wall of the chamber. The resulting figures yielded the total insulation of the three layers. The insulation of the pelt was obtained by subtracting the known value of the insulation of the meter and the wall (1.2-12% of the total insulation of three layers).

TABLE 1. The effect of wind on the thermal insulation ($\text{m}^2 \cdot ^\circ\text{C} \cdot \text{W}^{-1}$) of downy pelts of Chinstrap and Gentoo penguin chicks parallel to the direction of air movement.^a

Species	Age (days)	n	Pelt thickness ^b (mm)	Wind speed (m/s)						
				0	1	3	5.5	8	10	15
Chinstrap Penguin	10	4	8	0.258	0.210	0.198	0.161	0.127	0.113	0.092
	15	8	11	0.298	0.246	0.232	0.212	0.194	0.178	0.148
				± 0.028	± 0.028	± 0.027	± 0.027	± 0.024	± 0.019	± 0.009
25	12	21	0.488	0.457	0.431	0.429	0.415	0.372	0.262	
				± 0.029	± 0.027	± 0.030	± 0.029	± 0.036	± 0.040	± 0.039
Gentoo Penguin	10	4	8	0.272	0.224	0.211	0.192	0.180	0.174	0.159
	15	8	10	0.279	0.238	0.221	0.203	0.184	0.168	0.136
				± 0.017	± 0.014	± 0.014	± 0.016	± 0.018	± 0.015	± 0.011
	25	12	19	0.467	0.426	0.402	0.397	0.369	0.348	0.292
± 0.031				± 0.024	± 0.021	± 0.024	± 0.025	± 0.027	± 0.041	
40	12	27	0.610	0.592	0.588	0.581	0.508	0.441	0.312	
				± 0.030	± 0.032	± 0.052	± 0.074	± 0.088	± 0.070	± 0.060

^a Values represent means \pm SD.

^b Including 0.5 mm of skin in the pelts of 10- and 15-day-old chicks and about 1 mm in other chicks.

RESULTS

The thermal insulation of the first down of 10- and 15-day-old chicks was low, even in still air, and never exceeded $0.3 \text{ m}^2 \cdot ^\circ\text{C} \cdot \text{W}^{-1}$ (Table 1). Insulation increased as the coat of down grew thicker and doubled in value from 10 to 25 days of age when measured in still air. In down-covered 40-day-old Gentoo Penguin chicks, the insulation with no wind was the highest among all such values.

The pelt insulation of prefledged chicks with fully grown feathers, measured in still air, was $0.541 \pm 0.047 \text{ m}^2 \cdot ^\circ\text{C} \cdot \text{W}^{-1}$ ($n = 12$) for Chinstraps and $0.557 \pm 0.029 \text{ m}^2 \cdot ^\circ\text{C} \cdot \text{W}^{-1}$ ($n = 12$) for Gentoos. There was no statistically significant difference between these values ($P > 0.4$, t -test). The insulation of the ventral pelts of prefledged birds of both species was significantly greater than that of their dorsal pelts ($P < 0.001$, Table 2). The down of Gentoo chicks immediately before molting was a better insulator in still air than feathers (by about 10%; $P < 0.001$).

Heat loss from the pelts of 10- and 15-day-old chicks was strongly affected by wind, even at low velocities (Tables 1 and 3). The insulative value of these pelts decreased by nearly 20% at wind speed (u) = 1 m/s and 40–50% at $u = 10$ –15 m/s. In the pelts of 15-day-old chicks such deterioration of insulation occurred in wind flows both parallel and perpendicular to the pelts (Fig. 2).

As chicks grew older the thicker down became a better insulator in windy conditions. The insulation of downy pelts of 25- and 40-day-old chicks measured parallel to the direction of air movement remained, in general, fairly high for wind speeds up to 5.5 m/s but diminished rapidly when wind speeds exceeded this critical value (Table 1). For wind speeds less than 5.5 m/s and in parallel air flow, the reduction of insulation of the pelts of 25-day-old chicks did not exceed 15% of values in still air. The decrease in the insulation of the pelts of 40-day-old downy Gentoo chicks at $u \leq 5.5$ m/s did not exceed 5% (Fig. 2A, B).

In winds perpendicular to the pelts, the insulation of the down of older chicks remained high up to about 3 m/s. Contrary to the measurements with parallel air flow, the insulation of longer down was more affected by wind than the insulation of shorter down. At $u \geq 3$ m/s the insulation of the thickest downy pelts of 40-day-old Gentoo chicks was considerably lower than that of both 15- and 25-day-old chicks (Table 3, Fig. 2C).

The relationship of insulation to wind speed when the wind was parallel to the plumage was entirely different in the case of feathered pelts (Table 2, Fig. 2A, B). At lower wind speeds insulation diminished, but by less than 15% of the value measured in still air. At wind speeds greater than 5.5 m/s, however, the insulation value increased, and at $u = 15$ m/s achieved a mean of 125% of the value measured in still air

TABLE 2. Effect of wind on the thermal insulation ($\text{m}^2 \cdot ^\circ\text{C} \cdot \text{W}^{-1}$) of dorsal and ventral feathered pelts of Chinstrap and Gentoo penguin chicks parallel to the direction of air movement.* The slopes of the regression lines of the insulation on the pelt thickness (an increment of the insulation per 1 mm of pelt thickness) also are given.

	Chinstrap Penguin			Gentoo Penguin		
	Dorsal	Ventral	Slope	Dorsal	Ventral	Slope
Pelt thickness ^b (mm)	18	25		23	28	
Range	16-20	22-27		22-24	26-31	
Wind speed						
0 m/s	0.499 ± 0.009	0.582 ± 0.026	0.0111	0.532 ± 0.013	0.583 ± 0.012	0.0092
1 m/s	0.459* ± 0.014 (92)	0.551* ± 0.027 (95)	0.0124	0.498* ± 0.015 (94)	0.560* ± 0.012 (96)	0.0109
3 m/s	0.439* ± 0.016 (88)	0.552* ± 0.027 (95)	0.0150	0.493* ± 0.017 (93)	0.585 ± 0.016 (100)	0.0159
5.5 m/s	0.434* ± 0.019 (87)	0.594 ± 0.049 (102)	0.0218	0.508* ± 0.017 (95)	0.654* ± 0.033 (112)	0.0246
8 m/s	0.441* ± 0.026 (88)	0.652 ± 0.068 (112)	0.0285	0.551 ± 0.033 (104)	0.741* ± 0.077 (127)	0.0333
10 m/s	0.448* ± 0.034 (90)	0.709* ± 0.082 (122)	0.0353	0.605* ± 0.042 (114)	0.819* ± 0.092 (140)	0.0367
15 m/s	0.477 ± 0.055 (96)	0.769* ± 0.086 (132)	0.0393	0.678* ± 0.049 (127)	0.848* ± 0.155 (145)	0.0277

* Values of the insulation represent means ± SD; $n = 6$ in each case. Numbers in parentheses are the percentages of the value in still air (0 m/s). * = insulation value significantly different from that at 0 m/s ($P < 0.01$, paired-sample t -test).

^b Including 1 mm of skin. Average length of dorsal and ventral feathers measured by the method of Stonehouse (1967) was 37 mm in Gentoos and 36 mm in Chinstraps.

(Table 2). With the exclusion of dorsal pelts of Chinstrap chicks, the insulation value at $u = 15$ m/s was always greater than the one measured under zero wind conditions, and it reached a mean of 135% of the value measured in still air. The greatest increase of insulation (79%, from $0.575 \text{ m}^2 \cdot ^\circ\text{C} \cdot \text{W}^{-1}$ at $u = 0$ m/s to $1.03 \text{ m}^2 \cdot ^\circ\text{C} \cdot \text{W}^{-1}$ at $u = 15$ m/s) was observed for one of ventral pelts of a Gentoo preflledged chick (Fig. 3).

The thermal insulation of feathered pelts of both species measured at a given wind speed in air flow parallel to the plumage had a positive linear correlation with pelt thickness (Fig. 4; correlations were calculated for dorsal and ventral pelts together). All correlation coefficients were statistically significant (t -test, $P < 0.05$ for Gentoos at $u = 15$ m/s; $P < 0.001$ in all other cases). The increase in insulation value at high wind speeds was greater in the case of thicker pelts. The pelt must be at least 29 mm thick for insulation at increased wind speeds (e.g. 3 m/s) to be greater than in still air; for $u = 8$ m/s the pelt must be only 22 mm thick, and for $u = 15$ m/s only 19 mm thick (Fig. 4).

In air flow perpendicular to feathered pelts, insulation diminished over the entire range of wind speed (Table 4). However, the rate of this decrease was lower than in down (Fig. 2C).

DISCUSSION

There is a constant increase in the thermal insulative value of downy pelts with the age of chicks (Table 1). This increase occurs because of the increased thickness of down and possibly because of changes of its quality. The skin contributes negligibly to the total pelt insulation value. If we assume that the thermal conductivity of skin equals $0.50 \text{ W} \cdot \text{m}^{-1} \cdot ^\circ\text{C}^{-1}$ (Gates 1980), the skin contributes less than 1% of the insulation in both feathered and downy pelts. The insulation of chick pelts measured in still air was correlated significantly with the whole-body insulation of chicks at a given age ($r = 0.99$, $P < 0.001$, t -test; Fig. 5). The values of the whole-body thermal insulation, body core to environment, measured on live chicks (Taylor 1985) are the reciprocals of the whole-body conductances reported there.

TABLE 3. Thermal insulation ($\text{m}^2 \cdot ^\circ\text{C} \cdot \text{W}^{-1}$) of downy pelts of Gentoo Penguin chicks in winds perpendicular to the pelts.*

Age (days)	Wind speed (m/s)			
	1	3	5.5	10
15	0.225 ± 0.023	0.208 ± 0.028	0.174 ± 0.017	0.170 ± 0.012
25	0.428 ± 0.026	0.401 ± 0.029	0.305 ± 0.021	0.263 ± 0.017
40	0.522 ± 0.040	0.446 ± 0.030	0.324 ± 0.032	0.281 ± 0.038

* Values represent means \pm SD. Sample sizes as in Table 1.

The ratio of pelt insulation value to the whole-body insulation of the chicks indicates the importance of insulative properties of down and chick feathers in reducing heat loss. This ratio was not lower than 0.80 for 25-day-old and older Chinstrap and Gentoo chicks. Thus, the role of down and feathers in the reduction of heat loss in these chicks is approximately the same as in adult penguins of other species. The ratio calculated from the differences between the body, skin, and ambient temperatures (at the lower critical temperature) is 0.86 for Emperor Penguins (*Aptenodytes forsteri*; Jarman 1973, Le Maho et al. 1976) and about 0.80 for Humboldt (*Spheniscus humboldti*) and Little Blue penguins (*Eudyptula minor*; Drent and Stonehouse 1971, Stahel and Nicol 1982). On the other hand, this ratio in pygoscelid chicks is higher than in summer and in winter-acclimatized King Penguin (*Aptenodytes patagonica*) chicks (0.74 and 0.56, respectively; Barré 1984).

The low insulative value of the short down of 15-day-old Chinstrap and Gentoo penguin chicks (Table 1) has a bearing on their low whole-body insulation (Fig. 5). The insulation value of down in 10- and 15-day-old chicks both in still air and wind was much lower than the down insulation of older chicks. For this reason 10- and 15-day-old chicks still depend on the heat provided by adult birds, in spite of their own high ability to produce heat and their homeothermy at about 15 days of age (Taylor 1985). Brooding of chicks by parents becomes less effective as they grow due to their large size (Taylor 1985). However, parents guarding 15-20-day-old chicks could serve as effective wind screens. The cessation of brooding and guarding and the beginning of full exposure of chicks to the physical conditions of the en-

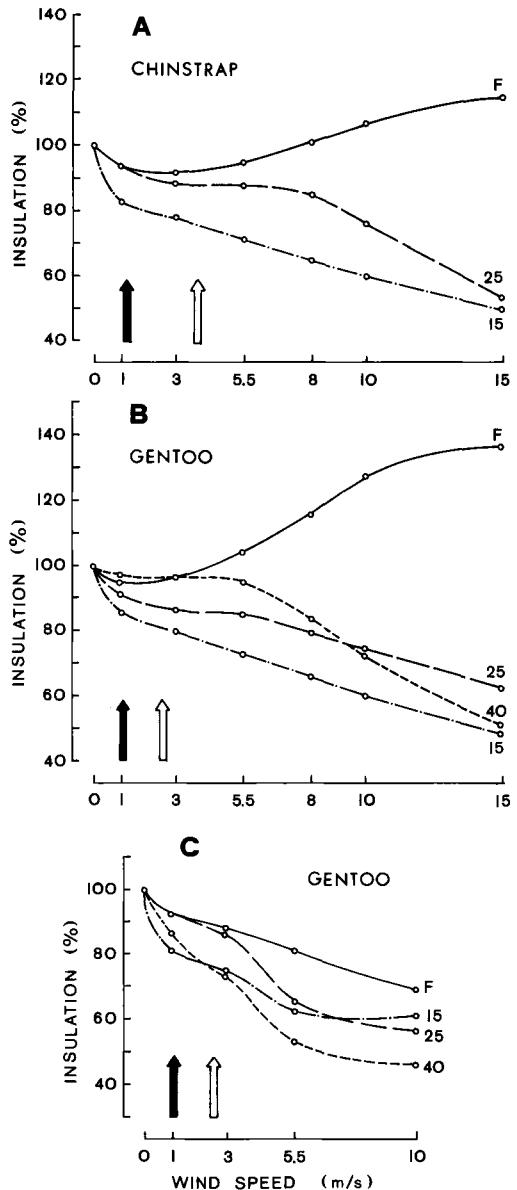


Fig. 2. Thermal insulation of the pelts of pygoscelid penguin chicks relative to wind speed. Insulation is expressed as a percentage of the value in still air. (A) Chinstrap Penguin, wind flow parallel to the pelt. (B) Gentoo Penguin, wind flow parallel to the pelt. (C) Gentoo Penguin, wind flow perpendicular to the pelt. The ages of the chicks are given next to the curves; F = feathered chicks. Black arrows indicate the average wind speed in the breeding colony of each species; white arrows indicate the average maximum wind speed.

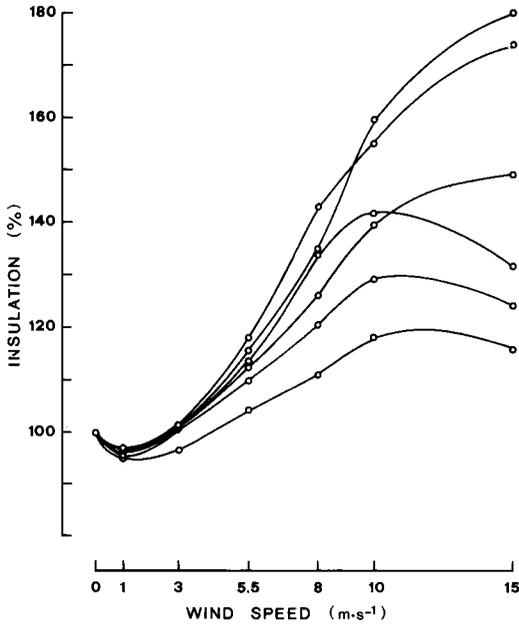


Fig. 3. The increase of thermal insulation of 6 feathered ventral pelts from prefledged Gentoo Penguin chicks as wind speed increased. Air movement was parallel to the pelts. Insulation is expressed as a percentage of the value in still air.

vironment coincides with the time that their down achieves high insulative value (i.e. between 15 and 25 days of age; Table 1). Barré (1978) found a similar correlation between the length of down in the chicks of King Penguins and the age of emancipation, which takes place after the chicks become homeothermic.

In still air or gentle wind the down of 25-day-old chicks was nearly equal, and shortly before their molt (40 days after hatching) was an even better insulator than feathers. This high insulation value of downy pelts of Gentoo chicks just before molting was due to the thickness of the coat of down at this age, which was even greater than the thickness of the feather layer in prefledged chicks (Tables 1 and 2). The highest insulation of 40-day-old Gentoos coincides with a very high whole-body insulation value ($0.735 \text{ m}^2 \cdot \text{C} \cdot \text{W}^{-1}$), which is greater than in Gentoo chicks shortly after molt (Fig. 5) and provides an exceptionally low lower critical temperature (-15°C ; Taylor 1985). Fully grown but still downy King Penguin chicks are probably also better insulated than adult birds. This can be inferred from the fact that during

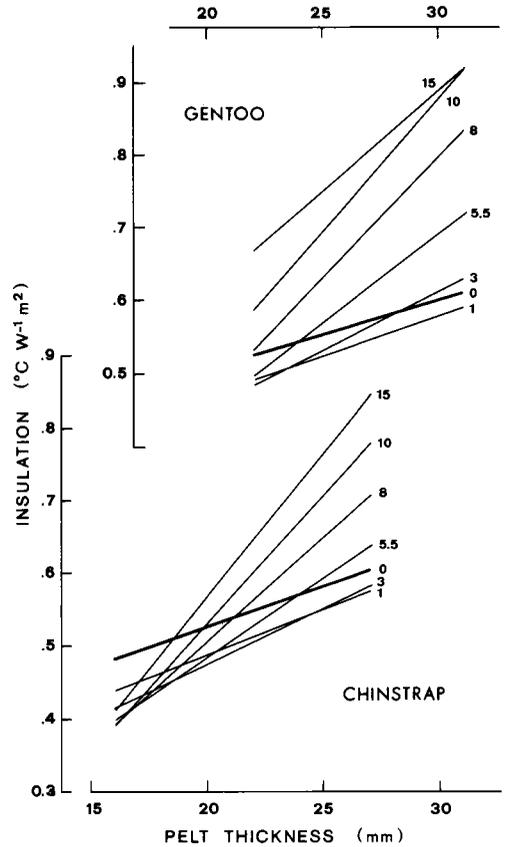


Fig. 4. Thermal insulation of the pelts of feathered Chinstrap and Gentoo penguin chicks as a function of pelt thickness at various wind speeds. Wind flow was parallel to the pelts. Wind speeds are given next to the regression lines. The linearity of the relationships was checked at $P < 0.05$ by the modified one-sample runs test, which is stronger than the ordinary test (Pawłowski 1976).

winter fast these chicks consume considerably less fat reserves than their parents (Mougin 1974, Barré 1976).

The insulation of feathered pelts in still air is similar to the values for pelts of adult Gentoo and Adélie (*Pygoscelis adeliae*) penguins given by Kooyman et al. (1976). There are no available data on the insulation properties of the integument of chicks or adult birds of other high-latitude species. The pelt insulation of young pygoscelid penguins, of 25 days of age and older, is very close to the insulation of summer pelts of arctic mammals and considerably lower than the insulation of winter coats of those animals (Hart 1956). The pelts of older

TABLE 4. Thermal insulation ($\text{m}^2 \cdot ^\circ\text{C} \cdot \text{W}^{-1}$) of dorsal and ventral feathered pelts of Chinstrap and Gentoo penguin chicks in winds perpendicular to the pelts.^a

Species	Wind speed (m/s)			
	1	3	5.5	10
Chinstrap Penguin				
Dorsal	0.409 ± 0.021 (82)	0.392 ± 0.027 (79)	0.379 ± 0.039 (76)	0.353 ± 0.035 (71)
Ventral	0.549 ± 0.027 (94)	0.524 ± 0.032 (90)	0.481 ± 0.028 (83)	0.362 ± 0.025 (62)
Gentoo Penguin				
Dorsal	0.466 ± 0.017 (88)	0.452 ± 0.022 (85)	0.442 ± 0.032 (83)	0.396 ± 0.041 (74)
Ventral	0.557 ± 0.043 (96)	0.530 ± 0.038 (91)	0.460 ± 0.020 (79)	0.373 ± 0.026 (64)

^a Values represent means \pm SD; $n = 6$. Numbers in parentheses are the percentages of the value in still air (0 m/s).

pygoscelid chicks have insulation values similar to mammal pelts of the same thickness (Scholander et al. 1950, Hart 1956).

Increased thermal insulation of feathers under increased wind speeds (Table 2, Figs. 2A, B and 3) has not been reported previously. The insulation properties of feathers in wind have been described only in the Sharp-tailed Grouse (*Tympanuchus phasianellus*; Evans and Moen 1975) and the Rock Dove (*Columba livia*; Walsberg et al. 1978). In both cases, the insulation value decreased proportionally with the reciprocal of the square root of the wind speed. Similarly, the increase of total pelt insulation has not been noted in the more extensive studies on fur (Moote 1955, Lentz and Hart 1960, Tregear 1965, Hutchinson and Brown 1969, Ames and Insley 1975, Degabriele and Dawson 1979).

The mechanism of the phenomenon is unknown and requires an experimental explanation. Stonehouse (1967) stated: "The penguin feathers seem especially well adapted for resisting wind movement. The short, stiff rachis of adjunct feathers, overlapping like tiles on a roof, are pressed more closely together rather than parted by strong winds, and are likely to be more efficient than mammal fur in retaining an undisturbed stratification of air close to the skin." This may explain the increase of penguin feather insulation in high wind flow par-

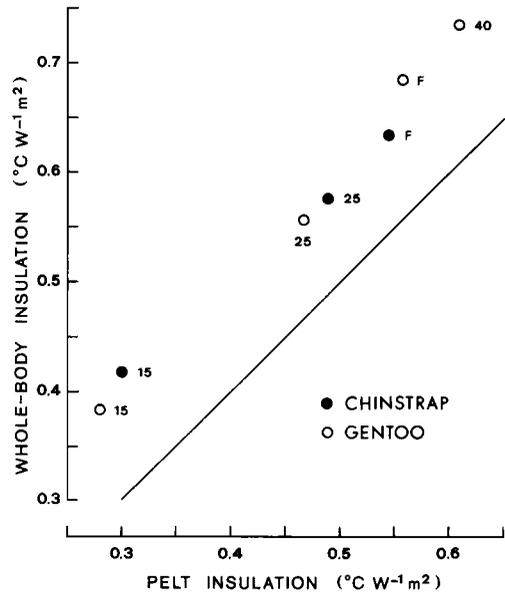


Fig. 5. Relationship between whole-body insulation and pelt insulation in Chinstrap and Gentoo penguin chicks at various ages. The diagonal line represents the equivalence of both types of insulation. Numbers next to circles indicate chick ages (days after hatching); F = feathered chicks.

allel to the plumage. The shafts of penguin contour feathers are flattened and elastic. The ends of the shafts are pointed toward the back of the body, and the top parts of vanes of neighboring feathers overlap flatly, forming a uniform surface. This structure and arrangement of feathers is primarily an adaptation to life in water. Under the influence of hydrostatic pressure the ends of the feathers lie more closely together, separating the insulating layer of air close to the skin from the water (Rutschke 1965). The pressure of the flowing air may produce an effect similar to hydrostatic pressure. This seems to be supported by the significant dependence between the rate of increase of insulation at a given wind speed and the thickness of the coat of feathers (Fig. 3). The longer the feathers are, the more elastic their shafts appear to be. On the other hand, it is difficult to explain in such a way the lack of increase in insulation when the pelts are placed perpendicular to the direction of air movement.

Nachtigall and Bilo (1980) stated that adult Gentoo Penguins have a surprisingly low coefficient of drag in water, lower than should re-

sult from their optimal shape. The authors suggested that this phenomenon is connected with the properties of their feathers, which damp the turbulence of water flowing around a penguin's body. It is thus possible that the increase in thermal insulation of feathers of Chinstraps and Gentoos in wind also is caused by the reduction of turbulence of air flowing over the pelt.

My results may be important for further investigation of the adaptations of penguins. If air flow reduces heat loss by the feathers, an analogous effect should be produced by water flowing around a penguin's body. If we accept Nachtigall and Bilo's (1980) hypothesis of damping turbulence, the laminar flow of water would enable the bird to move more quickly in water, and also would diminish heat loss. This is particularly important because heat loss in penguins is greater in water than in air (Kooyman et al. 1976, Stahel and Nicol 1982). However, this turbulence-suppression hypothesis requires supportive data.

The thermoneutral zones of Chinstrap and Gentoo penguin chicks 25 days old and older are 15–30°C wide, with a lower critical temperature as low as –15°C. These zones cover the range of air temperature variations common in the breeding colonies of both species at Point Thomas (King George Island, the South Shetlands) during the austral summer (Taylor 1985). The thermoneutral zones of these chicks were determined in a metabolic chamber in practically still air. On the other hand, heat loss in birds increases with the increase of wind speed (Goldstein 1983); air flow diminishes whole-body thermal insulation of birds and raises their lower critical temperature.

My results cannot give a quantitative estimate of rate of heat loss from the whole chick body despite the even distribution of collected pelts over the chick trunk. It is difficult to extrapolate from results obtained with a flat piece of pelt to heat transfer across the curved surface of a bird. However, these results provide an approximation of the extent to which heat loss from penguin chicks is affected by wind.

The slope of the regression line of energy metabolism on air temperature at low ambient temperatures can be considered in older downy Gentoo chicks as the whole-body conductance (Taylor 1985). The reciprocal of this conductance is whole-body insulation. I calculated a new slope of the regression line such that the

lower critical temperature was equal to the mean air temperature in a Gentoo Penguin breeding colony (2.3°C, Point Thomas colony; E. Moczydłowski unpubl. data). It was found that in air at 2.3°C the whole-body insulation should decrease by at least 14% in 25-day-old Gentoo chicks and by at least 25% in 40-day-old Gentoos if these birds are outside their thermoneutral zones.

The average wind speed in the Gentoo Penguin colony at Point Thomas during the austral summer 1979–1980 was 1.1 m/s (measured 35 cm above the ground when adult birds ceased brooding chicks). The average maximum wind speed on subsequent days of this period was 2.5 m/s. In a Chinstrap rookery these wind speeds were 1.2 and 3.8 m/s, respectively (E. Moczydłowski unpubl. data). These wind speeds did not lower the insulation of downy pelts of 25-day-old Gentoos by more than 14% in experimental air flows or by more than 4% (parallel) and 27% (perpendicular) in 40-day-old Gentoo pelts (Fig. 2B, C). Because the insulation of down is a major part of the whole-body insulation (Fig. 5), I inferred that the wind does not affect significantly the heat loss of older downy Gentoo chicks and that they remain within their thermoneutral zones even on windy days.

It is more difficult to estimate, on the basis of the available data, the effect of wind on heat loss in feathered chicks. These chicks probably suffered considerable heat loss through their practically bare flippers. However, wind speeds to at least 5 m/s have no important effect on the metabolic rate of adult Emperor Penguins (Le Maho et al. 1976) and King Penguins (Barré 1980). The increase of feather insulation in pre-fledged Chinstraps and Gentoos recorded in stronger winds parallel to the pelts probably is not important in the reduction of their heat loss on land. Only at the highest recorded wind speeds of 5.6 m/s in the Gentoo rookery and 13.0 m/s in the Chinstrap rookery did the insulation value exceed the insulation in still air (by 5% and 12%, respectively).

ACKNOWLEDGMENTS

I am grateful to Prof. Andrzej Myrcha for making possible my participation in the Fourth Antarctic Expedition of the Polish Academy of Sciences to King George Island. Measurements were made with the aid of Andrzej Depczyński. Prof. Krzysztof Cena loaned me the heat-flow meter. I am grateful to two

anonymous reviewers who suggested many important improvements in an earlier draft of the manuscript. I thank Dr. N. Volkman and Dr. W. Trivelpiece for correcting the English.

LITERATURE CITED

- AMES, D. R., & L. W. INSLEY. 1975. Wind-chill effect for cattle and sheep. *J. Anim. Sci.* 40: 161-165.
- BARRÉ, H. 1976. Etude de la dépense énergétique du poussin de Manchot royal (*Aptenodytes patagonica* J. F. Miller) dans les conditions ambiantes naturelles. *Comptes Rendus Acad. Sci. Paris* 285 D: 89-92.
- . 1978. Dépense énergétique du poussin de Manchot royal *Aptenodytes patagonicus* (J. F. Miller) au cours de la croissance. *J. Physiol., Paris* 74: 555-561.
- . 1980. Étude du métabolisme énergétique du Manchot royal (*Aptenodytes patagonicus* J. F. Miller) dans les conditions ambiantes naturelles. *Comptes Rendus Acad. Sci. Paris* 291 D: 493-496.
- . 1984. Metabolic and insulative changes in winter- and summer-acclimatized King Penguin chicks. *J. Comp. Physiol.* 154B: 317-324.
- BOYD, J. C., & W. J. L. SLADEN. 1971. Telemetry studies of the internal body temperatures of Adélie and Emperor penguins at Cape Crozier, Ross Island, Antarctica. *Auk* 88: 366-380.
- CHAPPELL, M. A. 1980. Thermal energetics of chicks of arctic-breeding shorebirds. *Comp. Biochem. Physiol.* 65A: 311-317.
- DEGABRIELE, R., & T. J. DAWSON. 1979. Metabolism and heat balance in an arboreal marsupial, the koala (*Phascolarctos cinereus*). *J. Comp. Physiol.* 134: 293-301.
- DRENT, R. H., & B. STONEHOUSE. 1971. Thermoregulatory responses of the Peruvian Penguin, *Spheniscus humboldti*. *Comp. Biochem. Physiol.* 40A: 689-710.
- EVANS, K. E., & A. N. MOEN. 1975. Thermal exchange between Sharp-tailed Grouse (*Pedioecetes phasianellus*) and their winter environment. *Condor* 77: 160-168.
- GATES, D. M. 1980. *Biophysical ecology*. New York, Springer-Verlag.
- GOLDSMITH, R., & W. J. L. SLADEN. 1961. Temperature regulation of some Antarctic penguins. *J. Physiol., London* 157: 251-262.
- GOLDSTEIN, D. L. 1983. Effect of wind on avian metabolic rate with particular reference to Gambel's Quail. *Physiol. Zool.* 56: 485-492.
- HART, J. S. 1956. Seasonal changes in insulation of the fur. *Can. J. Zool.* 34: 53-57.
- HUTCHINSON, J. C., & G. D. BROWN. 1969. Penetration of cattle coats by radiation. *J. Appl. Physiol.* 26: 454-464.
- JARMAN, M. 1973. Experiments on the Emperor Penguin, *Aptenodytes forsteri*, in various thermal environments. *Brit. Antarctic Surv. Bull.* 33/34: 57-63.
- KOORYMAN, G. L., R. L. GENTRY, W. P. BERGMAN, & H. T. HAMMEL. 1976. Heat loss in penguins during immersion and compression. *Comp. Biochem. Physiol.* 54A: 75-80.
- LE MAHO, Y. 1977. The Emperor Penguin: a strategy to live and breed in the cold. *Amer. Sci.* 65: 680-693.
- , P. DELCLITTE, & J. CHATONNET. 1976. Thermoregulation in fasting Emperor Penguins under natural conditions. *Amer. J. Physiol.* 231: 913-922.
- LENTZ, C. P., & J. S. HART. 1960. The effect of wind and moisture on heat loss through the fur of newborn caribou. *Can. J. Zool.* 33: 679-688.
- MCNABB, F. M. A., & R. A. MCNABB. 1977. Skin and plumage changes during the development of thermoregulatory ability in Japanese Quail chicks. *Comp. Biochem. Physiol.* 58A: 163-166.
- MOOTE, I. 1955. The thermal insulation of caribou pelts. *Textile Res. J.* 25: 832-837.
- MOUGIN, J. L. 1974. Enregistrements continus de températures internes chez quelques Spheniscidae. II. Le Manchot royal *Aptenodytes patagonica* de l'Île de la Possession (Archipel Crozet). *Compte Natl. Français Recherches Antarctiques* 33: 29-56.
- NACHTIGALL, W., & D. BILO. 1980. Strömungsanpassung des Pinguins beim Schwimmen unter Wasser. *J. Comp. Physiol.* 137: 17-26.
- PAWŁOWSKI, Z. 1976. [Mathematical statistics.] Warsaw, Państwowe Wydawnictwo Naukowe.
- PRÉVOST, J. 1961. *Ecologie du Manchot empereur Aptenodytes forsteri* Gray. Paris, Hermann.
- RUTSCHKE, E. 1965. Beiträge zur Morphologie der Pinguinfeder. *Z. Morph. Ökol. Tiere* 55: 835-858.
- SAPIN-JALOUSTRE, J. 1960. *Ecologie du Manchot Adélie*. Paris, Hermann.
- SCHOLANDER, P. F., V. WALTERS, R. HOCK, & L. IRVING. 1950. Body insulation of some arctic and tropical mammals and birds. *Biol. Bull.* 99: 225-236.
- STAHEL, C. D., & S. C. NICOL. 1982. Temperature regulation in the Little Penguin, *Eudyptula minor*, in air and water. *J. Comp. Physiol.* 148: 93-100.
- STONEHOUSE, B. 1967. The general biology and thermal balances of penguins. Pp. 131-196 in *Advances in ecological research*, vol. 4 (J. B. Cragg, Ed.). London, Academic Press.
- TAYLOR, J. R. E. 1985. Ontogeny of thermoregulation and energy metabolism in pygoscelid penguin chicks. *J. Comp. Physiol.* 155B: 615-627.
- TREGGAR, R. T. 1965. Hair density, wind speed, and heat loss in mammals. *J. Appl. Physiol.* 20: 796-801.
- WALSBERG, G. E., G. S. CAMPBELL, & J. R. KING. 1978. Animal coat color and radiative heat gain: a re-evaluation. *J. Comp. Physiol.* 126: 211-222.