EXPERIMENTS ON THE EMPEROR PENGUIN, *Aptenodytes forsteri*, IN VARIOUS THERMAL ENVIRONMENTS

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ABSTRACT. The daily weight loss of some male emperor penguins was determined under a variety of measured temperatures and wind speeds. The significance of these determinations is discussed. As an ancillary experiment, the skin, sub-skin and body-core temperatures of one bird were measured; this enabled the relative contributions of sub-dermal fat, skin and feathers-plus-air layer to the total thermal insulation of the bird in those conditions to be estimated. Some measurements of the air temperature in a huddle of birds were attempted. Weather conditions leading to huddling are evaluated from a statistical analysis of meteorological records from near two rookeries where huddling behaviour was regularly recorded. The results of these several lines of investigation are used in an attempt to quantify the benefit of huddling in combating adverse weather conditions.

WEIGHT LOSS AND THERMOREGULATION

The male emperor penguin near lat. 75°S. fasts from early April until late July. It is reasonable to suppose that its weight loss during this period represents loss of fat yielding, say, 9,500 kcal. per kg. consumed (Carpenter, 1939). It therefore seems relatively easy to determine the metabolic rate of such a fasting bird simply by weighing it at intervals. The experiments described here were undertaken partly to test whether this was indeed so and to obtain much needed data on the thermal regulation of this bird.

In the experiments, conducted at Halley Bay in 1962, a group of up to four birds was kept under various conditions and each bird weighed approximately twice weekly. In experiments where the birds were kept out of doors, the weighings were made whenever the weather changed markedly, so that conditions were reasonably constant between weighings. The greatest difficulty was one of finding suitable places where the birds could experience a wide variety of temperatures and winds, yet could not escape.

Ice caves round a submerged living hut were one place used, and these had zero wind speed but only a narrow range of temperature, between $-10\cdot4^\circ$ and $-14\cdot6^\circ$ C. A ventilating fan and some plywood made a makeshift wind tunnel which was used in these caves on some occasions.

Over half the exposures were made outdoors in a fast-vanishing windscoop which had the surprising property that at one end, where snow was rapidly being deposited, the wind speed was only about one-fifth of that recorded at the meteorological tower, and a small correction catered for this. Birds put into the scoop were always found at the low wind-speed end, so there was no need to confine them there.

A third type of environment was provided by taking single penguins in Dexion-and-chicken-netting cages and setting them out of doors some distance from the nearest building. Measurements with a hand anemometer close to the bird showed that the wind speed around it was roughly equal to that recorded at the station meteorological tower. One can do little more than make rough estimates of wind effect, for the result of a bird's exposure to wind depends so markedly upon its attitude.

Weighing the birds gave few problems. The bird to be weighed was put into a cage and set on platform scales in a level-floored ice cave. Ice lumps were removed and the bird was weighed several times to give a standard error of ± 20 g. Incidental errors, such as could be caused by a bird eating snow or excreting just before being weighed were guessed to be $\pm$ 100 g., or $\pm$ 50 g. per bird when the masses of the birds in a group were averaged. Weighing errors therefore are unlikely to contribute much to the variability of results. Estimated errors of temperature were also small.

The observed daily mass losses are given in Table I, together with the figures needed for deriving the thermal conductance of the bird's insulation, θ. This is defined as

$$\theta = \frac{\text{(heat produced} - \text{heat evaporated)}}{\text{(body-to-air temperature difference) (surface area) (time)}}\,.$$

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TABLE I. MASS LOSS OF EMPEROR PENGUINS IN VARIOUS ENVIRONMENTS

			Solitary birds exposed to wind				*Group of sheltered birds*					
Date	*Mean temp.* (°C)	*Mean wind* (m. sec.$^{-1}$)	*Mass* (kg.)	*Loss* (kg. day^{-1})	*Surface area* (m.$^{-2}$)	θ (kcal. day^{-1} m.$^{-2}$ °C^{-1})	*Number of birds**	*Mean mass* (kg.)	*Mean loss* (kg. day^{-1})	*Surface area* (m.$^{-2}$)	θ	θ *for zero wind*
Halley Bay (1962)												
25–29 May	−30·1	4·7	32·5	0·390	1·018	51·4	3	30·7	0·220	0·980	29·4	27·9
29 May–1 June	−32·1	4·2	30·9	0·197	0·985	25·2	3	29·9	0·227	0·971	29·8	28·6
1–5 June	−31·3	3·2	24·5	0·233	0·843	36·9	2	30·9	0·116	0·985	14·6	13·7
5–12 June	−35·9	3·0	23·5	0·207	0·821	30·5	2	30·4	0·226	0·974	28·0	27·1
12–15 June	−28·8	3·6	28·1	0·133	0·924	18·4	3	26·7	0·240	0·893	36·2	35·2
15–26 June	−21·3	8·7	27·8	0·185	0·918	30·0	3	26·3	0·135	0·884	22·1	19·6
26–29 June	−21·3	7·6	19·9	0·130	0·734	26·0	3	26·7	0·121	0·893	19·4	17·1
29 June–3 July	−21·3	4·0					4	24·6	0·148	0·846	25·8	24·6
3–6 July	−22·5	6·8					3	25·7	0·125	0·871	20·3	18·3
6–10 July	−22·9	10·4					3	25·4	0·137	0·864	22·5	19·4
10–13 July	−35·3	4·8					3	24·8	0·173	0·851	24·5	23·1
13–17 July	−30·6	12·5					3	24·3	0·084	0·839	11·9	8·1
17–24 July	−28·2	8·5					2	24·6	0·157	0·846	24·6	22·1
Weighted mean ± s.e.						31·7 ±3·3					23·7 ±1·7	21·7 ±2·0
Pointe Géologie average of several birds Apr.–Aug. 1956	(−17)	(13)	(27)	0·330†	0·900	60·6		(27)	0·200‡ (pen)	0·900	35·9	
									0·136‡ (rookery)	0·900	23·7	
Pointe Géologie two birds 16 Apr.–21 May 1956	(−15)	(15)	(35)	0·177‡	1·070	27·1						
21 May–3 Aug. 1956	(−17)							(27)	0·105‡ (rookery)	0·900	17·7	
3–17 Aug. 1956	(−17)	(19)	(20)	0·162‡	0·737	35·5						
straight mean						41·1					25·8	

* Variation caused by escape, replacement and accidental damage.

† From Stonehouse, 1967.

‡ From Prévost and Sapin-Jaloustre, 1964.

Evaporative water loss was calculated from the formula of Crawford and Lasiewski (1968); this estimate is almost certainly too low, for it would refer to measurements under standard conditions of metabolism, whereas the penguins were, in fact, exceeding their standard metabolic rate (SMR). This has only a small effect, however, on the value of thermal conductance finally evaluated. Solar radiation corrections were unnecessary as the sun was below the horizon for the whole period. Surface areas were calculated from Meeh's formula (surface area in square metres is approximately one-tenth of the two-thirds power of the mass in kilograms). The thermal conductance figures for the single bird exposed to wind were then compared with those for the remainder in the more sheltered environment, on the assumption that the wind caused an increase in conductivity that was proportional to the wind speed; any more complicated assumption would be unjustifiable. Wind was calculated to cause an increase of conductance of $1\cdot5 \pm 0\cdot85$ kcal. day^{-1} m.$^{-2}$ °C^{-1} per m. sec.$^{-1}$ of wind speed. A small wind correction was then applied to the figures for the birds in the windscoop to give the values for θ in calm conditions in the last column of Table I. These averaged to $21\cdot7 \pm 2\cdot0$ kcal. day^{-1} m.$^{-2}$ °C^{-1} (s.e. of 13 measurements).

The lower part of Table I contains a selection from the similar measurements made at Pointe Géologie (Prévost and Bourlière, 1957; Prévost and Sapin-Jaloustre, 1964; Birr, 1968). Although not strictly applicable, the published monthly mean meteorological data for 1963 were inserted where needed, and guesses made for penguin masses where only percentage weight losses were given. The data were then processed as in the upper part of the table. Only rough comparison is possible, and agreement between results from the two stations is as close as can be expected. Averaging the small sample of results in Table I, wind appears to raise the thermal conductance by about $0\cdot9$ kcal. day^{-1} m.$^{-2}$ °C^{-1} per m. sec.$^{-1}$ wind speed at Pointe Géologie, compared with the value of $1\cdot5$ in the Halley Bay experiment.

The variability in θ is higher than would be expected *a priori*. Both Halley Bay and Pointe Géologie data show this, and it may be that the species is unsuitable for accurate metabolic rate measurement. Taking a typical bird to have mass 25 kg. and surface area $0\cdot855$ m.^{2}, the formula of Lasiewski and Dawson (1967) gives a standard metabolic rate of 803 ± 126 kcal. day^{-1}. A bird at 38° C core temperature covered by a layer of conductance $21\cdot7 \pm 2\cdot0$ kcal. day^{-1} m.$^{-2}$ °C^{-1} has on these data a lower limit of thermoneutrality of $+1°$ C $\pm 7\cdot4°$ C. Therefore, the variability of results is most unlikely to be caused by the experimental conditions encroaching into the region of thermal neutrality. This high value for the lower limit of thermoneutrality may be related to the need to lose heat rapidly while swimming.

TEMPERATURE GRADIENTS WITHIN THE BIRD

A fairly fat male bird was anaesthetized on 26 June 1961 with veterinary Nembutal at an intramuscular dose of 600 mg. and kept unconscious with an ether pad. For measuring core temperature, a thermistor was introduced via the gullet by two concentric Perspex tubes. Fine connecting wires plaited with a nylon strengthening cord emerged through the angle of the beak and were attached to a multi-pole plug on a harness high on the bird's back. Also a sterilized thermistor was slipped through a slit in the lumbar skin, into a space made by separating the internal fat-laden tissue from the inner side of the skin about 30 mm. from the slit, which was then sewn closed round the leads. These were plaited as described for the gullet thermistor and led to other pins of the plug on the bird's back. A further thermistor was sewn on the outside of the skin at the base of the feathers. A fourth was glued and tied to the tips of the feathers in the same region, but this was soon preened off by the bird. Subcutaneous and cutaneous thermistors were duplicated on the right and left of the bird's midline.

The thermistors had all been encapsulated in Perspex in suitable shapes; the internal one was pill-shaped and smooth, while the sewn ones had extensions bearing holes so that local heating of the tissues reacting to the sewing did not influence the thermistor bead. The thermistors were carefully calibrated before and after the experiment and no calibration had shifted by more than 1° C.

After the operation, the bird was put in an ice cave of ambient temperature between $-10°$ and $-15°$ C. The core temperature of the bird was monitored continuously after the operation and, following recovery from the anaesthetic, about 3 days of continuous record were possible before the bird regurgitated the thermistor. The mean temperature was 38·1° C. There was some variation of this, not diurnal nor with any other recognizable rhythm, and the standard deviation of the temperature was ±0·37° C.

From time to time the temperatures of the other thermistors were measured. Periods of calm were alternated with periods of light breeze round the bird, with wind speeds of up to 2·5 m. sec.$^{-1}$, at which speed the first indication of movement of the feather tips was seen. This was taken to be the speed at which any possible insulation by a layer of still air outside the feathers had been destroyed while the feather insulation was still nearly intact. The temperature drop across each layer of insulation was proportional to the amount of insulation contributed by that layer and was as in Table II.

TABLE II. RELATIVE CONTRIBUTIONS (PERCENTAGES) OF THE LAYERS TO THE THERMAL INSULATION OF A SINGLE EMPEROR PENGUIN. AMBIENT TEMPERATURE BETWEEN −10° AND −15° C

Insulation layer	*In still air*	*In average wind* (1·6 m. sec.$^{-1}$)	*In maximum wind* (2·5 m. sec.$^{-1}$)
Subcutaneous fat, etc.	1·5±0·6 (s.d.)	1·9±0·1	1·8
Skin	12·5±1·3	15·2±1·7	17·1
Feathers and air layer around feathers	86·0±1·7	82·9±1·7	81·1

It must be emphasized that these results apply to one bird only, in one set of conditions, which were probably cooler than would be required for thermoneutrality. The insulation contributions from the layers may vary relative to one another or may remain much the same when the ambient conditions vary; this is not known. Prévost and Sapin-Jaloustre (1964) gave subcutaneous and rectal temperatures of individuals in a range of environments each different from that reported here, and the dorsal subcutaneous temperatures are never more than 2° C below the rectal ones. It seems safe to conclude that the feather layer is by far the most important thermal insulator. This is reasonable for a species that loses much of its fat before the coldest weather of the season comes along. Insulation in a tropical species, the Peruvian penguin, is similarly distributed (Drent and Stonehouse, 1971).

TEMPERATURE RISE IN HUDDLES

Using thermistors on stakes at various heights above snow level and encouraging birds to huddle around them, four measurements were made of the temperature difference between the air outside and that within the huddle. It is seen from the results in Table III that in round figures the huddled birds' micro-climate was 10° C above the ambient temperature.

TABLE III. TEMPERATURES MEASURED INSIDE AND OUTSIDE HUDDLES

Date 1961	*Type of huddle*	*Area per bird* (m.^{2})	*Height of thermometer* (mm.)	*Temperature in huddle* (°C)	*Temperature outside* (°C)	*Wind outside* (m. sec.$^{-1}$)
24 April	50 birds, captive, in pen	0·07	60	−7·5	−18·1	18·5
18 May		0·1	30	−23·5	−33·3	8·8
19 May		0·1	30	−4·5	−15·0	17·5
8 July	Natural huddle			−30	−39	Calm

ANALYSIS OF RECORDS OF HUDDLING BEHAVIOUR

Unpublished data were provided by M. H. Thurston giving the proportion of penguins huddled at the Emperor Bay rookery on 57 days between 19 April and 20 August 1961, and these were correlated, using several statistical methods, with the wind and temperature recorded at the Halley Bay station, then 2·5 km. east and somewhat higher than the rookery. The data of Stonehouse (1953) for the Dion Islands rookery (lat. 68°S.) were similarly correlated with weather data read from the published graphs, and with solar radiation data provided by J. C. Farman (personal communication).

For this part of the work, each bird was assumed to conform to the following measurements:

Mass	25 kg.
Surface area	0·855 m.^{2}
Cross-section presented to insolation	0·16 m.^{2}
Thermal conductance of insulating layer in zero wind	21·7 kcal. day^{-1} m.$^{-2}$ °C^{-1}
Evaporative water loss	119 kcal. day^{-1}
SMR (equation of Lasiewski and Dawson (1967))	803 kcal. day^{-1}

The method used was one of trial and error. For each day when huddling behaviour was known, the heat requirement for this standard penguin was worked out, several times, using the equation on p. 57 and a variety of coefficients to represent the increase of thermal conduction by wind. The coefficient was picked out which yielded results closest to the ideal, where all days on which the heat requirement was less than some critical value showed the colony unhuddled, while when the critical value was exceeded, the penguins huddled. For the Emperor Bay data, this occurred when the wind was assumed to raise the thermal conductance by 0·61 kcal. day^{-1} m.$^{-2}$ °C^{-1} per m. sec.$^{-1}$. The prediction that when the heat requirement exceeded 1,460 kcal. day^{-1} (180 per cent of SMR) huddling would occur, was correct for 74 per cent of days.

For the Dion Islands data, the same method was followed except that a second parameter had to be introduced to account for the effect of insolation. The computed heat requirement on days judged to be clear was reduced by the product of this parameter with the estimate in Fig. 1 of the total noon solar radiation falling through a clear sky on to the standard penguin of cross-section 0·16 m.^{2}. For cloudy days the estimate was halved. For best prediction here, the heat requirements were calculated on the assumptions that wind raised the thermal conductance by 0·73 kcal. day^{-1} m.$^{-2}$ °C^{-1} per m. sec.$^{-1}$, and that the heat requirement was reduced by 0·16 of the noon insolation. The critical heat requirement was then 1,190 kcal. day^{-1} (150 per cent of SMR).

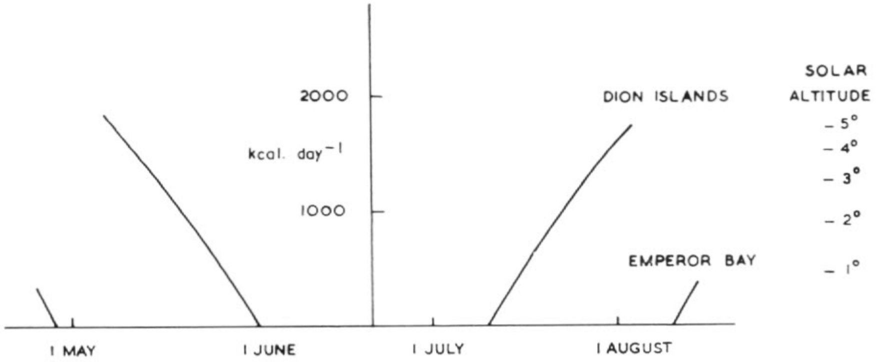

Fig. 1. Intensity of solar radiation falling on a penguin of cross-section 0·16 m.^{2}. Assumptions as in the text. Values interpolated from data provided by J. C. Farman.

The value for noon solar radiation is not very well known because of uncertainties of atmospheric absorption at such low solar elevations and an error of ±25 per cent would easily be possible in the assumed values. Also, it is a moot point whether noon flux or total daily radiation should be used, but the question happens to be unimportant in fitting this particular set of data.

The difference between the results for the two colonies is probably significant. The Dion Islands birds may be more apt to huddle than the Emperor Bay ones at the same heat requirement, or alternatively the Dion Islands birds may be less well insulated.

ESTIMATE OF THE BENEFIT OF HUDDLING

The benefit of huddling is three-fold. On the positive side, the air temperature is higher and the wind speed lower in a huddle, but on the negative side solar radiation is shielded from all but the penguins on the northern perimeter of the huddle.

Considering first the temperature benefit, this obviously depends on the wind speed and closeness of huddling, but a 10° C benefit has been shown to be possible.

The benefit from reduced wind speed is much less certain, but it can be estimated on an order-of-magnitude basis. A huddle of, say, 5,000 birds in a reasonably compact shape has about 2·5 per cent of its occupants on the perimeter on the windward side. (This ignores the lone birds that are always to be found standing off from the compact huddle.) This percentage varies approximately with the square root of the number of birds in the huddle, but 5,000 might be typical of the Emperor Bay rookery in 1961. These windward peripheral birds will be exposed to a wind of speed different from, but of the same order as, that measured with a free-standing anemometer. In addition, the whole huddle will have some wind exposure at head level. Suppose that the wind speed tapers off from the unimpeded wind speed at the level of the tops of the birds' heads to zero at neck level; the head might be responsible for 10 per cent of the bird's heat loss, a guess made on the basis of its size and relative feather-layer thickness. The face and beak are tucked down during huddling. The effect of the wind blowing on the head of each bird in this way would therefore be 5 per cent of the effect on a solitary bird. If we consider the huddle as a whole, and add in 2·5 per cent for the effect of the wind blowing on the full profile of the windward peripheral members, the effect of huddling on the community

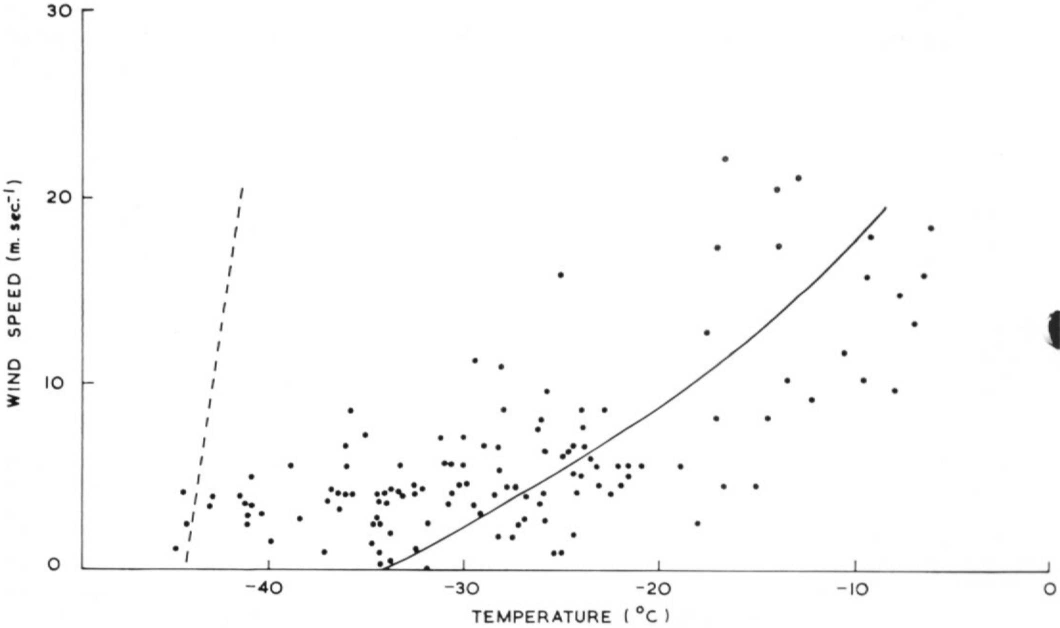

Fig. 2. Daily weather means at Halley Bay between 19 April and 20 August 1961. Huddling is predicted to occur on days represented as above and left of the solid line. Equivalent metabolic rate would be required of huddled birds when conditions were those of the broken line.

is estimated to be equivalent to a reduction of wind speed to 7·5 per cent of that actually existing.

The temperature and wind benefits gained by huddling at Emperor Bay (where insolation is unimportant during the incubation season) may be summed up graphically. Fig. 2 is a plot of daily weather means at Halley Bay for each day between 19 April and 20 August 1961. The mean wind speed for each day is plotted as ordinate of a point and mean temperature as its abscissa. The line for a heat requirement of 1,460 kcal. day^{-1} is drawn solid and it is seen that 67 per cent of the points lie on the inclement side of this line. Birds that are huddled would experience a micro-climate equivalent to this if the ambient conditions were those represented by points on the broken line (whose intercept is 10° C lower and whose course is adjusted by a factor of 7·5 per cent in the wind speed). It is seen that only 3 per cent of the points lie on the inclement side of this line. (The 7·5 per cent figure can be quite seriously in error without affecting the validity of the result much.) The solid line represents conditions inducing a metabolic rate of 80 per cent above standard in solitary birds, whereas conditions on the broken line would induce that rate in huddled birds. Huddling is seen to be a powerful method of combating weather conditions that might strain the metabolic resources of the birds.

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