

# WINTER BREEDING IN EMPEROR PENGUINS: A CONSEQUENCE OF THE SUMMER HEAT?

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**ABSTRACT.**—During their Antarctic breeding season Emperor Penguins (*Aptenodytes forsteri*) fast as long as 115 days and walk as far as 200 km from the sea to their rookeries and back. The breeding males stand on the ice incubating a single egg for about 62 days. We examined the thermal exchanges between Emperor Penguins and their environment in an attempt to answer the question: Why do these penguins breed during the winter? Existing physiological data for the temperature regulation of Emperor Penguins were used in conjunction with meteorological data from the Antarctic to model thermal interactions between the animal and its environment.

Computer simulations for the energy budget of Emperor Penguins in a variety of microclimatic conditions indicate that the heat load imposed on these birds during the Antarctic summer does not limit their choice of breeding season. We conclude that the physiological and morphological characteristics associated with heat exchange do not constrain Emperor Penguins to winter breeding.

In 1902 Edward Wilson, a physician participating in Robert Falcon Scott's first expedition to Antarctica, discovered that Emperor Penguins (*Aptenodytes forsteri*) breed during the Antarctic winter (Wilson 1907). By contrast, all other Antarctic penguins breed during the summer. In the course of their unique breeding cycle, Emperor Penguins may fast for 115 days (Isenmann 1971) and walk as far as 200 km from the sea to their rookeries and back (Budd 1962).

Aspects of the breeding biology of Emperor Penguins have been extensively studied (e.g., Stonehouse 1953, Prévost 1961, Isenmann 1971, Bougaeff 1974), and energetic costs for thermoregulation and locomotion have been quantified (Le Maho et al. 1976, Pinshow et al. 1976). The intriguing question of why Emperor Penguins breed during the winter has not been treated as thoroughly. Stonehouse (1953) suggested that the phenomenon is related to the short time available for chicks to achieve independence. Simpson (1976) and Schmidt-Nielsen (1979) left the question open.

This report does not directly address the question of why Emperor Penguins are winter breeders. Rather, we ask why these birds do not breed during the summer. Specifically, would an adult Emperor Penguin become heat stressed if it bred during the Antarctic summer? We have tried to resolve this

using mechanistic models and the concept of the thermodynamic energy balance.

## MODEL DEVELOPMENT

The practical difficulties of simultaneously measuring physiological and micrometeorological variables for an animal under natural conditions are formidable. It is, however, possible to amalgamate physiological data collected from animals under controlled laboratory conditions with appropriate micrometeorological data. We applied the modelling principles of Porter and Gates (1969) and Porter et al. (1973) to construct a mathematical model that examines the thermal response of Emperor Penguins to different environmental conditions. This model is based on the following three equations, symbols for which are defined in Table 1.

Simulated micrometeorological conditions, and the relevant physical characteristics of an Emperor Penguin, were used to determine the operative environmental temperatures ( $T_e$ ). This value ( $T_e$ ) is a calculated temperature, equivalent to that of an organism's thermally complex, natural environment, and conceptually similar to the  $T_e$  of Bakken (1976) (see Fig. 1).

The  $T_e$  for an Emperor Penguin was defined as

$$Q_{sol} + \sigma\alpha A_r T_{1w}^4 + h_c A_c T_a = \sigma\epsilon A_r T_e^4 + h_c A_c T_e \quad (1)$$

for which we obtained a numerical solution using the *regula falsi* method (Stanton 1961). This equation makes it possible to relate the physiological response data collected from animals in a controlled environment to the variable natural environment that an animal actually experiences.

The second equation gives the energy balance for the plumage surface,

TABLE 1. Mathematical symbols.

Symbol	Physical quantity	Units
$A_b$	Body surface area of animal	$m^2$
$A_c$	Area of animal for convective heat exchange	$m^2$
$A_r$	Area of animal for radiative heat exchange	$m^2$
$c_p$	Specific heat of animal	$3.35 \text{ KJ} \cdot \text{kg} \cdot \text{K}^{-1}$
$E$	Rate of evaporative heat loss	$\text{W}$
$h_c$	Convective heat transfer coefficient	$\text{W} \cdot \text{m}^2 \cdot \text{K}^{-1}$
$K_B$	Thermal conductance from animal core to skin	$\text{W} \cdot \text{m}^2 \cdot \text{K}^{-1}$
$K_p$	Thermal conductance across plumage	$\text{W} \cdot \text{m}^2 \cdot \text{K}^{-1}$
$M$	Metabolic power input	$\text{W}$
$m$	Body mass	$\text{kg}$
$Q_{\text{sol}}$	Absorbed solar radiation	$\text{W}$
$T_a$	Air temperature	$^{\circ}\text{C}$
$T_c$	Core (cloacal) temperature	$^{\circ}\text{C}$
$T_{\text{lw}}$	Radiating temperature for environment	$^{\circ}\text{C}$
$T_r$	Radiating surface temperature of animal	$^{\circ}\text{C}$
$T_s$	Skin temperature	$^{\circ}\text{C}$
$t$	Time	$\text{s}$
$U$	Wind speed	$\text{m} \cdot \text{s}^{-1}$
$U_z$	Wind speed at animal height	$\text{m} \cdot \text{s}^{-1}$
$\alpha$	Absorptance for thermal radiation	decimal fraction of 1
$\epsilon$	Emittance for thermal radiation	decimal fraction of 1
$\sigma$	Stefan-Boltzmann constant	$5.67 \times 10^{-8} \text{W} \cdot \text{m}^2 \cdot \text{K}^{-1}$

$$Q_{\text{sol}} + \sigma\alpha A_r T_{\text{lw}}^4 + K_p T_s + h_c A_c T_a = \sigma\epsilon A_r T_r^4 + K_p T_r + h_c A_c T_r \quad (2)$$

where it is assumed that the equation  $K_B T_c + K_p T_e = K_p T_s$  describes the heat flow from the animal's core to its surface. Equation 2 was solved for the surface temperature ( $T_r$ ) with the same numerical technique used to solve for  $T_e$ .

The third equation describes a transient energy balance. The rate of change in the core temperature ( $T_c$ ) of a resting penguin is expressed as

$$-m c_p \frac{dT_c}{dt} + M - E = K_B (T_b - T_c) \quad (3)$$

where the temperature differential ( $dT_c/dt$ ) was solved numerically with a discrete approximation (Greenspan 1973). Emperor Penguin core temperature is known to remain relatively constant (Le Maho et al. 1976, Pinshow et al. 1976). We, therefore, assumed that a significant rise in core temperature and/or evaporative water loss would indicate thermal stress.

The three equations were solved simultaneously in conjunction with calculations for the parameter values indicated below.

## PARAMETER EVALUATION

Steady state data for the metabolic power input ( $M$ ), evaporative power output ( $E$ ), and core (cloacal) temperature ( $T_c$ ), as functions of air temperature ( $T_a$ ) in a black body metabolic chamber, are available from Pinshow et al. (1976). In addition we used data for Emperor Penguin skin temperature ( $T_s$ ) collected by Pinshow (unpubl.). A value of 23.7 kg was used for body mass ( $m$ ), and body surface area ( $A_b$ ) was estimated from the allometric equation for penguins (Pinshow et al. 1976). Thermal conductance across the plumage ( $K_p$ ) was calculated from the data for  $M$ ,  $E$ ,  $T_s$  and  $A_b$ . A plumage depth of 1 cm was assumed based on measurements made by Pinshow (unpubl.).

As  $K_p$  is related to the difference between skin temperature and feather surface temperature, changes in which take place through erection of the feathers, a polynomial regression equation relating  $K_p$  to ( $T_s - T_r$ ) was calculated and used in the model. Similarly,  $K_B$  is related to the difference between core and skin temperatures through vasomotor responses and a corresponding equation relating  $K_B$  to ( $T_b - T_s$ ) was used.

To simplify the heat transfer calculations, we geometrically represented an Emperor Penguin as a cylinder with hemispherical ends. One half of the surface of this cylinder was assumed to be black, and the other half white, corresponding to the dorsal and ventral color pattern.

Solar reflectances (290–2,600 nm) of Emperor Penguin plumage were measured with a Beckman Model DK-2A Spectroreflectometer. Absorptance was calculated from the reflectance data using the SOLREF modification of the SOLRAD computer program (McCullough and Porter 1971). The mean absorptances of black and white plumage are 0.82 and 0.32 respectively. Thermal absorptance ( $\alpha$ ) and thermal emittance ( $\epsilon$ ) were both assumed equal to 0.97 (Porter and Gates 1969).

Wind speed at penguin height ( $U_z$ ) was estimated using the profile for neutral conditions given in Sellers (1965). A convective heat transfer coefficient ( $h_c$ ) was calculated according to Mitchell (1976), and a factor of 1.5 was assumed to account for air turbulence in a natural environment (Kowalski and Mitchell 1975). Convective heat loss was considered negligible.

Micrometeorological conditions of the Antarctic sea-ice, where Emperor Penguins might spend the summer, were simulated mathematically using the equations of Porter et al. (1973). To solve these equations we used data from a standard meteorological station (2 m high) to calculate the air temperature and wind speed at the average height of an adult penguin, and the incident solar and thermal radiation. Meteorological data that are appropriate for such calculations were gathered during the austral summer of 1957 at Station Little America V (78°11'S, 162°10'W; Archives of the U.S. Weather Service, Asheville, North Carolina). This coastal site is at the southern edge of the Emperor Pen-

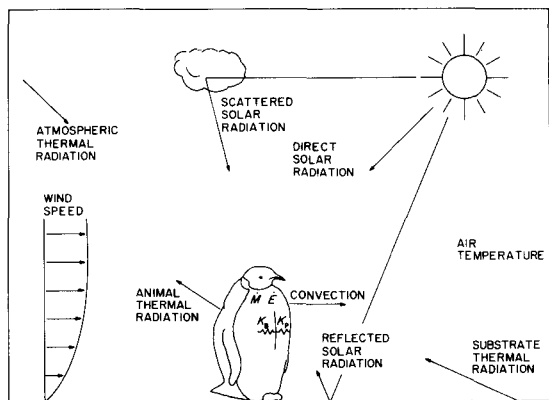


FIGURE 1. Schematic diagram of the Antarctic environment showing energy fluxes to and from an Emperor Penguin. See Table 1 for abbreviations.

gull's breeding range. The data include hourly measurements of substrate and air temperatures, wind speed, direct and reflected solar radiation, and twice daily measurements of overcast sky temperature. Temperature of the clear sky was calculated following Idso and Jackson (1969).

Emperor Penguins breed as far north as 66°S (Stonehouse 1967) but, due to perennial surface ice and snow and the low water temperatures along the Antarctic coast, it seems unlikely that higher  $T_e$ 's would be calculated for the lower latitudes. Unfortunately, suitable meteorological data were not available for a northerly rookery.

## RESULTS

Computer simulations were made for 15 December 1957, the date of highest radiant energy flux in the available data. We allowed the microclimatic conditions of that day to impinge on the model penguin many consecutive times. The model stabilized after one 24-h cycle after which the calculated model parameters repeated themselves for each additional day (Fig. 2).

The relatively large long-wave and short-wave radiative heat gains made by the penguin are balanced by concomitant convection and long-wave reradiation. The magnitudes of metabolic heat input and heat lost by the evaporation of water fluctuate little and are relatively small when compared with the contributions of radiation and convection to the total heat budget.

Under the warm summer conditions to which the model penguin was exposed, heat storage was not significant and core temperature remained almost constant at about 38°C. Body and plumage conductances varied little. Either a significant rise in core temperature or in evaporative heat loss (which might be needed to maintain constant core temperature) would indicate an intolerable heat load.

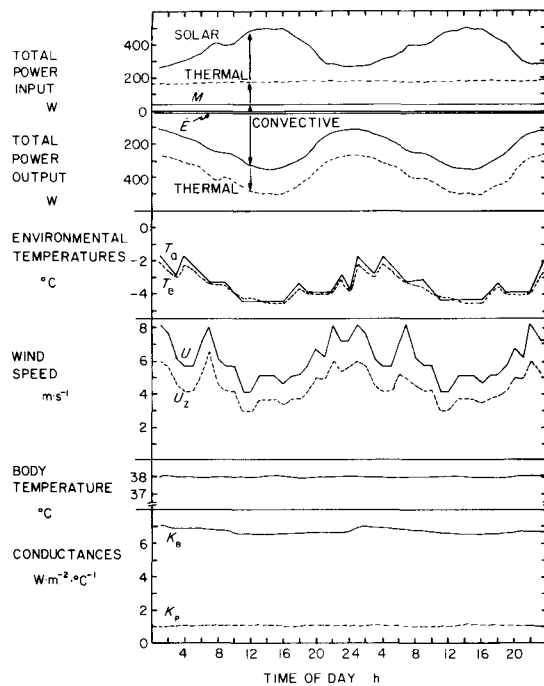


FIGURE 2. Family of curves relating model variables and parameters to time of day. Micrometeorological data for 15 December 1957 were used for a number of consecutive days, two of which are displayed here (see text for details). The upper two curves show the additive magnitudes of power inputs and outputs to and from the bird. Metabolic power input and the rate of evaporative heat loss are exaggerated slightly for clarity. See Table 1 for abbreviations.

## DISCUSSION

Our results suggest that the heat load during the Antarctic summer does not cause undue stress to Emperor Penguins standing on the ice for extended periods. We reason, therefore, that Emperor Penguins are not constrained by their thermoregulatory capabilities to breed in winter. Explanations for their hibernal breeding pattern probably lie in their ecology rather than in their physiology.

One may speculate on the phenomenon using the ecological and behavioral information at hand. For example, Emperor Penguins may have evolved winter breeding in order to avoid predators. This would be an advantage enhanced by the fact that Emperor Penguins incubate only one egg at a time and raise a single chick per year. Two important predators of other Antarctic penguins during breeding are the South Polar Skua (*Catharacta maccormicki*; Muller-Schwarze and Muller-Schwarze 1973) and the leopard seal (*Hydrurga leptonyx*; Muller-Schwarze and Muller-Schwarze 1975, Øritsland 1977). The skua arrives in the Ant-

arctic during October by which time Emperor Penguin chicks are too large to be suitable prey. Predation by leopard seals on Emperor Penguins has been reported (e.g., Hamilton 1946, Prévost 1964), but examination of seal stomach contents shows few Emperor Penguin remains (Øritsland 1977). The Southern Giant Fulmar (*Macronectes giganteus*) has been observed to eat Emperor Penguin chicks (Prévost 1961, Prévost and Sapin-Jaloustre 1965), and Mougin (1966) reported that these birds accounted for up to 8% of total Emperor Penguin chick mortality at the Pointe Géologie rookery during two years. Some Southern Giant Fulmars even winter in the Antarctic to take advantage of the hibernal breeding habits of the Emperor Penguin (Watson 1975). The killer whale (*Orcinus orca*) is another potential predator, but its impact on Emperor Penguins has not yet been studied.

Except for the King Penguin (*Aptenodytes patagonica*), which also incubates one egg on its feet as does the Emperor Penguin, all other penguins build nests and lay at least two eggs. On the one hand the Emperor and King penguins' method of incubation limits their potential number of offspring, but on the other hand, their eggs are well protected from predators and the elements.

Availability of food may also pertain to the evolution of winter breeding in Emperor Penguins. These birds feed mainly on squid and small fish, and their diet includes euphausiid and schizopod crustaceans (Watson 1975). These prey items are all eaten by other Antarctic animals but data on the food habits of the penguins and possible competition for resources are too limited to permit conclusions to be drawn.

Because of their ungainly and energetically costly mode of waddling (Pinshow et al. 1977), Emperor Penguins are probably limited to breeding on flat surfaces. The only suitable areas available to them in the Antarctic are on the ice. Subantarctic beaches, on which King Penguins breed, might be suitable in this respect, and it is conceivable that Emperor Penguins were, in the past, competitively excluded from using this terrain.

According to Stonehouse (1953) and Isenmann and Jouventin (1970), Emperor Penguins must begin their breeding cycle during the winter because the chicks require five months to reach independence. This takes place in January and February and coincides with the breakup of the sea ice and the summer plankton bloom, a time

when food is presumably abundant. Emperor Penguins lay the smallest egg relative to adult body mass of any bird (Lack 1968), and among penguins, their chicks grow at relatively the slowest rate (Stonehouse 1970). It is therefore possible that Emperor Penguins could breed closer to the sea and later in the year in order to allow more frequent feeding and faster development of the chicks.

The pressures which led to the unique breeding cycle of Emperor Penguins will apparently only be elucidated through further study of their ecology and evolutionary history.

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