Heat Transfer through Penguin Feathers

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Morphological measurements of penguin feathers are used to construct a thermal model of heat transfer through the coat. Assuming uniform distribution of the feathers and their associated afterfeathers, it is possible to model heat transfer through the coat of the penguin using standard theory. It is shown that convection does not occur in the coat of the penguin and that radiative heat loss is minimized. The theory predicts a thermal conductivity of $2.38 \, \mathrm{W \, m^{-2} \, K^{-1}}$ which compares well with an empirically measured value of $1.93 \, \mathrm{W \, m^{-2} \, K^{-1}}$.

Introduction

Penguins are a specialized group of non-flying, aquatic birds that live in the southern hemisphere, most famously in the Antarctic. The ability of some species to withstand extreme cold whilst fasting for up to 120 days (during egg incubation) has excited much attention. Several studies have investigated the thermal resistance of penguin "coats" (feather and skin assembly) and found it to be surprisingly low—an average of $0.74 \, \mathrm{m^2 \, K \, W^{-1}}$ or 7.4 Tog (Drent & Stonehouse, 1971; Jarman, 1973; Pinshow *et al.*, 1974; Kooyman *et al.*, 1976).

Penguin feathers are heavily modified, being short (30–40 mm), stiff and lance shaped. Insulation is provided by a long (20–30 mm) afterfeather. Penguins are unique in that the feathers are evenly packed over the surface of the body (30–40 per $\mathrm{cm^2}$) rather than arranged in tracts.

For insulation the penguin requires a thick, air-filled, windproof coat (similar to an open-cell foam covered with a windproof layer) that eliminates convection and reduces radiative and convective heat losses to a minimum.

However, when diving, the penguin requires a thin, smooth and waterproof coat with no trapped air (positive buoyancy would be a big disadvantage to an active swimming hunter—Wilson *et al.*, 1992). It achieves this by using muscles attached to the shaft of the feather to "lock down" the feathers to create a water-tight barrier (Kooyman *et al.*, 1976). In addition, the feather rachis is flattened dorso-ventrally allowing it to bend and conform to the body shape readily with increasing water pressure.

When the penguin emerges back onto land the muscles re-erect the feather and provide a thick air-filled coat. However, only the shaft of the feather has muscle control. The rest of the feather parts cannot be actively moved. To achieve

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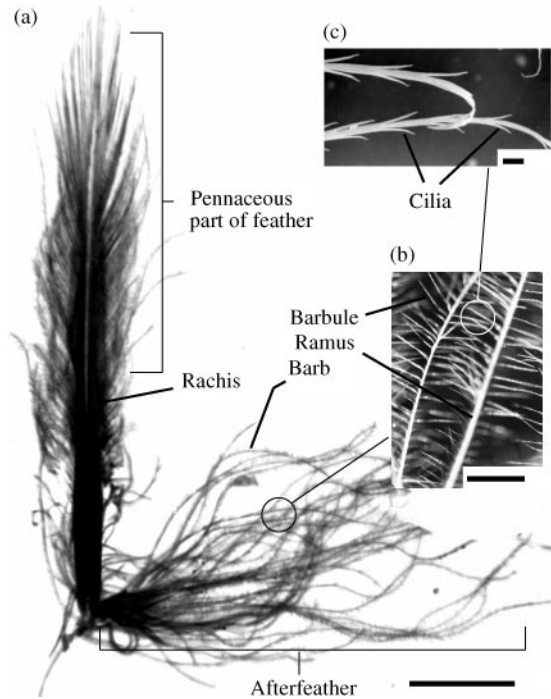E-mail: c.dawson@rdg.ac.uk.

FIG. 1. (a) Feather of *Pygoscelis papua* showing the prominent afterfeather—scale bar 5 mm, (b) light micrograph of two barbs from the afterfeather—scale bar 500 μm and (c) scanning electron micrograph of two barbules entangled by their cilia—scale bar 10 μm.

effective insulation it is important that the rest of the feather parts are able to "self-organize" to give an evenly distributed insulation system.

Materials and Methods

Specimens of skin and feathers from Gentoo penguins, *Pygoscelis papua*, were examined at various magnifications using light and scanning electron microscopes. Five feathers from the breast and five from the back were taken from each of three specimens (one male, two females—adult plumage but ages unknown). Naming of the feather parts follows Lucas and Stettenheim (1976)—see Fig. 1.

Results

No significant differences were observed between feathers taken from different sites on the skin or between the specimens. Therefore all results have been pooled.

The barbs of the afterfeather are attached at their base to the rim of the superior umbilicilus.

There are 47 ($\pm$ 4) barbs per feather. The barbs are uniform in length on a single feather but vary a little from feather to feather (24 $\pm$ 5 mm). Emerging at an angle of 60–80° to the ramus are the barbules. There are 1250 barbules per barb ($\pm$ 130). They are uniform in length (335 $\pm$ 12 μm), emerge from the ramus every 20 μm and are arranged spirally. The arrangement of the barbules is approximately constant along the whole length of the barb. The barbules taper towards their tip but are 6 μm in diameter along most of their length. Coming off the barbule at intervals are forward-facing projections or cilia.

The cilia may be functionally equivalent to nodes on the barbules of downy feathers in ducks but the shape is very different—hence the different name. They increase in number and length towards the tip of the barbule and are 25–30 μm long at the tip of the barbule. They project at an acute angle to the barbule.

Modelling

To construct a thermal model of the feather system it is necessary to make some simplifying assumptions:

(a) The afterfeather is entirely responsible for the insulation of the penguin; the main part of the feather provides a wind and water-proof outer layer.
(b) The overall effect of the interacting barbules is to form horizontal layers within the insulated air space.
(c) The barbs of each afterfeather are evenly distributed and that the barbules are evenly distributed around the ramus of the barb (Table 1).
(d) The barbs are extended to their full length of 24 mm; barbules from one barb interact with its nearest six neighbours.

Using these assumptions it is possible to construct a schematic diagram of the feather insulation (Fig. 3).

There are three ways that heat can be exchanged; convection, radiation and conduction. Convection occurs when currents are set up in a fluid (in this case air). It is assumed that external

TABLE 1
Dimensions of feather elements

No. of feathers per cm^2 skin	35
Area each feather has to insulate	3 mm^2
No. of barbs per feather	47
Spacing between barbs assuming even distribution	0.3 mm
No. of barbules per feather	1250
Diameter of barbule	6 μm
Length of barbule	335 μm
Circumference of barb	2.11 mm
No. of barbules to completely fill circle	351
No. of completely filled layers per barb	3.5
No. of layers with seven barbs interacting	24

Note: Used to calculate the spacing of the layers of barbules within the coat of the penguin. The number of barbules needed to create a layer is calculated by dividing the circumference of the barb by the diameter of the barbule. Assuming equal distribution of the barbules and seven interacting barbs there are 24 layers spaced 1 mm apart—also see Figs. 2 and 3.

air currents cannot enter the downy afterfeathers. Therefore, only natural (as opposed to forced) convection can occur and only if the Rayleigh number (*Ra*) is greater than ca. 1700 (Bejan, 1993). *Ra* is a product of two dimensionless numbers; the Prandtl number (*Pr*) of the fluid and the Grashoff number (*Gr*). *Pr* for dry air is well known and for the range of temperatures encountered by penguins is about 0.7 (Bejan, 1993). *Gr* is calculated using

$$Gr = \frac{\rho^2 g\beta\Delta t l^3}{\mu^2},\tag{1}$$

where *Gr* is the Grashoff number; ρ the density of fluid (kg m^{-3}); g the acceleration due to gravity; β the coefficient of volumetric thermal expansion [K^{-1}—also see Fig. 3(b)]; Δt the temperature difference (K); l the characteristic length [m—also see Fig. 3(b)]; μ the dynamic viscosity of fluid (kg s^{-1} m^{-1}) (Incropera & DeWitt, 1996). The characteristic length l is the distance between the layers of barbules which is 1 mm (Fig. 3). Therefore, *Ra* is approximately 0.2, well below the *Ra* at which natural convection can occur. Thus convection is not a cause of heat loss within the feather layer of penguins.

If a thin layer of material is placed between two surfaces at different temperatures, the layer will absorb radiation from the hotter surface and

re-emit this radiation in all directions (i.e. half will radiate back towards the hotter surface—thus one layer reduces heat losses due to radiation by a half:

$$q_r = \frac{\sigma(T_1^4 - T_2^4)}{n + 1(2/\varepsilon - 1)},\tag{2}$$

where q_r is the radiative heat transfer (W m^{-2}); σ the Stefan–Boltzman constant (W m^{-2} K^{-4}); T_1 & T_2 the skin and air temperature, respectively (K); n the number of layers or radiation shields (24 used here); and ε the emissivity of keratin (0.8) (Bejan, 1993). The layers of barbules act as radiation shields, and using the values shown in Fig. 3 the calculated losses due to radiation are 3.1 W m^{-2} (without layers the value would be 78 W m^{-2}). The arrangement of the feathers significantly reduces the heat loss due to radiation.

Heat loss due to conduction,

$$k_{\text{total}} = (1 - \varepsilon)k_{keratin} + \varepsilon k_{air}\tag{3}$$

where k is the conduction (W m^{-1} K^{-1}); and ε the porosity of system (Dunn & Reay, 1976), treats the feather insulation as an open cell meshwork. The porosity of the system was calculated from the volume fraction of air in the feathers:

$$\varepsilon = (\text{total volume} - \text{volume of keratin})/$$
$$\text{total volume}\tag{4}$$

where ε is the porosity of system; total volume is the volume of feathers per unit area of skin (m^3); and volume keratin is the weight of feathers per unit volume of feathers/density of keratin (m^{-3}).

Discussion

The barbs attached to the rachis will move as the rachis is moved, i.e. muscle movements will directly alter their position. However, most of the insulation is provided by the afterfeather and the position of its barbs is not under direct muscular control. Rearrangement of the barbs of the afterfeather must therefore be done passively by storing strain energy in bending the barbs during compression and using this stored elastic energy to re-establish optimum spacing once the
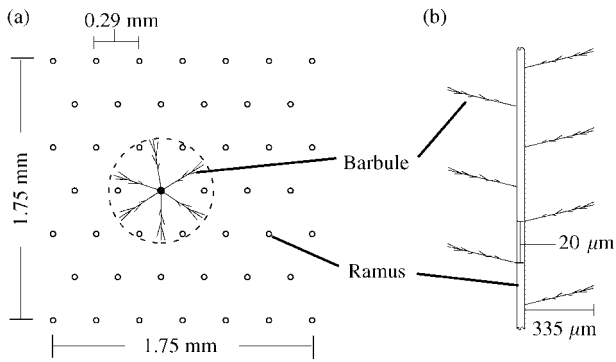
(a)

(b)

FIG. 2. Schematic diagram showing spacing of barbs and barbules of the afterfeather. (a) Plan view of afterfeather showing spacing of the rami of the barbs (small open circles) with one barb drawn showing the spiral arrangement of the barbules around the ramus (small solid circle with radial projections). The large dotted circle shows the extent of barbules of one barb (dotted circle, diameter 0.67 mm). (b) Side view of single barb with distance between neighbouring barbules indicated. Barbs are 24 mm long, with an average of 1250 barbules per bar. Compare with Table 1 to see how spacing of "layers" within the penguin coat were calculated.
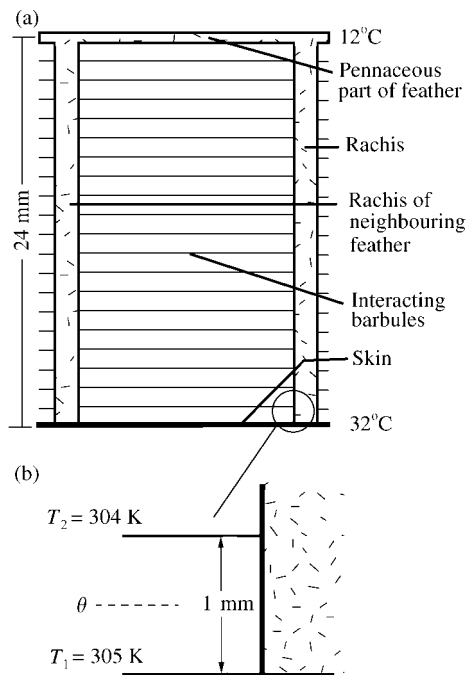
(a)

(b)

FIG. 3. Schematic diagram showing structuring of air space within the feather coat of a penguin. The temperatures indicated on the diagram were used to calculate Ra and radiative heat loss—see text for details. (a) Side view of coat showing two feathers. The horizontal layers show the net effect of the interacting barbules which subdivide the air space beneath the windproof pennaceous layer. The space is also divided vertically by the rami of the barbs but this is not shown here. (b) Enlarged view of the space between the skin and the first layer of barbules. The gap size indicated is the characteristic length l and θ is the film temperature: $(T_1 + T_2/2) - \beta = 1/\theta$.

penguin emerges onto land. Modelling of the optimal spacing between hairs to provide efficient insulation has been carried out by Bejan (1990a, b) but as yet this has not been extended to the more complex feather insulation.

The function of the cilia is, most probably, to entangle one another and allow the barbules to move in only one direction relative to one another via a "stick slip" mechanism [Fig. 1(c)]. The net effect of the arrangement of the barbules is to produce a regular, uniform division of the air space within the coat with well defined dimensions (Fig. 2).

The thermal conduction predicted by the model assumes that all the keratin in the feathers is involved in the conduction pathway. Whilst this is not true, it was not possible to measure the proportion of keratin in the conduction pathway. As a result the thermal conductivity predicted by the model should be greater than that actually measured. The heat loss due to radiation has not been included as it is not possible to express the loss in $W\,m^{-2}\,K^{-1}$. However, for the temperatures given in Fig. 3 the radiative heat loss is less than 6% of the total. The model shows, that for penguin feathers at least, it is safe to assume that convective heat loss does not occur and that radiative heat losses are small. Using the temperatures shown in Fig. 3, the model predicts a thermal conductivity of $2.38\,W\,m^{-2}\,K^{-1}$ which is close to an empirically measured value of $1.93\,W\,m^{-2}\,K^{-1}$ for adult Gentoo Penguin (Kooyman et al., 1976). However, further experimental work is required to test the validity of the model proposed here.

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