Air movement and heat loss from sheep.

III. Components of insulation in a controlled environment

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The rate of sensible heat loss from a Clun Forest ewe was studied at several fleece depths in a temperature-controlled chamber. A simple resistance analogue was used to describe the heat flow from different body regions.

Heat loss from the trunk depends largely on the mean fleece depth $l$. The fleece resistance was about $1.5 \text{s cm}^{-1}$ per centimetre depth. Heat transfer through the fleece was accounted for by molecular conduction, thermal radiation and free convection. The fleece conductivity $k_b$ attributed to free convection depends on the mean temperature difference $(T_{st} - T_{ct})$ across the fleece according to the relation $k_b = 8.9 (T_{st} - T_{ct})^{0.53}$. Estimates of the sensible heat flux from the trunk at environmental temperatures, $T_a$, between $0$ and $30 \degree C$ range from about $8 \text{ W} (l = 7.0 \text{ cm}, T_a = 30 \degree C)$ to about $160 \text{ W} (l = 0.1 \text{ cm}, T_a = 0 \degree C)$.

In contrast, the sensible heat loss from the legs depends mainly on the local tissue resistance. For environmental temperatures between $0$ and $30 \degree C$, the calculated tissue resistance for this region of the body varied from about $8$ to $1 \text{ s cm}^{-1}$. The corresponding heat loss from the legs was between $10$ and $20 \text{ W}$, compared with between $3$ and $7 \text{ W}$ from the head.

The fastest heat loss from the legs occurred at an environmental temperature of about $12 \degree C$. Although the proportion of the heat loss from the extremities depends on environmental temperature, the total heat loss (sensible or latent) was closely related to the mean skin temperature of the trunk.

Introduction

A housed animal is usually surrounded by still or slowly moving air and by walls whose radiative temperature is close to air temperature. When deep body temperature exceeds environmental temperature, sensible heat must flow through the body tissue and coat of the animal to the environment. When this flux exceeds the rate at which heat is produced by metabolism in a thermoneutral environment, evaporative heat loss is minimal and any decrease of environmental temperature must be balanced by an increase in the metabolic rate. Bennett (1972) reported that the summit metabolism of a sheep is about $10 \text{ W kg}^{-1}$, about five times its heat production in a thermoneutral environment. Conversely, if the heat produced...
by metabolism cannot be dissipated fast enough by convection and radiation, the animal must increase its evaporative heat loss to remove surplus heat. Sheep respond to heat by panting. Brockway et al. (1965) reported that cutaneous evaporation from sheep with fleeces was practically constant at environmental temperatures up to 35 °C and accounted for a small component of the total evaporative loss, although Knapp & Robinson (1954) found that cutaneous evaporation was an important mechanism of heat loss from shorn sheep at environmental temperatures between 30 and 40 °C. Hofmeyr et al. (1969) concluded that, while sweating can be important over the initial period of exposure to heat stress, respiratory evaporation is usually rapid enough to maintain homeothermy; they indicated that wool cover may impede evaporation from the skin surface. In addition to changes in metabolism and evaporation, vasomotor changes regulate the heat flow between the body core and the skin surface. These changes in blood flow are pronounced on extremities such as the legs, but have not been observed on the trunk.

Prediction of the rates of heat production or evaporative heat loss necessary for the maintenance of a steady deep body temperature in a specified environment requires a knowledge of the total thermal insulation between the body core of an animal and its surroundings. Three main resistances to sensible heat flow act in series, provided by the body tissue, the coat and the environment. The unit of resistance used in this paper has the dimensions of time per unit length, and 1 s cm⁻¹ is equivalent to 0.078 m² K W⁻¹.

Values of these resistances, averaged over the whole body, have been determined from measurements of the rate of metabolic heat production, the rate of evaporative heat loss, and the corresponding mean temperature differences. The average tissue resistance for Down Cross sheep, calculated from the data of Blaxter et al. (1959), ranges from 0.9 for vasoconstriction to 0.3 s cm⁻¹ for vasodilation. Systematic differences are reported between breeds. Maximum tissue resistances of about 1.1, 1.6, 1.8 and 2.3 s cm⁻¹ have been calculated for Down Cross, Blackface, Suffolk and Cheviot sheep respectively (Armstrong et al. 1960; Joyce & Blaxter 1964; Webster & Blaxter 1966). These values are between two and three times the reported tissue resistance when the blood vessels are dilated. However, in calculation of the average tissue resistance, the total metabolic rate rather than the heat flux through the body tissue is normally used (see, for example, Blaxter 1967). As the latent heat flux from the respiratory tract of a sheep can be a significant part of the total heat loss, the values reported must underestimate the true resistances. For the above breeds, the average coat resistivity, defined as the coat resistance per unit depth, measured at low rates of air movement (windspeed < 0.4 m s⁻¹) ranges from about 1.4 to 2.0 s cm⁻² (Blaxter et al. 1959; Doney 1963; Joyce et al. 1966; Webster & Blaxter 1966). Values of the environmental resistance at similar windspeeds lie between about 1.2 and 2.2 s cm⁻¹ (Blaxter et al. 1959; Joyce & Blaxter 1964; Joyce et al. 1966; Webster & Blaxter 1966).

These figures indicate that the total resistance to sensible heat loss from sheep
depends largely on the coat depth. Heat transfer through this layer can occur by several processes simultaneously: conduction along the fibres, molecular diffusion, convection and radiation (Cena & Monteith 1975a, b; McArthur & Monteith 1980b). However, the legs and head, which comprise about 30% of the total skin surface area, have little coat insulation in comparison with the trunk, where the mean fleece depth may exceed 10 cm. Consequently, large regional variations exist in tissue and coat resistance and in the sensible heat flux density.

The aim of this study was to investigate the rates of heat loss by convection and long-wave radiation from an adult sheep indoors. A simple resistance analogue was used to describe the sensible heat flow from different body regions, and its component resistances were determined experimentally. From the analogue, the total heat balance of the sheep was related to the mean fleece depth and to environmental temperature. Particular attention was given to assessment of the thermal properties of the fleece.

**Theory**

Figure 1 is a resistance analogue describing the pathways of sensible heat flow between the body core at temperature $T_b$ and the environment specified by the air temperature $T_a$ and mean radiative temperature $T_e$. The trunk, legs and head, treated as separate body regions, are denoted by the second subscripts t, l and h respectively. The quantities $r_s$ and $r_c$ are the mean thermal resistance of the body tissue and the coat respectively. (E.g. $r_{sl}$ is the mean tissue resistance of the legs.) For the trunk, the mean fleece resistance is indicated by $r_f$. The environmental resistance $r_e$ between the coat surface and the surroundings comprises a boundary layer resistance $r_a$ and radiative resistance $r_R$ in parallel. The symbols $C$ and $L_n$ are the heat losses by convection and long-wave radiation exchange respectively, and $G$ is the sensible heat transfer through the coat. The mean temperature of the skin surface is denoted by $T_s$ and the radiative temperature of the coat surface by $T_c$.

The average sensible heat flux density for an animal is usually based on the total skin surface area, evaluated, for example, as $0.09 \, \text{kg/kgs}^{0.667}$ (Mitchell 1927). As the exchange of heat with the surroundings occurs by convection and radiation from the outer surface of the coat, it is more convenient to refer $G$ to the outer surface area, such that, for each region,

$$G = C + L_n.$$  

The sensible heat flux density $G_s$ at the skin surface is simply

$$G_s = GA/A_s,$$  

where $A_s$ is the skin surface area and $A$ is the surface area of the coat. The thermal surface of the fleece-covered trunk was assumed to be a few millimetres below the actual hair tips (Clark et al. 1973). By treating the trunk as a horizontal cylinder.
with hemispherical ends, the area $A_t$ of this surface can be estimated with acceptable accuracy as
\[ A_t = \pi d (d + y), \]
where $d$ is the mean (outer) diameter and $y$ is the length of the cylindrical section.

As the depth of hair on the legs and head is small in comparison with the diameter of these regions, it was assumed that
\[ G_{1,h} = G_{s1,h}. \]

The total sensible heat flux $H_{tot}$ is then defined by
\[ H_{tot} = G_tA_t + G_lA_l + G_hA_h. \]

For each region of the body, the thermal resistances to sensible heat transfer can be defined as follows.

**Radiative resistance $r_R$.** The heat flux density $L_n$ by long-wave radiation exchange between a surface behaving as a black body radiator at absolute temperature $T_e$
and the surroundings which are radiating at absolute temperature $T_e$ is given by

$$L_n = \sigma(T_e^4 - T_m^4),$$

where $\sigma$ is the Stefan–Boltzmann constant ($= 5.67 \times 10^{-8}$ W m$^{-2}$ K$^{-4}$). If $T_m$ (expressed in kelvin) is the average of $T_c$ and $T_e$, and $T_m \gg (T_e - T_c)$, it can be shown that

$$L_n = \rho c_p(T_c - T_e)/r_R,$$

where $\rho c_p$ is the volumetric heat capacity of air and $r_R = \rho c_p/4\sigma T_m^3$ is the resistance to radiative transfer (Monteith 1975). The value of $r_R$ depends only on the absolute temperatures of the surface and the radiative environment. For values of $T_m$ between 273 and 303 K, $2.8 > r_R > 2.0$ s cm$^{-1}$.

Boundary layer resistance $\tilde{r}_a$. The boundary layer resistance governing convective heat transfer depends on the rate of air movement, the body geometry and the nature of the interface (Mitchell 1974; McArthur & Monteith 1980a). This resistance is defined by

$$C = \rho c_p(T_c-T_e)/\tilde{r}_a.$$

The mean value $\tilde{r}_a$ for each region of the body was determined by studying the energy balance of a model sheep. With use of this value of $\tilde{r}_a$, values of heat flux densities for convection from the live sheep were evaluated from measurements of the mean temperature difference between the radiative surface of the coat and surrounding air. A small correction was made to the value of $\tilde{r}_a$ for the trunk to allow for the change in diameter with increasing fleece depth.

The average boundary layer resistance $\tilde{r}_{am}$ for the whole body can be calculated with acceptable accuracy from

$$\tilde{r}_{am} = A_{tot}/(A_t/\tilde{r}_{at} + A_1/\tilde{r}_{a1} + A_h/\tilde{r}_{ah}),$$

where $A_{tot}$ is the total (outer) surface area.

Environmental resistance $\tilde{r}_e$. Combining equations (1), (7) and (8), the total sensible heat flux density $G$ can be written as

$$G = \rho c_p(T_c-T_e)/\tilde{r}_e + \rho c_p(T_a-T_e)/r_R,$$

where $\tilde{r}_e = \tilde{r}_a r_R/(\tilde{r}_a + r_R)$ is the thermal resistance of the environment. Indoors, the condition $T_a = T_e$ is usually satisfied, so that

$$G = \rho c_p(T_c-T_a)/\tilde{r}_e.$$

Coat resistance $\tilde{r}_c$. The mean thermal resistance of the coat is defined by

$$G = \beta'\rho c_p(T_s-T_e)/\tilde{r}_c,$$

where $\beta'$ is a term that accounts for the effects of body curvature (McArthur & Monteith 1980b). For a cylindrical body with hemispherical ends and covered with an insulating layer of depth $\hat{t}$,

$$\beta' = [(1-\hat{t}/d)y + (d-2\hat{t})]/(y+d).$$
For the trunk, the value of $\beta'$ was calculated from measurements of the mean fleece depth $l$ and the dimensions $d$ and $y$. For the legs and head, the assumption $\beta' = 1.0$ introduces little error.

**Tissue resistance $\bar{r}_s$.** The thermal resistance $\bar{r}_s$ of the skin and body tissue is defined by

$$ G_s = \rho_c c_p (T_b - T_s)/\bar{r}_s. \quad (13) $$

*Sensible heat loss.* Assuming that the evaporative heat flux from the skin surface is a negligible component of the total heat flow, the rate of sensible heat loss $G_s$ from each region of the body can be evaluated by combining the above equations to give

$$ G_s = \rho_c c_p [(T_b - T_a) + (\bar{r}_a/\tau_R) (T_b - T_e)] / [(\bar{r}_s + \bar{r}_c A_s/\beta' A) (1 + \bar{r}_a/\tau_R) + \bar{r}_a A_s/A]. \quad (14) $$

**Apparatus and experimental procedure**

**Model studies**

Boundary layer resistance values for each region of the body were determined from the energy balance of the life-size thermal model described by McArthur & Monteith (1980a). Steady-state measurements were recorded in a controlled temperature chamber in which the rate of air movement, measured with an omnidirectional hot wire anemometer (Hastings, type N-78), was approximately 0.3 m s$^{-1}$. The mean radiative temperature $T_e$ of the walls and the floor was usually within 1 K of the air temperature $T_a$.

**Measurements**

For each region of the model, the convective heat flux density $C$ was determined from the measured power input corrected for radiation losses. The surface temperature of the trunk (fleece-covered) was measured at 60 evenly distributed sites by means of a portable infrared radiometer (Barnes Engineering Co., model PRT-10L) held normal to the surface; the mean surface temperature $T_{ct}$ was calculated as the arithmetic average of these measurements. The mean surface temperature of the legs, $T_{cl}$, and head, $T_{ch}$, was measured with surface-mounted thermocouples. Air temperature in the chamber was measured with an Assmann ventilated psychrometer. The mean radiative temperatures of the walls etc. in the chamber were measured by means of a miniature net radiometer fitted on one side with a black body cavity at known temperature. Net radiation losses were calculated according to equation (7). The energy balance of each region was studied separately and at power inputs in the range 20 to 60 W m$^{-2}$. Values of $\bar{r}_a$ were calculated in accordance with equation (8).

**Animal studies**

The steady sensible heat loss from a Clun Forest ewe (body mass $\approx 56$ kg) was studied at intervals over one year in the controlled temperature chamber used for the model studies. The sheep stood restrained in a metabolism crate at the centre
of the room, but the sides of the crate were removed to prevent disturbance of the fleece. At each fleece depth, the heat flux densities were estimated at air temperatures between about 0 and 25 °C. Measurements were not made at air temperatures outside this range as rapid body movement associated with shivering or panting could have decreased the boundary layer resistance. Vapour pressure in the chamber was not controlled, but relative humidity did not exceed 50%. An equilibration time of at least 6 h was allowed at each temperature setting (Webster 1966). Measurements were made over periods of approximately 30 min.

Measurements

(i) Trunk. Before each series of observations, the fleece depth was measured at 60 evenly distributed sites on the trunk with a calibrated probe held normal to the skin surface. The mean fleece depth \( \bar{l} \), calculated as the arithmetic average of these measurements, varied between 1.1 and 6.6 cm. Skin surface temperature was measured at 12 sites on the trunk by means of a 42 s.w.g. copper-constantan thermocouple contact probe, and fleece surface temperature was measured at 60 sites with the infrared radiometer. The net long-wave radiation loss was measured at 12 sites by a miniature net radiometer (Funk type) held parallel to and about 2 cm from the fleece surface. Average values of skin temperature, fleece surface temperature and net radiation were used in calculations. The net radiation loss was also calculated from equation (7) with use of the measured values of \( \bar{T}_{ct} \) and \( \bar{T}_e \). On all but two occasions, agreement between the measured and calculated values of \( L_{nt} \) was better than ±2 W m⁻². Rectal temperature \( T_b \) was measured with a calibrated thermistor probe inserted to a depth of about 8 cm. The value of \( T_b \) was 39.0 (± 0.1 °C) in each case.

(ii) Legs and head. The surface temperatures at 10 sites on each leg and at 8 sites on the head were measured with the infrared radiometer. The mean surface temperature of each region was evaluated and the net radiation loss calculated. It was assumed that the radiative temperature of the surroundings 'seen' by the head was the mean value for the chamber, \( \bar{T}_e \). For the legs, however, a small arbitrary correction (ca. 1K) was made to the value of \( \bar{T}_e \) to allow for radiation exchange with other parts of the body.

The mean skin temperature could not be measured exactly. Point measurements of skin temperature cannot be assumed representative of the mean value, and it was impractical to attach a large number of thermocouples to the skin surface of these regions. There was some fleece growth on each region and a small increase in coat resistance with time must have occurred. To minimize this change, the heat losses from the legs and head were determined when the mean fleece depth on the trunk was between 4 and 6 cm. The total resistances \( r_1 \) and \( r_h \) (figure 1) between the body core and coat surface were evaluated.
Results and discussion

Model studies

The energy balance of each region of the model sheep was studied in the chamber at a temperature setting of approximately 12 °C. The area of the effective trunk surface was 1.10 m², and the surface areas of the leg and head regions were 0.22 and 0.10 m² respectively. Figure 2 shows the relation between the convective heat flux density $C_t$ and the mean temperature difference $(T_{ct} - T_a)$ between the trunk surface and the surrounding air.

![Figure 2. Heat loss from model: convective heat flux density $C_t$ plotted against the mean temperature difference $(T_{ct} - T_a)$ between the fleece surface and the surrounding air.](http://rspb.royalsocietypublishing.org/)

Therefore, the boundary layer resistance $r_a$ of 2.7, 1.9 and 2.6 s cm⁻¹ were evaluated for the trunk, legs and head respectively. These values are estimated to be accurate to within ±10%.

Because the values of $r_a$ are comparable in magnitude with the resistance $r_R$ to radiative transfer, heat losses by convection and radiation will occur at similar rates when the radiative temperature of the surroundings is close to air temperature. The average boundary layer resistance $r_{am}$ for the whole body, calculated by means of equation (9), was about 2.5 s cm⁻¹. It follows that for environmental temperatures between 0 and 30 °C, the average environmental resistance $r_{em}$ for the whole body, which comprises the boundary layer resistance and radiative resistance acting in parallel, lay in the range 1.1 to 1.3 s cm⁻¹.
Trunk

Figure 3 shows the mean fleece depth plotted against time. The rate of fleece growth decreased from about 1.0 cm per month immediately after shearing to about 0.4 cm per month at large fleece depths. The initial growth rate can be compared with corresponding values of about 1.0 and 2.5 cm per month reported for Cheviot and for Blackface sheep respectively (Armstrong et al. 1960). The variation of the quantity $\beta'$, calculated from equation (12), is shown by line $a$ in figure 3. Values of $\beta'$ lie between 1.0 ($\bar{l} = 0$) and 0.77 ($\bar{l} = 7.0$ cm). The corresponding values of $A_t$, evaluated by means of equation (3), are shown by line $b$. The measured values of $d$ (at $\bar{l} = 0$) and $y$ were 0.30 and 0.53 m respectively.

With the exception of a small area (less than 0.08 m$^2$) of the belly, where the local fleece depth did not exceed 3.5 cm, fleece growth on the trunk was fairly uniform. The wool fibres grew almost normal to the skin surface, although, owing to crimping, hair length exceeded the recorded values of fleece depth.

The total rate of sensible heat flow through the fleece was determined by equation (1). Values of the mean temperature difference $\left(\bar{T}_{et} - \bar{T}_{at}\right)$ did not exceed 7.5 K. Figure 4 $a$, $b$ shows the heat flux density $G_t$ plotted against the mean temperature difference $\left(\bar{T}_{at} - \bar{T}_{et}\right)$ across the fleece. Results are presented for mean fleece depths of 1.1, 2.3, 3.7, 4.7, 5.1 and 6.6 cm. A straight line, forced through the origin, was fitted to each set of experimental points; all the correlation coefficients exceeded 0.996. The relation between the quantity $(\bar{r}_f/\beta')$, evaluated from the slopes of the lines in accordance with equation (11), and the mean fleece depth is presented in figure 5. Values of $(\bar{r}_f/\beta')$ increase systematically with fleece depth, reaching a value of about 13.6 s cm$^{-1}$ at $\bar{l} = 6.6$ cm. For comparison, figure 5 also shows the values of $\bar{r}_{at}$ (line $a$) and $r_R$ (line $b$) when the temperature $T_m$ is 283 K. When the mean fleece depth is greater than about 1 cm, the quantity $(\bar{r}_f/\beta')$
mean temperature difference, \( (T_a - T_m)/K \)

**Figure 4.** Heat loss from trunk; sensible heat flux density \( G_i \) plotted against mean temperature difference \( (T_a - T_m) \) across the fleece. (a) Mean fleece depth \( l = 1.1, 3.7 \) and \( 5.1 \) cm; (b) \( l = 2.3, 4.7 \) and \( 6.6 \) cm.

**Figure 5.** Variation of the quantity \( \bar{r}_f/\beta' \) with mean fleece depth \( \bar{l} \). Lines \( a \) and \( b \) show boundary layer resistance \( r_\text{bl} \) and resistance \( r_R \) to thermal radiation exchange, respectively.

**Figure 6.** Fleece resistance \( \bar{r}_f \) plotted against mean fleece depth \( \bar{l} \) (solid line). The broken line indicates the thermal resistance of an equivalent depth of still air.

exceeds the environmental resistance \( \bar{r}_e \). The curvilinear relation shown in figure 5 can be attributed to the effects of body curvature. Because fleece surface area increases with depth (figure 3) the results show that the addition of unit depth of fleece becomes less effective with increasing coat depth.

Figure 6 shows the fleece resistance \( \bar{r}_f \) plotted against the mean fleece depth \( \bar{l} \). For comparison, the dashed line shows the thermal resistance of an equivalent depth of still air (at 25°C), which exceeds the fleece resistance by a factor of about.
3. The experimental points can be described by a straight line fitted through the origin and with a slope of 1.5 s cm\(^{-2}\). The corresponding thermal conductivity \(k_t\) of the fleece is 86 mW m\(^{-1}\) K\(^{-1}\). Heat transfer by molecular diffusion and thermal radiation alone cannot account for this value: the thermal conductivity of still air is about 25 mW m\(^{-1}\) K\(^{-1}\) and the fleece conductivity attributable to radiation is about 20 mW m\(^{-1}\) K\(^{-1}\) (Cena & Monteith 1975b). As the rate of air movement in

the chamber was slow, free convection within the fleece is a likely mechanism of heat transfer. Neglecting conduction along the fibres, figure 7 shows the fleece conductivity \(k_b\) (\(= k_t - 45\)) attributed to free convection plotted against the mean temperature difference \((T_{st} - T_{ct})\) across the fleece. The results shown are for mean fleece depths of 1.1, 2.3, 3.7, 4.7 and 5.1 cm. (The points for \(l = 6.6\) cm are omitted as the heat flux density \(G_t\) was small and scatter in the points was large.) The increase in \(k_b\) from about 25 mW m\(^{-1}\) K\(^{-1}\) at \((T_{st} - T_{ct}) = 8\) K to about 50 mW m\(^{-1}\) K\(^{-1}\) at \((T_{st} - T_{ct}) = 25\) K can be accounted for by increased convection of the air within the fleece by buoyancy forces.

Measurements of the heat transfer by free convection from smooth cylinders have shown that the conductance of the boundary layer is proportional to \(\delta T^n\), where \(\delta T\) is the difference between the mean temperature of the surface and the temperature of the surrounding fluid. The exponent \(n\) has a value of 0.25 when the régime is laminar and is 0.33 when it is turbulent. By minimizing the root mean square difference between the experimental values of \(k_b\) and the values predicted by the relation

\[
  k_b = B(T_{st} - T_{ct})^n,
\]

(15)
the independent variables were evaluated as $B = 8.9$ and $n = 0.53$. This relation is indicated by the solid line in figure 7. The rate of heat loss from a warm cylinder ($\delta T = 25$ K), with a diameter of 0.33 m, to the surrounding air (still) is about 100 W m$^{-2}$. When insulation is provided by a 5 cm depth of fleece with $(\bar{T}_{st} - \bar{T}_{ct}) = 25$ K, the heat loss by molecular conduction and convection from the skin (trunk) surface of a sheep exposed to slowly moving air is only about 40 W m$^{-2}$. The inhibition of upward movement of warm air from the skin surface is therefore an important function of the fleece. However, the results in figure 7 indicate that in slowly moving air a temperature difference of 25 K across a sheep’s fleece will reduce the fleece resistivity to about 50% of its maximum value, and that free convection may often be the main mechanism of heat transfer through the coat. Although values of $(\bar{T}_{st} - \bar{T}_{ct})$ exceeding 25 K are common in winter, this dependence of coat insulation on temperature difference is usually ignored in estimations of heat loss.

The tissue resistance $\bar{r}_{st}$ for the trunk was evaluated as 1.0 (± 0.2) s cm$^{-1}$. The uncertainty in this resistance value may be attributed in part to variations in the small evaporative heat loss from the skin surface. In addition, tissue resistance may change with time.

**Legs**

Figure 8 shows the relation between the resistance $\bar{r}_{l}$ ($= \bar{r}_{sl} + \bar{r}_{cl}$) and the mean temperature difference $(T_{b} - \bar{T}_{sl})$ between the body core and the outer surface of the legs. Values of $\bar{r}_{l}$ range from about 1.5 s cm$^{-1}$ at the higher environmental temperatures ($T_{a} > 20$ °C) to about 8.5 s cm$^{-1}$ at low temperatures ($T_{a} < 2$ °C). This increase in the value of $\bar{r}_{l}$ may be attributed to a reduction in blood flow to the legs. The contribution to the resistance $\bar{r}_{l}$ provided by the coat can be estimated if it is assumed that the resistivity of the coat on the legs has the same value as the fleece. The dashed line in figure 8 shows the estimated value of $\bar{r}_{cl}$ when the mean coat depth on the legs is 3 mm. At the higher environmental temperatures, the coat contributed about 30% of the total resistance $\bar{r}_{l}$ compared with only 6% at the lower temperatures.

Figure 9 shows the quantity $\bar{r}_{sl}^{-1}$ plotted against the estimated mean temperature difference $(T_{b} - \bar{T}_{sl})$ between the body core and the skin surface. The quantity $\bar{r}_{sl}^{-1}$, which is a tissue conductance, decreases almost linearly with $(T_{b} - \bar{T}_{sl})$ to about 27 °C, corresponding to $\bar{T}_{sl} = 12$ °C. For skin temperatures above 12 °C, the relation can be described by

$$\bar{r}_{sl}^{-1} = 0.96 - 0.031 (T_{b} - \bar{T}_{sl}),$$

which implies that the blood flow to the legs is controlled by the local skin temperature $\bar{T}_{sl}$. To prevent damage to the leg tissue, the tissue conductance must reach a minimum value, set somewhat arbitrarily at 0.125 cm s$^{-1}$, as indicated by the horizontal line in figure 9. When the environmental temperature falls below 0 °C, the tissue conductance must increase above its minimum value (cold-induced vasodilation) to prevent freezing of the tissues.
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Head

Figure 10 shows the head resistance $\bar{r}_h$ plotted against the mean temperature difference $(T_b - T_{ch})$. The substantial scatter in the results may be attributed to experimental error in determination of the mean surface temperature. The variation of surface temperature over the head was often larger than the calculated mean difference between surface and environmental temperature. The relation between $\bar{r}_h$ and $(T_b - T_{ch})$ can be represented approximately by the solid line drawn by eye through the experimental points, which implies that when the environmental temperature is between 0 and 30 °C, the resistance $\bar{r}_h$ lies between 6 (± 2) s cm$^{-1}$ and 3 (± 1) s cm$^{-1}$. The dashed line in figure 10 shows the coat resistance for an average coat depth of about 0.5 cm.
At an environmental temperature of \(-0.7\, ^\circ\text{C}\), the surface temperature of the poorly insulated parts of the head did not fall below \(5\, ^\circ\text{C}\) whereas local surface temperatures on the lower parts of the legs were between \(0\) and \(1\, ^\circ\text{C}\). These observations are consistent with a preferential flow of blood to the head, presumably to prevent local cooling in the brain.

**Total heat balance**

To maintain a steady body temperature, a balance must be achieved between the rate at which heat is produced by metabolism and the rate of loss by sensible and latent heat transfer. Changes in the metabolic rate or the latent heat loss in response to environment changes can be predicted from an analysis of the sensible heat flow.

**Sensible heat loss**

Figure 11 shows the dependence on environmental temperature of the heat flux density \(G_{st}\) at the skin surface of the trunk, predicted from equation (14). The curves, which correspond to fleece depths of 0.1, 1.0, 3.5 and 7.0 cm respectively, apply to slow air movement (windspeed \(\approx 0.3\, \text{m s}^{-1}\)) and to an environment in which \(T_a = T_e\). The heat production of a sheep (body mass = 50 kg) in a thermoneutral environment lies between about 60 and 100 W depending on the feeding level (Graham et al. 1959). Line \(a\) corresponds to maintenance feeding level; line \(b\) corresponds to well fed sheep. The intersections of the horizontal dashed lines with the solid curves indicate the environmental temperature below which the rate of sensible heat loss from the trunk exceeds metabolism.

Figure 12a shows the predicted dependence of \(G_l\), the heat flux density at the surface of the legs, on environmental temperature (assuming \(T_e = T_a + 1.0\)). With the further assumption that \(\bar{r}_{el} = 0.5\, \text{s cm}^{-1}\), figure 12b shows the corresponding values of the mean skin temperature \(\bar{T}_{sl}\) (line (i)) and the tissue resistance \(\bar{r}_{sl}\) (line (ii)) plotted against environmental temperature. The graphs indicate that the rate of heat loss from the legs is slow (ca. 9 W) at the higher environmental temperatures. This rate increases with decreasing environmental temperature and reaches a maximum value of about 20 W at approximately \(12\, ^\circ\text{C}\). At an environmental temperature of approximately \(5\, ^\circ\text{C}\), the temperature difference between the skin surface and the environment is minimal and a heat flux of about 10 W is expected. This fall in \(G_l\) with decreasing temperature is attributable to the sharp increase in tissue resistance (figure 9) when the mean skin temperature falls below about \(15\, ^\circ\text{C}\). For environmental temperatures below \(0\, ^\circ\text{C}\), the dashed part of the curve in figure 12a is included to indicate the rate of heat loss needed to maintain the mean skin temperature of the legs at about \(6\, ^\circ\text{C}\), a value that allows for a temperature drop between the upper and lower parts of the legs but with \(T_{sl} > 0\, ^\circ\text{C}\) at all positions. These estimates of heat loss are consistent with the observations of Webster & Blaxter (1966) that the rate of sensible heat loss from the shanks of Cheviot and Suffolk sheep was very small at air temperatures of \(5\) and \(0\, ^\circ\text{C}\) respec-
tively, and that the rate of heat loss from the lower leg increased threefold when air temperature was lowered from 0 to \(-10^\circ C\).

It is likely that a change in the coat resistance \(r_{cl}\) with depth, associated with the growth of fleece on the upper half of the leg, will make the sharp change in tissue

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**Figure 11.** Heat loss from trunk: computed variation of sensible heat flux density \(G_{st}\) with environmental temperature \(T_s\). Lines \(a\) and \(b\), respectively, show the rate of heat production of a sheep (body mass \(\approx 50\) kg) on a low and on a high plane of nutrition; \(l\), mean fleece depth.

**Figure 12.** Heat loss from legs: (a) computed variation with environmental temperature \(T_s\) of the sensible heat flux density \(G_s\); (b) mean skin temperature (line (i)), tissue resistance (line (ii)), environmental temperature (line (iii)).

resistance \(r_{sl}\) occur at a different environmental temperature to that shown in figure 12b. The measurements for the head show that the rate of sensible heat loss from this region increases systematically from about \(3 \ (\pm 1)\ W\) at an environmental temperature of \(30^\circ C\) to about \(7 \ (\pm 2)\ W\) at \(0^\circ C\).

Figure 13 shows the sensible heat flux \(H_t\) from the trunk, expressed as a percentage of the total sensible heat flux \(H_{tot}\) plotted against environmental temperature for fleece depths of 0.1, 1.0, 3.5 and 7.0 cm respectively. The proportion
of the heat loss occurring from the extremities (legs and head) depends on fleece depth and environmental temperature. At the lower environmental temperatures ($T_a \approx 0 \, ^\circ C$) the extremities contribute less than 30% of the total heat flux. This fraction increases as environmental temperature is raised and at $30 \, ^\circ C$, with a fleece depth of 7.0 cm, the extremities contribute about 60% of the total sensible heat flow. At subzero temperatures, if vasodilation occurs, the ratio $H_t/H_{tot}$ will decrease below the maximum value shown in figure 13.

The average tissue resistance for the whole body was evaluated by inserting the mean sensible heat flux density (based on total skin surface area) and the mean skin temperature (obtained by weighting the skin temperatures of the different regions according to the area that they represent) into equation (13). The average tissue resistance ranged from about 1.0 to 2.5 s cm$^{-1}$, depending on the blood flow to the legs. The value of 2.5 s cm$^{-1}$ is similar in magnitude to the maximum tissue resistance figures quoted earlier for other breeds. However, the present minimum value of 1.0 s cm$^{-1}$ cannot be readily compared with other reported figures. The present results show that values of tissue resistance expressed as an average for the whole body conceal large local variations in this quantity. But the fact that these variations occur in appendages, where the corresponding changes in sensible heat loss are small in comparison with the metabolic rate, implies that alterations in the

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**Figure 13.** Sensible heat flux $H_t$ from the trunk, expressed as a percentage of the total sensible heat flux $H_{tot}$, plotted against environmental temperature $T_a$; $l$, mean fleece depth.

**Figure 14.** Computed latent heat flux $\lambda E'$ plotted against environmental temperature $T_a$; $l$, mean fleece depth.
average tissue resistance do not reflect clearly an animal's ability to withstand cold.

**Latent heat loss**

The minimum latent heat fluxes by respiratory and by cutaneous evaporation from sheep are about 5 and 10 W respectively (Brockway *et al.* 1965). With the assumption that the rate of heat production is $M = 80$ W, the total latent heat flux $\lambda E'$, expressed in watts, can be estimated by means of

$$\lambda E' = M - H_{\text{tot}}.$$  \hspace{1cm} (17)

**Figure 15.** Respiratory heat loss: computed latent heat flux $\lambda E'_R$ plotted against mean skin (trunk) temperature $T_{st}$.

**Figure 16.** Computed sensible heat flux plotted against mean skin (trunk) temperature $T_{st}$.

Figure 14 shows calculated values of $\lambda E'$ plotted against environmental temperature for fleece depths of 0.1, 1.0, 3.5 and 7.0 cm. For Clun Forest sheep indoors, the environmental temperature above which evaporative heat loss must increase with temperature ranges from about 3 °C at $l = 7.0$ cm to about 28 °C at $l = 0.1$ cm. These values are consistent with measurements reported from calorimeter studies on Down Cross sheep (Blaxter *et al.* 1959).

Assuming that the cutaneous evaporative heat flux $\lambda E'_g$ remains constant at 10 W, the respiratory latent heat flux $\lambda E'_R$ can be calculated as

$$\lambda E'_R = \lambda E' - \lambda E'_g.$$  \hspace{1cm} (18)

Figure 15 shows values of $\lambda E'_R$ plotted against the calculated mean skin tempera-
ture $T_{st}$ of the trunk. Above $T_{st} = 35 \, ^\circ C$, the points lie close to a straight line with a slope of 16 W K$^{-1}$. Below $T_{st} = 35 \, ^\circ C$, the respiratory latent heat flux is minimal. The points shown on figure 15 were determined from equation (17) and values of $H_{tot}$ calculated for 4 K intervals between $T_a = 2$ and 30 $^\circ C$, and for fleece depths of 0.1, 1.0, 3.5 and 7.0 cm. The deviation from a straight line relation above $T_{st} = 35 \, ^\circ C$ is attributable to variations in the sensible heat loss from the legs, which depends on $T_{sl}$ rather than $T_{st}$. These results predict that evaporative heat loss from sheep depends largely on the mean skin temperature of the trunk surface.

Finally, figure 16 shows the total sensible heat flux $H_{tot}$ plotted against $T_{st}$. As the variations with environmental temperature in the sensible heat loss from the legs and from the head, associated with changes in skin blood flow, are comparatively small, the points in figure 16 lie close to a straight line; the slope is approximately $-10 \, W \, K^{-1}$.

To assess the effectiveness of shelter, or of any other modification of the thermal environment, it is necessary to evaluate all the components of heat loss from an animal in relation to the relevant climatological variables and the animal’s physiological responses to thermal strain. Applied in the field, the procedure is always much more complex than the corresponding analysis for animals in chambers where the thermal régime can be controlled and precisely monitored. It is essential to test this type of analysis by measuring metabolic rates and heat losses of animals in the field, but such measurements have rarely been made, because of obvious problems of management and instrumentation. The study described in this paper, in particular figures 15 and 16, points to the significance of the mean skin temperature of the trunk $T_{st}$, a quantity that can be measured with comparative ease on free-ranging animals, as an index of strain that is closely related to heat loss. In practice, it would be necessary to ‘calibrate’ the animal in a temperature-controlled chamber by measuring its rate of metabolic heat production and respiratory evaporation rate in relation to $T_{st}$, if necessary over a wider range of $T_{st}$ values than was considered here.

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