Thermal properties of the pelages of selected African ungulates

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In wild African ungulates the thickness of the pelage decreases with increasing body size. Thermal conductance decreases with increasing pelage depth, despite the fact that conductivity increases with increasing depth. Forced convection has a more pronounced effect upon the insulation of thin pelages than on thicker pelages, because in thin pelages the boundary layer is of greater importance. The colour differences between the ungulate species result in weighted mean absorptances for solar radiation which vary between 0,25 and 0,85. The thermal properties of the pelages of African ungulates play an important role in the physiological ecology of these animals.

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By wilde hoefdiere van Afrika verminder pelsdikte met toenemende liggaamsgrootte. Termiese geleiding verminder met toenemende pelsdikte, ten spyte daarvan dat geleidingsvermoë groter word met 'n toename in pelsdikte. Dwangkonveksie het 'n duideliker uitwerking op die insulasie van dun pelse as dikker pelse, omdat die grenslaag by dun pelse van groter belang is. Die kleurverskille tussen hoefdierspesies veroorsaak dat die beswaarde gemiddelde absorpsie vir sonstraling tussen 0,25 en 0,85 varieer. By Afrika-hoefdiere speel die termiese eienskappe van die pelse 'n belangrike rol in die fisiologiese ekologie van hierdie diere.

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The pelages of mammals provide a barrier between the animal and its environment, and the physical characteristics of the pelage can feature prominently in the thermal adaptations of animals to specific climatic zones. Scholander, Walters, Hock & Irving (1950), for example, have demonstrated the value of a thick pelage in arctic mammals while Schmidt-Nielsen (1959) has shown that a thick pelage can also be advantageous to an animal in a desert environment.

The most important thermal properties of the pelage are depth, density and colour. Scholander *et al.* (1950) established that insulation increases with increasing fur thickness. The insulative value of the fur does not depend on the hairs, as such, but on the still layer of air trapped therein and thereon. According to Monteith (1973) the air trapped in the fur is not perfectly still and free convection and radiation occur simultaneously with conduction.

The thermal insulation of a pelage is affected by forced convection and Lentz & Hart (1960) and Moote (1955) found that conductivity increased with an increasing windspeed. According to Cena & Monteith (1975a), thin furs are affected to a much greater extent by forced convection than thicker furs. It is, however, not only the total thickness of the fur which determines the insulative value, but also the density of the fur. Tregear (1965) concluded that the conductivity of fur with a density less than 1000 hairs cm^{-2} is greatly affected by forced convection.

The colour of a mammal's pelage is also involved in thermal adaptation to specific environmental conditions. Bonsma & Pretorius (1943) found that cattle with light-coloured coats were better adapted to hot conditions than similar animals with dark-coloured coats. Riemerschmid & Elder (1945) demonstrated that light-coloured cattle coats reflect more solar radiation than the darker ones. However, the reflectance of a coat does not give a true indication of the heat load at skin level because, as Hutchinson & Brown (1969) have shown, radiation penetrates more deeply into light than into darker coats. Nevertheless, they still found that white coats had a lower heat load at the surface of the skin than similarly insulated dark coats. The difference, however, decreased with increasing windspeed. Recently, Finch, Dmi'el, Boxman, Shkolnik & Taylor (1980) have demonstrated the thermal and metabolic advantages of a dark colour for Bedouin goats under winter conditions in the Negev. The metabolic rates of the black goats during winter were 25% lower than those of white goats, when standing in full sunlight. No difference was recorded when these animals were in the shade.

The purpose of this study was to determine the role of certain pelage characteristics in the adaptation of selected

African ungulates to their environments. Little or no work has been done on the physical properties of the pelages of indigenous African ungulates. The experiments were designed to measure characteristics such as thickness, conductance and reflectance. These variables were then related to body size and the ecological distribution of the species concerned. It is hoped that this knowledge might contribute to a better understanding of the animals' ecology and their thermal physiology.

Materials and Methods

Pelage thickness

The pelts of 16 different ungulate species were borrowed from museums and used in this experiment. A total of 131 pelts were studied of which only six (two springbok and four steenbok) were collected during the summer months. The summer pelts were not separated from the winter pelts because their thicknesses did not differ significantly from their winter equivalents ($p > 0,1$ in both cases). Certain pelts were cured while others were tanned as well. A preliminary study of the different pelages showed that measurements on the midflank region, halfway between the spinal column and the ventral midline, would give the best assessment of the mean pelage thickness of the animal. The pelage depth was measured in this region with vernier calipers and the mean was determined from five measurements. Unfortunately, no information was available on the live mass of the animals whose pelts were used in this study. Therefore an average body mass for each species was obtained from the ranges in the literature (Zaloumis & Cross 1975; Burton 1962; Shortridge 1934; Dorst & Dandelot 1970).

Insulation

Heat transfer through the pelage was determined by employing a guarded hot plate technique. The apparatus consisted of a small brass disc (diameter = 5,8 cm and height = 0,32 cm) which was fitted into a larger brass block (diameter = 9,2 cm and height = 6,0 cm). The disc and block could be heated independently. The heating of the brass block was controlled by a variac, while circuit sensors controlled the temperature of the block at 41,6°C. The disc was heated independently from a power pack and the energy input was measured by a Hewlett Packard multimeter. The heater element of the disc was isolated from the block by layers of felt and polyurethane foam. With the block at a steadily controlled temperature, the heat input into the disc could only be lost through the upper surface when the block and disc were at the same temperature. Copper-constantan thermocouples were inserted into the block and disc and the temperatures were read on a digital thermometer (Bat 8, Bailey Instruments) to 0,1°C. The direct current output from the digital thermometer was also connected to a multimeter and differences of 0,005°C were then detectable.

The brass block and disc were mounted in a polyurethane foam box with the upper surfaces of the block and disc *ca.* 0,5 cm higher than the surface of the polyurethane foam box (Figure 1). Tanned pelts which were pliable were selected and placed on top of the apparatus. A thin layer of petroleum jelly was placed between the undersurface of the pelt and the disc, to displace the air and ensure maximum contact between the two surfaces. The apparatus was kept in a temperature-controlled room at 10 ± 1°C.

A windtunnel (100 × 26 × 26 cm) with a circular opening in the lower surface was placed on top of the apparatus. The undersurface of the pelt was a few millimetres higher than the floor of the windtunnel and the opening in the windtunnel's floor was large enough to prevent its margins from disturbing the lie of the fur in the area of measurement. The assumption was made that air flow in the windtunnel was laminar and windspeed was measured with a vane anemometer (height = 8 cm) placed on top of the pelt. Measurements were taken at a windspeed of 0,1, 2, 3 and 4 m s^{-1}.

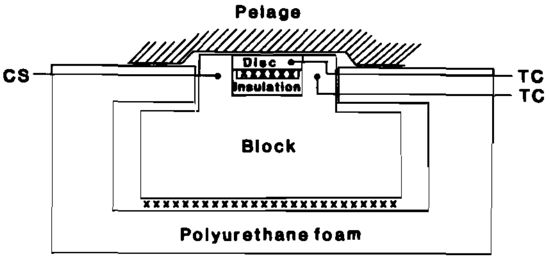

Figure 1 The guarded hot plate apparatus. TC = Thermocouple; CS = Circuit sensor; xxx Heater.

The skin temperature was determined with a copper-constantan thermocouple, inserted obliquely from the undersurface through the skin so that the tip was flush with the skin surface without disturbance of the fur. The fur surface temperature and temperature gradient in the boundary layer of air were measured with a series of thermocouples spaced 2 mm from one another and attached to a vertical rod which was attached to the roof of the windtunnel. The rod could be moved up and down and the displacement could be measured accurately to the nearest millimetre on a vernier scale.

All measurements were made on the midflank region of the pelts of eight different species. The thickness of each pelage was averaged from several measurements with vernier calipers on the specific area which covered the disc. The pelts were positioned so that the wind blew along the lie of the fur.

When a specific pelt was studied the procedure was as follows. The pelt was mounted on the apparatus and the energy input into the disc was altered until the temperature difference between the block and disc was less than 0,01°C, which was regarded as the equilibrium point. The skin, surface and boundary layer temperatures were then measured as well as the energy input into the brass disc. This procedure was repeated at a windspeed of 1, 2, 3 and 4 m s^{-1}. The whole procedure was repeated at least three times so that an average heat loss could be determined at each windspeed. The pelts of three klipspringers and Namaqua-Afrikaner sheep were only measured in still air.

The following equations were used in the calculations:

$$k = \frac{Q\,d}{A\,(T_{sk} - T_s)} \tag{1}$$

$$C_f = \frac{Q}{A\,(T_{sk} - T_s)} \tag{2}$$

$$C_{f+a} = \frac{Q}{A\,(T_{sk} - T_a)} \tag{3}$$

$$I = \frac{1}{C} \tag{4}$$

where

k is conductivity of the fur (W m^{-1} K^{-1})
Q is energy input into the disc (W)
d is the thickness of the fur (m)
A is the surface area of the disc (m^2)
T_{sk} is the skin temperature (K)

T_s is the fur surface temperature (K)
C_f is the conductance of the fur (W m^{-2} K^{-1})
C_{f+a} is the conductance of fur and boundary layer of air (W m^{-2} K^{-1})
T_a is the air temperature (K)
I is the insulation (K m^2 W^{-1}).

Reflectance

A double pyranometer, calibrated under solar radiation and certified by the C.S.I.R.O. of Australia was used to measure the reflectance of the various pelts. The outer glass dome measured 4 cm in diameter and the black sensitive surface, 2 cm. When the pyranometer was unrestricted and held 5 cm above the horizontal pelt, the angle of acceptance of radiation was 180° and 100% radiation can only be received from an infinitely flat surface. A pelt with a diameter of 100 cm would therefore give an angle of acceptance of *ca.* 170°. According to Hutchinson, Allen & Spence (1975) the radiation received from a pelt, as a percentage (%) of that received from a limitless flat surface, can be calculated by the following equation:

$$\% = 100 \sin^2\gamma \qquad (5)$$

where 2γ is the angle of acceptance.

Thus 99% of the radiation registered, would be received from the pelt when the latter has a diameter of 100 cm. In this experiment an unrestricted pyranometer was used for pelts with a length and width greater than 100 cm.

Most of the pelts, however, measured between 25 and 100 cm in width and a restricted pyranometer was needed. A strip of thick black tape (height = 4,5 mm) was fixed to the base of the glass dome. The angle of acceptance was then reduced to *ca.* 120° and 100% of the radiation received was from the pelt, when the latter had a diameter greater than 25 cm. In certain instances, the reflectance of specific areas on the pelts which measured less than 25 cm in diameter was measured. For these measurements, the pyranometer was restricted to an angle of acceptance of *ca.* 12° and when the pyranometer was held 5 cm above the pelt, all the radiation received came from an area with a diameter of 3 cm.

Reflectance measurements were taken at different angles of solar incidence. The pelts were mounted on a platform which could be adjusted from a horizontal to a vertical position when θ was changed (Figure 2). The solar elevation (α) during each measurement was calculated using standard equations. Thus the size of θ could be calculated for each specific angle of incidence (β) required, when the incident solar elevation was known. The pelts were always orientated in such a way that the azimuth angle was zero and that the direct rays were parallel with the lie of the hair.

In all the measurements the pyranometer was held 5 cm above the pelt surface with the receiving surface parallel to the pelt's surface. Four thin steel legs of equal length were attached to the pyranometer to ensure that the distance from the pelt was always kept constant. A board coated with Vadec white matt paint was used as the standard. The paint was tested in the manufacturer's laboratories and was found to have a reflectance of 0,9 in the visible range. This standard was used to correct for the effect of the steel legs and the pyranometer's shadow on the reflected radiation received by the pyranometer.

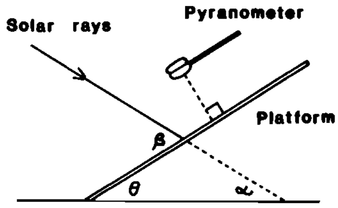

Figure 2 Adjustable platform used for reflectance measurements. Solar elevation is α and angle of incidence is β.

The following procedure was used during each measurement. The platform was fixed at the required angle and then the total solar radiation incident on the platform was measured with the unrestricted pyranometer. A small black shield was used to obscure the direct rays in order to measure diffuse radiation from the sky. Next the total radiation reflected from the standard and pelt respectively were measured at that specific angle of incidence. Riemerschmid & Elder's (1945) suggestions were followed and the diffuse component of the total reflected radiation was measured only at 30°, 15° and 5° angles of incidence. The mean reflectance for diffuse radiation was then used to calculate the diffuse component of the total reflected radiation at higher angles of incidence. The reflectance of the pelt for total, diffuse and direct radiation was then calculated in the following way:

$$r_p = r_s \left(\frac{Z_p}{Z_s}\right) \qquad (6)$$

where
r_p is reflectance of the pelt
r_s is reflectance of the standard (0,9)
Z_p is radiation reflected from the pelt and
Z_s is radiation reflected from the standard.

In both springbok and bontebok, four different pelts were used and mean reflectance was determined for every angle of incidence.

When an animal as a whole is considered, direct radiation falls onto the pelt at different angles of incidence at any one time. A weighted mean absorptance for direct radiation was therefore obtained by the method of Riemerschmid & Elder (1945).

Reflectance and pelage thickness both contribute towards the final heat load at the skin surface. This effect was investigated in the following way. Several pelts of different colours and various thicknesses were selected. Copper-constantan thermocouples connected to a Bailey Bat digital thermometer, were inserted obliquely from the undersurface through the skin to determine skin surface temperature. A Barnes infrared thermometer was used to measure the fur surface temperatures. The pelts were mounted on polyurethane foam sheets and placed outdoors in the sun. When skin and surface temperatures were measured, ambient temperature, windspeed and solar radiation intensity were determined simultaneously. Windspeed was measured with a hot-wire anemometer and with a three-cup anemometer while solar radiation was measured with a Kipp and Zonen solarimeter.

Species names

Table 1 provides a list of the scientific and common names of all the species used. Determinations made on each species are also indicated.

Results and Discussion

Pelage thickness

The pelage depth ranged from 1 – 28,2 mm and decreased with increasing body mass, which ranged from 12,5 – 727 kg (Figure 3). A power curve describing the association between average body mass and mean depth for each species was

Table 1 The scientific and common names of all the species studied, to measure the depth (*d*), reflectance (*r*) and insulation (*I*) of their pelages

Scientific name	Common name	Measurements
Raphicerus melanotis	Grysbok	*d r I*
Oreotragus oreotragus	Klipspringer	*d I*
Raphicerus campestris	Steenbok	*d r I*
Pelea capreolus	Vaal ribbok	*d*
Antidorcas marsupialis	Springbok	*d r I*
Ovis aries	Namaqua-Afrikaner sheep	*r I*
Aepyceros melampus	Impala	*d*
Alcelaphus buselaphus	Hartebeest	*r*
Damaliscus dorcas phillipsi	Blesbok	*d r*
Damaliscus dorcas dorcas	Bontebok	*d r I*
Connochaetes gnou	Black wildebeest	*d r*
Damaliscus lunatus	Tsessebe	*d*
Oryx gazella	Gemsbok	*d r*
Hippotragus niger	Sable antelope	*d*
Connochaetes taurinus	Blue wildebeest	*d r*
Equus burchelli	Zebra	*d r*
Tragelaphus strepsiceros	Kudu	*d I*
Taurotragus oryx	Eland	*d r I*

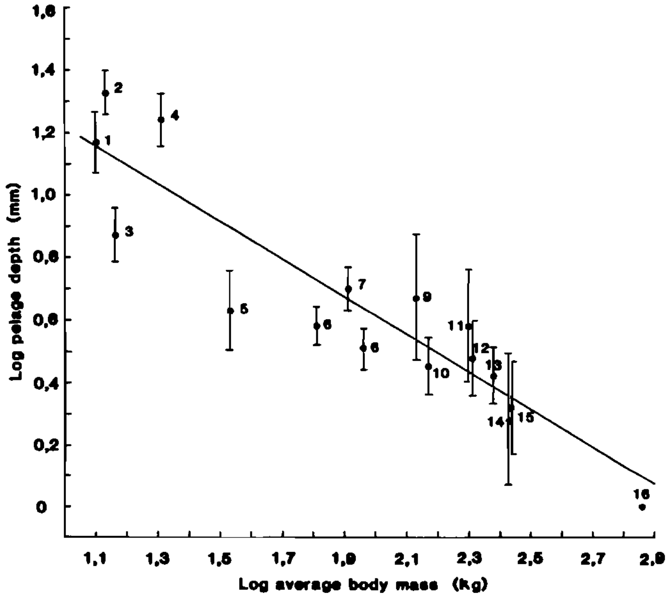

Figure 3 The relationship between pelage depth and average body mass in selected African ungulates. 1 = Grysbok (n = 2); 2 = Klipspringer (n = 15); 3 = Steenbok (n = 23); 4 = Vaal ribbok (n = 8); 5 = Springbok (n = 17); 6 = Impala (n = 10); 7 = Blesbok (n = 4); 8 = Bontebok (n = 5); 9 = Black wildebeest (n = 3); 10 = Tsessebe (n = 4); 11 = Gemsbok (n = 5); 12 = Sable antelope (n = 5); 13 = Blue wildebeest (n = 10); 14 = Zebra (n = 6); 15 = Kudu (n = 12); 16 = Eland (n = 2). See Table 1 for scientific names.

calculated and the following regression equation was obtained:

$$d = 65\ W^{-0,6} \qquad (7)$$

where d = depth in mm, and W = body mass in kg.

Eighty-three per cent of the total variation in depth can be accounted for by the fitted regression ($r^2 = 0,83$) and a Student's t test established that the regression is highly significant ($p < 0,001$). The regression equation was $d = 48\ W^{-0,55}$ and $r^2 = 0,69$ when the individual depth values were used with the average mass of each species in the calculations. Once again a Student's t test established that the regression is highly significant ($p < 0,001$).

In contrast to these results, Scholander *et al.* (1950) found that pelage depth in arctic mammals increased with increasing animal size. However, a near maximum value for insulation was already reached at a body mass of *ca.* 5 kg and no further significant increase in thickness occurred. This apparent contradiction between the results of Scholander *et al.* and the present study can be explained by the marked difference between the arctic environment and that of the African savanna as well as the relationship between body mass and the surface area. The ratio of surface area to volume decreases with an increasing body mass. Small animals would thus experience a high rate of heat gain or loss and the low thermal inertia which goes with the small volume would cause a rapid increase or decrease in body temperature. Small animals therefore need to be well insulated and a thick pelage affords protection not only against heat loss but also against heat gain from the environment. There is, however, a physical limit to the thickness of the pelage for a certain animal size and Scholander *et al.* found that within the smaller range, pelage depth increased with increasing body size. The results of Scholander *et al.* show that a maximum insulative value was reached in a relatively small animal (5 kg) and the larger animals with their relatively smaller body surface areas had no need for a thicker pelage. In warm climates a thick pelage in larger mammals would afford protection against heat gain but would also reduce heat loss. The depth of an ungulate's pelage is therefore a reflection of an evolutionary compromise and the present results show that, under the predominantly hot conditions of the African savanna, natural selection seems to have favoured the facilitation of heat loss rather than the prevention of heat gain or reduction of heat loss. This argument is supported by the sharp decline in pelage depth which occurs with increasing body mass.

It is also of interest that a positive relationship between body size and cutaneous evaporative water loss has been established by Robertshaw & Taylor (1969). They found that smaller bovids rely to a greater extent on respiratory evaporation while cutaneous evaporation becomes more important with increasing body size. Whether this phenomenon is related to pelage depth is not yet clear. Cena & Monteith (1975b) found that in sheep the resistance against water vapour diffusion increased with increasing wool thickness. Furthermore, Hutchinson, Brown & Allen (1976) postulated that sweating would wet a thicker fur more readily and thus evaporation would be thermally less effective. The warm-climate animals are also subjected to cold spells and again a thicker pelage would be of greater importance to the smaller animal.

The pelage thickness of the klipspringer, vaal ribbok, steenbok and springbok deviate considerably from the calculated power curve. The klipspringer and vaal ribbok both occupy montane areas and are frequently exposed to fluctuating environmental conditions. The thicker than expected pelage would be of considerable value to these animals during cold, windy conditions which are often experienced in their habitat. However, the klipspringer's thick pelage is also considered as a protective device against bruising in the rocky environment in which it lives. Nevertheless, Norton (1980) has reasoned that the pelage cannot render effective protection against bruising because the hairs fall out too readily. He also felt that the thick pelage more probably plays a role in the thermoregulation of the animal.

The steenbok and springbok have a particularly thin pelage compared with other animals in their size class. Both animals occur in hot arid areas and this may explain the unusually thin pelage. In the case of the springbok the thin pelage would also facilitate the dissipation of the large amount of metabolic heat which is generated while sprinting across a hot, arid plain. Springbok are generally recognized as being among the swiftest of the African antelope.

Insulation

Before the total insulative properties of the animals' coats are evaluated the thermal conductivity values obtained for the various animal coats will be discussed. In this investigation the conductivities for the furs ranged from 22,4 – 74,5 mW m^{-1} K^{-1} in still air. These values correspond well with values found in the literature. For example, Scholander *et al.* (1950) reported that the coat conductivities of arctic animals ranged from 35,0 – 95,0 mW m^{-1} K^{-1} and perusal of his data shows that the range extended much lower for tropical animals. Furthermore, Hammel (1955) found that the conductivities of the inner fur fell between 34,8 – 51,0 mW m^{-1} K^{-1}, while Tregear (1965) reported a range of 29,3 – 75,3 mW m^{-1} K^{-1}. The present results (Figure 4) show that thermal conductivity increased with increasing pelage depth. In other words, the rate of heat transfer was faster in the thicker coats. The same trend was reported by Birkebak (1966) who recalculated the data of Scholander *et al.* (1950), Hammel (1955) and Hart (1956) in terms of thermal conductivity and expressed them as a function of fur thickness. Birkebak's examination yielded the same unexpected trend as found here, namely that the conductivity values of the thin furs tend to be lower than that of still air (25,7 mW m^{-1} K^{-1} at 20°C). He explained it on the basis of very small air spaces trapped within the fur which resulted in high resistance against heat transfer. Thickness measurements of thin furs, however, are very difficult to make and small errors can lead to highly erroneous conductivity values. For example, the conductivity value of the eland's pelage will increase by 50% if a pelage depth of 1,5 mm instead of 1,0 mm was used in the calculations. Similar calculations for the thicker pelage of a klipspringer show an increase of only 2% in the conductivity value. Therefore, despite the similarity between Birkebak's and the present results, the low conductivity values obtained for the eland (22,4 mW m^{-1} K^{-1} in still air) and kudu (29,4 mW m^{-1} K^{-1} in still air) are probably erroneous and need further investigation.

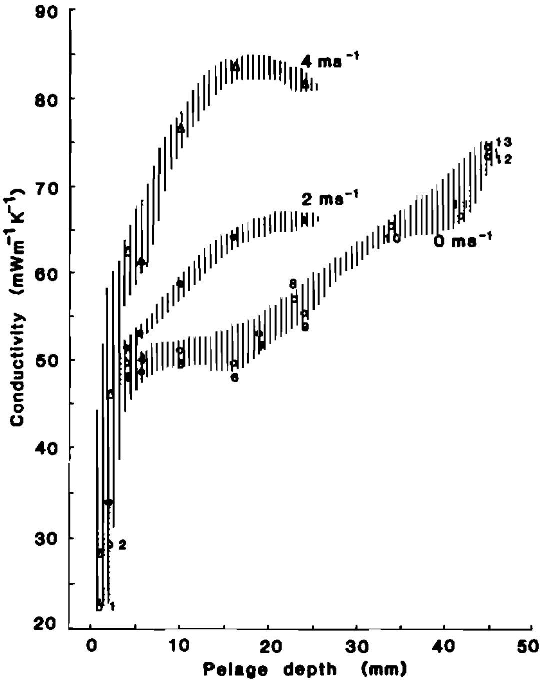

Figure 4 The effect of windspeed upon the relationship between conductivity and pelage depth. 1 = Eland; 2 = Kudu; 3 = Bontebok; 4 = Springbok; 5 = Steenbok; 6 = Grysbok; 7, 8, 9, 10 = Klipspringer; 11, 12, 13 = Sheep. See Table 1 for scientific names.

The relationship between thermal conductivity and pelt thickness is illustrated in Figure 4. All the pelts, except for the eland's, had conductivity values higher than that of still air. Cena & Monteith (1975a) found that the high thermal conductivities of animal furs can be ascribed to (i) air conduction, (ii) radiative transfer, and (iii) free convection. The positive relationship between conductivity and pelage thickness, therefore, suggests that radiant transfer and free convection become of increasing importance with increasing pelage thickness. Nevertheless, various other physical pelage characteristics such as hair diameter, hair density, etc. could also influence the thermal conductivity. Cena & Monteith (1975c) for instance, found that the interception function (*p*) for long-wave radiation depended on (i) the mean diameter of the hairs, (ii) the density of the hair, and (iii) the angle between the hairs and the normal to the skin surface. In all likelihood the relationship may not be between conductivity and pelt thickness as such, but rather between conductivity and the angle between the hairs and the normal to the skin surface. If diameter and density of the hairs remain constant, an increase in thickness would coincide with a reduction of this angle and this would result in a lower interception function. The lower intercept function again would lead to a higher radiative heat transmittance. This would also explain the observation by Hammel (1955) that the conductivity of erected fur was higher than that of the flattened fur. Hammel put this difference down to increased free convection and it is quite possible that both free convection and radiative transfer would increase when the angle between the hairs and the normal to the skin surface decreases.

Figure 5 shows three linear relationships between thermal insulation and pelage depth for conductivity values of 25,0; 50,0 and 75,0 mW m^{-1} K^{-1} respectively. The data points on this graph are the measured insulation values of the individual pelages and it is clear that insulation increases with increasing pelage depth. The relationship between thermal insulation and pelage depth was not strictly linear because the conductivity value increased with increasing depth. The logarithmic values, however, gave a coefficient of determination (r^2) of 0,98 and the correlation between pelage depth and insulation can be shown by a power curve.

The total resistance of a pelage to heat transfer includes the resistance of the air trapped within the fur and the resistance of the boundary layer of still air above the fur surface. The effect of windspeed on pelage insulation was only determined on seven individual pelts belonging to seven different species. The pelage thickness of the pelts varied between 1 and 24 mm. Figure 5 shows that the best association between insulation and pelage thickness could be illustrated by a power curve. However, when the thicker pelages (> 24 mm) were excluded, as in this instance, a linear correlation gave a better coefficient of determination than a power curve. Figure 6 shows that the importance of the boundary layer decreased with increasing pelage depth and windspeed.

Table 2 summarizes the measured and calculated contributions of the boundary layer to the total insulation at windspeeds of 0 and 2 m s^{-1}. The calculated contributions were determined from the regression equations. It is clear that at

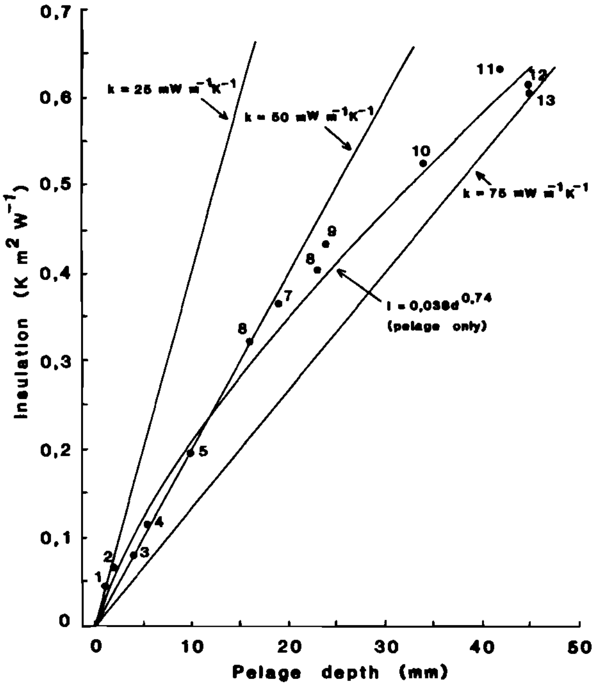

Figure 5 The effect of thermal conductivity (*k*) upon the relationship between thermal insulation (*I*) and pelage depth (*d*). •Insulation values of individual pelages in still air. 1 = Eland; 2 = Kudu; 3 = Bontebok; 4 = Springbok; 5 = Steenbok; 6 = Grysbok; 7, 8, 9, 10 = Klipspringer; 11, 12, 13 = Sheep. See Table 1 for scientific names.

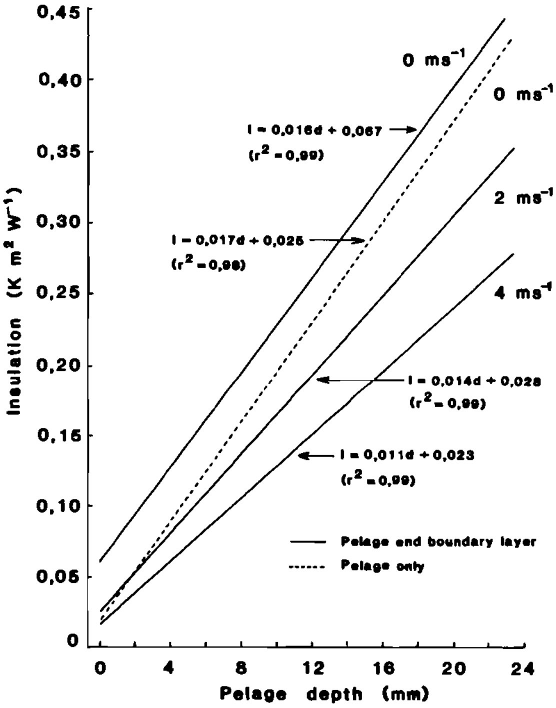

Figure 6 The effect of windspeed upon the relationship between thermal insulation (*I*) and pelage depth (*d*).

Table 2 The contribution of the boundary layer towards the total thermal insulation of various pelts at windspeeds of 0 and 2 m s^{-1}

Species	Pelage depth (mm)	Measured contribution		Calculated contribution	
		0 m s^{-1} (%)	2 m s^{-1} (%)	0 m s^{-1} (%)	2 m s^{-1} (%)
Eland	1,0	43	4	49	9
Kudu	2,0	35	1	40	7
Bontebok	4,0	35	10	29	4
Springbok	5,5	25	7	23	3
Steenbok	10,0	19	0	14	1
Grysbok	16,0	4	0	8	0
Klipspringer	24,0	5	0	4	0

Table 3 Regression equations (pelage only) which show the relationship between thermal insulation (*I*) and pelage thickness (*d*) at different windspeeds

Windspeed (m s^{-1})		r^2
0	$I = 0{,}017\ d + 0{,}025$	0,99
1	$I = 0{,}016\ d + 0{,}032$	0,99
2	$I = 0{,}014\ d + 0{,}028$	0,99
3	$I = 0{,}012\ d + 0{,}025$	0,99
4	$I = 0{,}011\ d + 0{,}023$	0,99

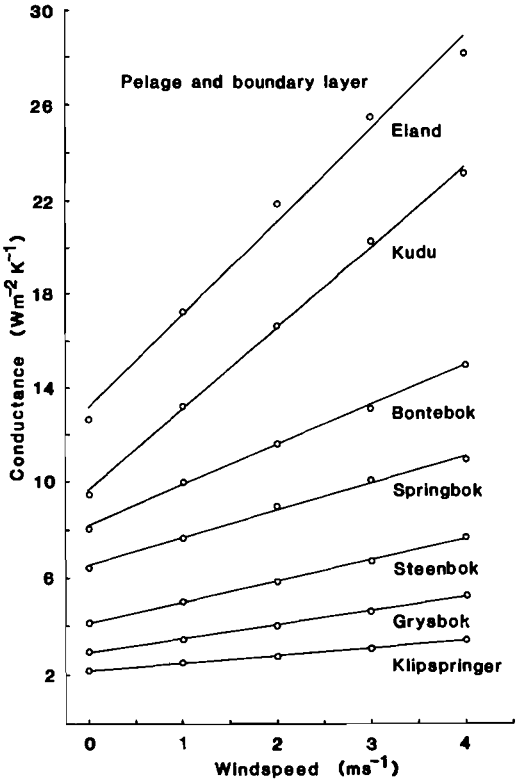

Figure 7 The relationship between thermal conductance (*C*) and windspeed (*s*). Eland: $C = 3{,}92\,s + 13{,}22$ ($r^2 = 0{,}99$); Kudu: $C = 3{,}42\,s + 9{,}68$ ($r^2 = 0{,}99$); Bontebok: $C = 1{,}68\,s + 8{,}21$ ($r^2 = 0{,}99$); Springbok: $C = 1{,}13\,s + 6{,}57$ ($r^2 = 0{,}99$); Steenbok: $C = 0{,}88\,s + 4{,}12$ ($r^2 = 0{,}99$); Grysbok: $C = 0{,}57\,s + 2{,}93$ ($r^2 = 0{,}99$); Klipspringer: $C = 0{,}30\,s + 2{,}18$ ($r^2 = 0{,}99$).

a windspeed of only 2 m s^{-1}, the contribution from the boundary layer was reduced to a small fraction. Forced convection did not only disturb the boundary layer but reduced the thermal insulation of the fur as well. This can be seen from the slopes of the regression lines which decreased with increasing windspeed (Table 3).

The effect of forced convection on the individual pelts is illustrated in Figure 7. Conductance rather than insulation units were used, because the former increased linearly with increasing windspeed as shown by Campbell, McArthur & Monteith (1980). Tregear (1965) found that the relationship between conductance and windspeed was less than linear and that increasing the windspeed from 0 to 3,58 m s^{-1} (0 to 8 mph) had a greater effect than an increase from 3,58 to 8,05 m s^{-1} (8 – 18 mph). His figures, however, indicated that the relationship between conductance and windspeed was more or less linear for windspeeds between 0 and 4 m s^{-1}. The present data also show that the effect of forced convection was more pronounced on the thinner pelages. For example, at 0 m s^{-1} the conductance of the eland's pelage was 6,07 times greater than that of the klipspringer. This difference increased to 8,55 times at a windspeed of 4 m s^{-1}. This phenomenon is also apparent from Tregear's results.

The thickness of the boundary layer at 0 m s^{-1} varied from 10 mm for the klipspringer to 22 mm for the eland. The reduction in the thickness of the boundary layer with increasing windspeed for three examples is illustrated in Figure 8. The thermal gradient within the fur was not measured but one can assume that the wind actually penetrated the fur itself. This assumption is supported by the reduction in skin temperature at increased windspeeds. It is also clear that forced convection resulted in a greater reduction in skin temperature in the thin pelages, such as in the eland (1 mm), kudu (2 mm) and bontebok (4 mm).

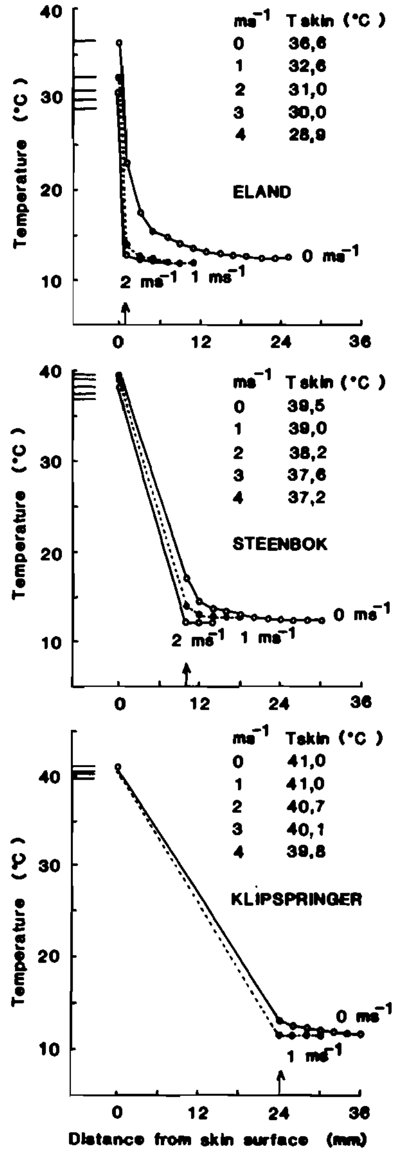

Figure 8 The effect of windspeed upon the temperature gradient across the pelage and boundary layer. ↑ Indicates fur surface.

Tregear (1965) found that a moderate windspeed could destroy the boundary layer of still air and that the level of wind penetration within the fur was dependent on the windspeed and the hair density. His results indicated that a windspeed of 8,05 m s^{-1} (18mph) penetrated a rabbit's pelage only slightly, the fur being about 8 mm thick and having a density of 4100 ± 260 hairs cm^{-2}. Cena & Monteith (1975a), however, found that a windspeed greater than 3 m s^{-1} penetrated the fur of a rabbit's pelage, which was 18 mm thick. They questioned Tregear's results and suggested that the method of exposing the coat might have led to a situation where the wind velocity at the coat surface was much less than the free stream velocity. The present results show that although forced convection had a greater effect on thin pelts, even the thicker pelts, like that of the klipspringer and grysbok, were affected by a windspeed greater than *ca.* 2 m s^{-1}. They are therefore in agreement with the results of Cena & Monteith (1975a).

Reflectance

Figure 9 shows the reflectance of the pelts for direct solar radiation at various angles of incidence. In the case of the springbok and bontebok, the reflectance indicates the mean obtained from four different pelts, while individual pelts were used for all the other species. In all the pelts studied, reflectance values increased with a decreasing angle of incidence. Riemerschmid & Elder (1945) came to the same conclusion when studying cattle coats. Hutchinson *et al.* (1976) argued that the increasing reflectance found by Riemerschmid & Elder could be ascribed to an increase in gloss, which would result in an increase in specular as opposed to diffuse reflection. In the present study this trend was more pronounced in certain pelts. For example, the reflectance value of the following pelts increased by more than 0,35 units when the angle of incidence decreased from 90° to 5°: black wildebeest, eland, gemsbok, black stripes of zebra and brown lateral line of springbok. In contrast, the grysbok, for example, showed an increase in reflectance of only 0,15 units with a decreasing angle of incidence. It is possible that this difference between the coats is the result of differences in gloss. On the other hand, other optical properties may be involved and the drying and tanning processes might have influenced the gloss characteristics. Further speculation at this stage is therefore not warranted.

The weighted mean absorptance of the coats for direct solar radiation varied from 0,25 to 0,85 and are shown in Table 4. These results clearly illustrate the effect of coat colour on the absorptance of solar radiation. The darker coats, as expected, had the highest absorptance values, while the white coats had the lowest values. The absorptance values obtained in this experiment for the eland (0,71) and hartebeest (0,66) compare favourably with values in the literature. Finch (1972) reported values of 0,75 and 0,64 respectively for the eland and hartebeest.

Surprisingly, the weighted mean absorptance for the four different white-coloured coats differed considerably. For example, the white areas on the springbok's pelt (belly and pronk) gave the lowest absorptance values (0,28 and 0,25 respectively). The shorn sheep had a dull, slightly yellowish-white colour and irregular surface which could explain the higher absorptance of 0,33. The white zebra stripes (0,49) had the highest absorptance, which can possibly be explained by the high absorptance of the black skin beneath the very short

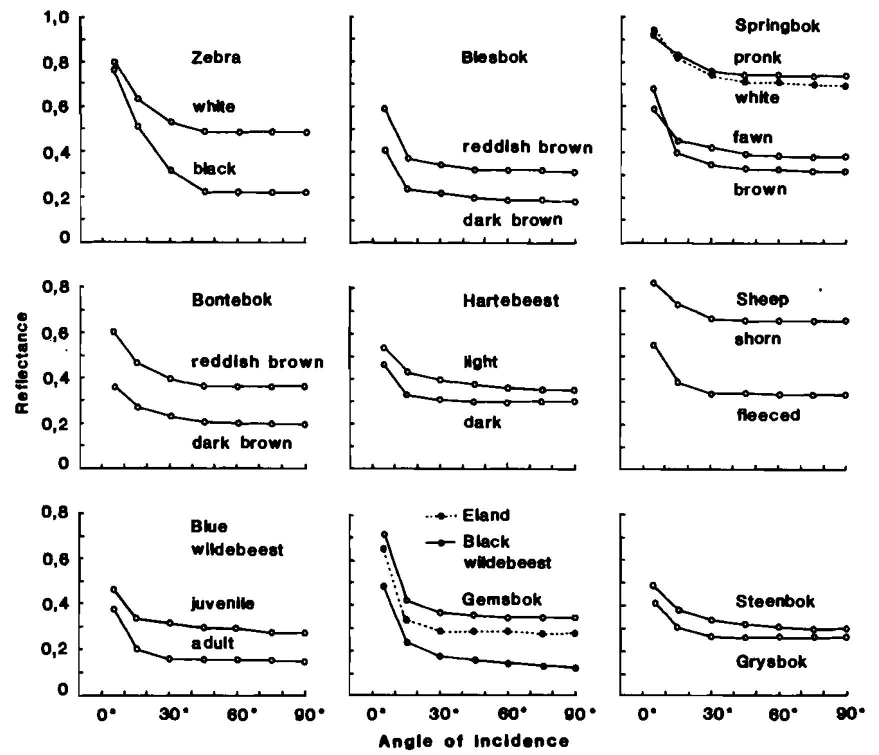

Figure 9 The effect of the angle of incidence of the sun's rays upon the reflectance of various pelages.

Table 4 The weighted mean absorptance of selected African ungulate pelts for direct solar radiation

Species	Colour	Weighted mean absorptance
Steenbok	sandy brown	0,68
Grysbok	dark red-brown with white hairs	0,73
Gemsbok	pale grey	0,63
Eland	dark fawn	0,71
Hartebeest	reddish fawn	0,66
Black wildebeest	black	0,85
Blue wildebeest adult	grey-brown	0,84
Blue wildebeest juvenile	blue-grey	0,70
Zebra black stripes	black	0,74
Zebra white stripes	white	0,49
Namaqua-Afrikaner sheep fleeced	dirty yellowish white	0,66
Namaqua-Afrikaner sheep shorn	clean yellowish white	0,33
Springbok back	fawn	0,60
Springbok lateral line	chocolate brown	0,66
Springbok belly	white	0,28
Springbok pronk	white	0,25
Bontebok back	reddish brown	0,62
Bontebok rump and sides	dark brown	0,79
Bontebok belly	white	0,28
Blesbok back	reddish brown	0,67
Blesbok rump and sides	dark brown	0,80

hair.

The juvenile blue wildebeest had a much lower absorptance value than the adult. The juvenile also had a thicker pelage than the adult. This might be a result of the relatively large surface area of the juveniles. The lighter, thicker pelage would provide better protection against the heat load from the environment and thus counteract the relatively larger surface area. On the other hand, the lighter colour would be more cryptic on the African savanna and provide greater protection to the juveniles, as they are particularly prone to predation. The dark colour of the adults could be an advantage for sunbasking on cold sunny days. The latter would reduce metabolic demands for thermoregulation, as in the Bedouin goat, during the most critical season of the year.

A knowledge of the physical properties of an animal's pelage allows one to speculate on their possible importance in influencing the distribution and ecological physiology of a particular species. The blue wildebeest, eland, steenbok, hartebeest, gemsbok, zebra and springbok are all animals which occur in very hot and sometimes very arid areas. The eland is the largest of these and would experience a very high heat load from the environment with its thin pelage and an absorptance of 0,71. However, the large size has certain functional advantages in the sense that it provides the animal with a high thermal inertia. Moreover, it is well known that the eland exhibits large fluctuations in body temperature and it has been reported that these animals also seek shade during the periods of intense solar radiation. Consequently, the eland's pelage contributes very little to alleviate the heat load from the environment but would facilitate heat loss at night when temperatures fall. The zebra is also a large semi-arid species with a thin pelage. The zebra, however, has a striped colour pattern which may be involved in its adaptation to the hot environment. Baldwin (1971), for example speculated that the striped pattern facilitates thermoregulation by the differential absorption of solar radiation. According to him, this effect is combined with changes in the circulatory pattern beneath the differently coloured stripes. This, however, has not been proved experimentally and the striped pattern remains an enigma. A more acceptable explanation is that the striped pattern is involved in crypsis or that the ratio of black to white when viewed laterally is 3:1 and changes to 1:3 when viewed from behind the animal (Joubert & Louw 1976). The latter difference would allow the animal to alter the solar load appreciably by altering the orientation of the long axis of the body to the incoming radiation, depending on the prevailing environmental conditions.

The blue wildebeest appears to be at a serious disadvantage. The thin pelage would not provide significant protection against solar heat gain and, furthermore, the animal has a very high absorptance (0,84) for solar radiation. This species pants instead of sweats (Taylor 1970) and would therefore probably maintain a very high skin surface temperature under hot conditions. The pelage thus does not contribute towards a reduction in heat load and this animal can only survive in hot environments when water is freely available. During cool sunny conditions, however, which are typical of the African savanna during winter, the dark thin pelage would facilitate heat gain, thereby reducing the energy requirements for maintaining body temperature. In fact, Berry (1980) has clearly shown that these animals orientate laterally towards the sun to exploit solar radiation under cool sunny conditions.

The gemsbok and hartebeest both have pelts with a fairly low absorptance which would reduce the environmental heat load. The hartebeest also has a reasonably thick pelage for its size. The gemsbok is known to penetrate deep into desert environments and to be able to survive for long periods without drinking water. Taylor (1968 and 1970) has reported that the gemsbok exhibits wide fluctuations in its body temperature (adaptive hyperthermia) and as a result, conserves water very efficiently. He compared the gemsbok and blue wildebeest and concluded that the superior water-conserving ability of the gemsbok is largely due to the ability of the former species to store large amounts of heat. My results suggest that the superior reflectance value of the gemsbok's pelage would also contribute towards the animal's ability to live under desert conditions.

Finally, the springbok and steenbok also live in a hot environment and it has frequently been reported that both species are able to survive under arid conditions without drinking water. The steenbok is a small antelope with a thinner than expected pelage thickness (based on body size). However, this animal is able to seek out a favourable microhabitat because of its small size. In contrast, the springbok frequently occurs on hot arid plains where little or no shade exists. The low absorptance value obtained for the springbok pelage undoubtedly reduces heat gain under these conditions. Furthermore, unpublished results of Hofmeyr, M.D. & Louw, G.N. (1985) show that springbok orientate with their long body axes parallel to the solar rays during hot summer days to reduce environmental heat load. The thin pelage represents a thermal disadvantage, but is probably of great importance when sprinting away from predators. Hofmeyr, M.D. & Louw, G.N. (1985) concluded that springbok do not rely on hyperthermia or thermolability and that their adaptation to hot arid environments resides in their thermal behaviour and specific pelage qualities.

As described previously, Hutchinson & Brown (1969) and Cena & Monteith (1975c) maintain that short-wave radiation is not absorbed on the surface but penetrates the fur to various degrees. Penetration is greater in lighter and sparser coats and this effect must also be taken into consideration. Thus, coat colour, thickness and density must all be considered together when the value of the coat is evaluated as a protection against heat gain. It would seem then that a thick, light-coloured coat would afford greater protection than a thin, dark-coloured coat.

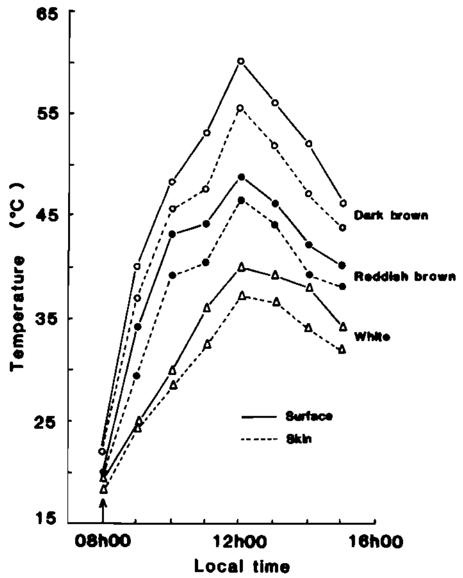

Figure 10 The heating effect of the sun upon the surface and skin of three differently coloured areas on the bontebok's pelt when windspeed was low. Dark brown: a = 0,79; d = 2,5 mm; reddish brown: a = 0,62; d = 2,8 mm; white: a = 0,28; d = 2,0 mm where a = absorptance and d = depth.

Figure 10 illustrates skin and surface temperatures, measured on three different areas of a bontebok's pelt. From 09h00 to 15h00 the windspeed never exceeded 2 m s^{-1} and the absorptance for solar radiation was the most important factor influencing surface temperature. Consequently, the dark brown surface had a much higher temperature than the white surface. Furthermore, the skin temperatures indicate that the high absorptance of the dark brown fur resulted in a much higher heat load at skin level than in the case of the white fur. On this particular day the skin underneath the reddish brown fur exhibited a heat load between that of the white and dark brown fur. In contrast, Figure 11 shows that the heat load on the skin covered by the white and reddish brown fur became approximately equal, when windspeed increased. During these measurements, windspeed fluctuated between 2 – 4 m s^{-1}. The penetrance of radiation was probably greater into the sparse, white fur than into the denser reddish-brown fur, although in the present investigation no actual measurements of density were made. Nevertheless, at low windspeeds, the lower absorptance of the white fur outweighed the difference in penetrance. At higher windspeeds, however, the heat load on the coloured furs was greatly reduced and the difference in absorptance became less important. Thus, reddish brown and white furs had approximately the same heat load at skin level. The same general phenomenon was reported by Hutchinson & Brown (1969). Finally, Figure 12 illustrates how both coat colour and thickness can influence the heat load at skin surface. The springbok and hartebeest had approximately the same heat load at the skin surface because the springbok had the advantage of a lower absorptance while the hartebeest had the advantage of a thicker pelage. The black wildebeest had the highest heat load with its high absorptance value, despite the fact that the fur in this particular animal was thicker than in the springbok and hartebeest. During these measurements, windspeed never exceeded 1 m s^{-1}.

Conclusions

(i) In warm-climate ungulates, pelage thickness decreased with increasing body weight. Thus it would seem that natural selection has favoured heat loss rather than

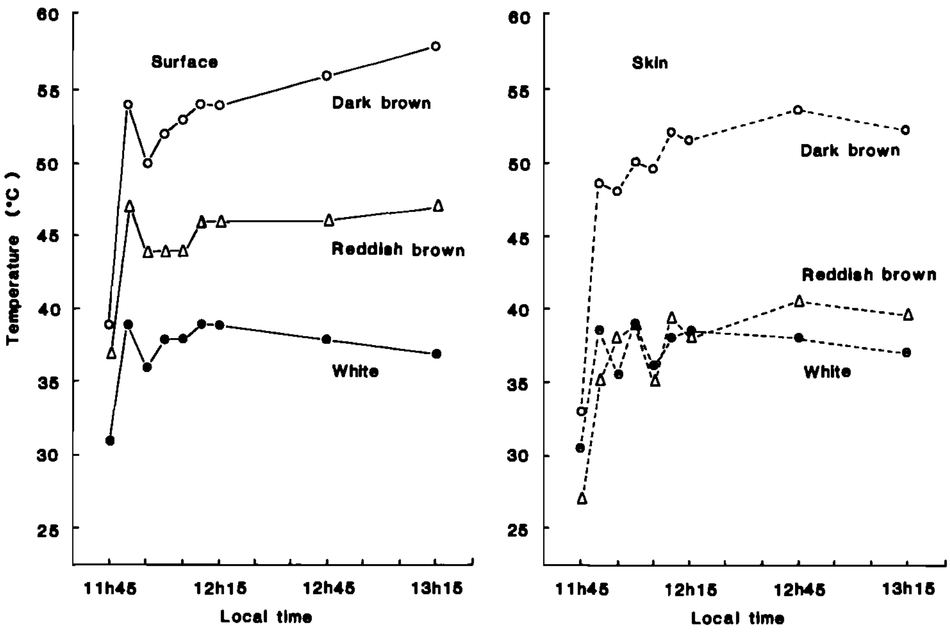

Figure 11 The heating effect of the sun upon the surface and skin of three differently coloured areas on the bontebok's pelt when windspeed was high.

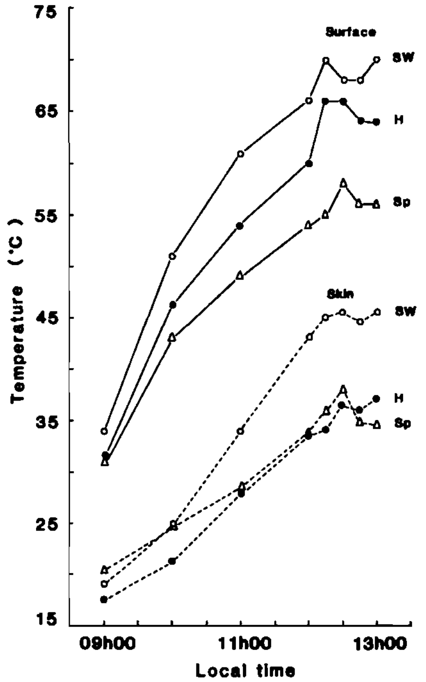

Figure 12 The effect of solar radiation on the surface and skin temperatures of three different pelts. SW = Black wildebeest: a = 0,85; d = 8 mm, H = Hartebeest: a = 0,66; d = 7 mm, Sp = Springbok: a = 0,60; d = 5 mm, where a = absorptance and d = depth.

protection against heat gain. This is contrary to the results of Scholander *et al.* (1950) on arctic mammals, where heat retention has been favoured and larger mammals also developed a thick pelage.

(ii) Thermal conductivities of pelts with a thickness between 1 and 45 mm, ranged from 22,4 – 74,5 mW m^{-1} K^{-1} and the conductivity increased with increasing pelage thickness.

(iii) Thermal insulation increased with increasing pelage thickness. Thus the effect of a thicker insulation was greater than the increase in conductivity.

(iv) The total resistance of the pelts to heat transfer includes both the resistance of the air trapped within the fur and the resistance of the boundary layer of still air above the fur. The importance of the boundary layer decreased with increasing pelage thickness and was already insignificant for a pelage of *ca.* 24 mm. However, it contributed nearly half of the total insulation for a pelage of 1 mm thickness. The boundary layer was also affected by forced convection and a windspeed of 2 m s^{-1} was sufficient to reduce the contribution of the boundary layer to insignificance. Furthermore, forced convection also disturbed the thermal resistance of the air trapped within the fur and the conductivity of the fur increased with increasing windspeed. The effect of forced convection was greater on thin than on thick pelages. However, a windspeed greater than *ca.* 2 m s^{-1} even disturbed the fur of a 24-mm pelage and caused a reduction in skin temperature.

(v) Total conductance increased linearly with increasing windspeed, when the windspeed increased from 0 to 4 m s^{-1}. The effect was, however, greater on the thin pelages, mainly because the boundary layer made such a large contribution towards total insulation.

(vi) The angle of incidence of solar radiation affected the amount of radiation reflected from a pelage and reflectance increased with a decreasing angle of incidence. This effect was more pronounced in certain pelts which can probably be accounted for by a difference in gloss characteristics. The weighted mean absorptance of the pelts varied between 0,25 and 0,85. The highest absorptance values were obtained from dark-coloured pelts while white pelts yielded the lowest values.

(vii) A knowledge of the thermal properties of the pelages of wild ungulates can facilitate the evaluation of the physiological ecology and distribution of these animals. In a large-sized African ungulate, a thin pelage appears to be advantageous. Although the thin pelage enhances heat gain and loss, this effect is counteracted by the relatively small surface area over which heat exchange can take place. Moreover, a thin pelage facilitates heat loss during locomotion and during the night. The latter is of particular importance for large ungulates, such as the eland and oryx, which exhibit adaptive hyperthermia. A dark colour would result in a very high skin temperature which can only be alleviated by cutaneous evaporation or convective cooling. In the smaller ungulates, which rely to a greater extent on respiratory evaporation, a thicker pelage becomes of greater importance. A lighter and thicker pelage would be beneficial in a warm environment to reduce heat load from the environment. The gemsbok and springbok exhibited the lowest absorptance values and both of these occur in warm, arid regions.

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