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THERMAL PHYSIOLOGY OF SELECTED AFRICAN UNGULATES WITH EMPHASIS ON THE PHYSICAL PROPERTIES OF THE PELAGE

by

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Thesis submitted for the degree of PhD. in the
Department of Zoology, University of Cape Town

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ABSTRACT

Thermal Physiology of Selected African Ungulates with Emphasis on the Physical Properties of the Pelage

by M.D. Hofmeyr, Zoology Department, University of Cape Town

The study consisted of three main sections.

In Chapter 1 certain physical characteristics of the pelages of wild African ungulates were studied for the first time. One of the more interesting results to emerge from these studies was that the thickness of the pelage decreases exponentially with increasing body size and disappears completely in the very large ungulates such as the rhinoceros and elephant. This relationship is closely associated with the progressive increase in relative surface area which occurs with decreasing body size and could be interpreted as an effect of natural selection to ensure reduction in heat loss in the smaller ungulates. This phenomenon could, however, also be the result of enhancing heat loss in the larger ungulates, particularly when they are required to sprint away from predators under the hot conditions prevailing in the African savanna. The latter conclusion is supported by the fact that the springbok, among the swiftest of antelope, has a pelage thickness which is significantly less than that predicted by the regression line. These studies also showed that conductance decreased exponentially with increasing pelage depth, despite the fact that conductivity increased with increasing depth. Total insulation was largely determined by air trapped within the pelage and the boundary layer of still air above the pelage. The importance of the boundary layer, however, decreased with increasing pelage thickness. Consequently forced convection, which disturbed the still air, had a more pronounced effect upon the insulation of thin pelages than on thicker pelages. Nevertheless, windspeeds greater than *ca.* 2 m s^{-1} could penetrate the thicker pelages and thereby increase their conductance dramatically. Important differences in respect to reflectance of the different colours of the various pelages were established and these have been discussed in terms of their thermal and ecological significance.

In Chapter 2 a complete thermal balance was constructed for the Namaqua-Afrikaner sheep, while restrained in a metabolic cage in an outdoor environment. The results showed that the major avenue of heat gain under hot conditions was from thermal radiation from the ground surface. The major avenues of heat loss under hot conditions were via reradiation and, under windy conditions, convection. Detailed results with respect to the major influences on respiration rate, cutaneous water loss and vasomotor tone have been described and discussed. In general, these results have again emphasised the important role of the pelage in providing protection against both heat loss and heat gain, thereby facilitating the maintenance of a stable body temperature.

In Chapter 3 the first studies on free-ranging and restrained springbok have again highlighted the importance of studying thermoregulation under natural conditions as opposed to studies in artificially controlled climate chambers. The results show that springbok are able to maintain a stable body temperature (37 - 41°C) under a variety of climatic conditions and even when dehydrated. They exhibit all the expected physiological responses to thermal stress such as sweating, thermal panting, shivering and marked changes in vasomotor tone; the latter being reflected in sudden changes in the temperature of the ears and horns which are used as thermal windows. In sharp contrast to the Namaqua-Afrikaner sheep, however, the thin pelage of the springbok offers minimal protection against heat loss and heat gain. Consequently they rely heavily on behavioural thermoregulation to compensate for this disadvantage. Important behavioural adjustments include shade-seeking, seeking cover under cold, windy conditions and by reducing the profile area exposed to direct solar radiation by orientation of the long axis of the body towards the sun. The effect of the latter adjustment is enhanced by the colour pattern of the pelage. Finally, the springbok was found to possess efficient renal function which would naturally compensate to some extent for excessive evaporative water loss under hot, arid conditions.

In general then it can be concluded that, although marked variation exists in the physical quality, colour and thickness of the pelages of African ungulates, the pelage is of critical importance in the thermal physiology of these animals. For example, my heat balance studies have again confirmed that the primary compensation to high environmental heat loads was via physical processes which occurred automatically on the external surface of the animal and did not necessarily involve physiological responses. Equally important, it has also become clear that the quality, colour and thickness of the ungulate pelage represents an interesting evolutionary compromise, imposed upon the animal by natural selection in its specific ecological niche. The latter conclusion is clearly demonstrated by the marked differences found between the artificially-selected Namaqua-Afrikaner sheep and the naturally-selected springbok.

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CHAPTER 3

THERMOREGULATION AND RENAL FUNCTION IN THE SPRINGBOK, ANTIDORCAS MARSUPIALIS

GENERAL INTRODUCTION

The ungulates include some of the largest land animals and, in consequence, they cannot avoid climatic stress as do small mammals. A great deal of information concerning the physiology of thermoregulation in domestic ungulates is available but relatively little is known about thermoregulation in wild ungulate species. Moreover, in the past, thermoregulation studies were conducted mainly in climatic chambers and consequently the effects of certain important environmental parameters were ignored.

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 *et al.* (1950), for example, have demonstrated the value of a thick pelage in arctic mammals. The thick pelage provides good protection against heat loss and thus extends the ambient temperature limits which the animal can tolerate without the need to increase metabolic heat production. Schmidt-Nielsen (1959) has shown that a thick pelage can also be advantageous to an animal in a desert environment. The thick, dorsal fur in the camel provides protection against excessive heat gain from the environment and thereby assists with water conservation.

The colour of a mammal's pelage is also involved in the thermal adaptations to specific environmental conditions. Bonsma and Pretorius (1943) found that cattle with light-coloured coats were better adapted to hot conditions than similar animals with dark-coloured coats. Riemerschmid and Elder (1945) have 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 and Brown (1969) have shown, radiation penetrates more deeply into light than into darker coats. Also, Finch *et al.* (1980) have demonstrated the thermal and metabolic advantages of a dark colour for Bedouin goats under winter conditions in the Negev.

The importance of behavioural thermoregulation in mammals only becomes apparent when the animals are studied in their natural environment. Clapperton *et al.* (1965) found, for example, that the contribution from direct solar radiation towards total heat gain in an animal can be markedly altered by altering the orientation of the long axis of the body towards the sun. Consequently solar heat gain can be optimised in a cold environment and reduced in a warm environment. Furthermore, shade seeking behaviour and various postural adjustments can also influence the heat exchange between an animal and its environment.

Mammals can only maintain a stable body temperature if heat gain equals heat loss. The thermal interplay between an animal and its environment can therefore only be fully appreciated if all the avenues of heat gain and loss are studied. Finch (1972 and 1976) conducted such a study on three different ungulate species and her research represents a major advance in environmental physiology. The heat balance of animals can also help to give a better understanding of how certain animals can exploit environments which are totally unfavourable to other animals.

The purpose of this study was first ~~of all~~, to determine the role of certain pelage characteristics in the adaptation of selected African ungulates to their environments. Secondly, I wished to study thermoregulation in two ungulate species in an outdoor environment and to construct ~~compound~~ a complete heat balance for one of them.

The physical characteristics of the pelages of wild African ungulates have not been studied before and the experiments described in Chapter 1 have been designed to measure important characteristics such as thickness, reflectance and conductance. These variables have then been related to body size and the ecological distribution of the species concerned. In Chapter 2 I have constructed a complete heat balance of a domesticated, indigenous ungulate, the Namaqua-Afrikaner sheep, with emphasis again on the role of the pelage in its thermal physiology. Finally, in Chapter 3 I have contrasted the thermoregulation of the artificially-selected, slow-moving Namaqua-Afrikaner sheep with that of a swift-footed, wild ungulate - the springbok. The emphasis here, has been on the importance of behavioural thermoregulation but, again, the role of the pelage has been a major consideration.

CHAPTER 1

PHYSICAL PROPERTIES OF THE PELAGES OF SELECTED UNGULATES

INTRODUCTION

The pelages of mammals play an important role in their adaptations to different thermal environments. In a homeotherm, a stable body temperature can only be maintained if heat production equals heat loss. In the thermoneutral zone, heat production is kept at a basal level and the animal maintains a stable body temperature by (1) vasomotor alterations, (2) changes in the depth of the pelage by piloerection, (3) evaporative cooling, and (4) by behavioural means. The range of the thermoneutral zone is determined by the efficiency of the above physiological and behavioural traits and also by the physical properties of the pelage. The most important physical properties of the pelage are depth, density and colour. Thickness in the following discussion being synonymous with depth.

Scholander *et al.* (1950) found that fur thickness in arctic mammals increases with the size of the animal up to the 5 kg fox (*ca.* 50 mm). From the 5 kg fox to a 500 kg moose, the thickness did not vary much in most of the mammals he studied. Furthermore, he established that insulation increases with increasing fur thickness and, therefore, the thermoneutral zone increases as well.

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. Conductance is the reciprocal value of insulation and indicates the heat flow per unit time per unit area per degree temperature difference. Thermal conductivity is an expression of how easily heat flows in a given material (Schmidt-Nielsen 1979). Birkebak (1966) recalculated the results of Scholander *et al.* (1950), Hammel (1955) and Hart (1956) in terms of thermal conductivity and showed that thermal conductivity increased with increasing fur thickness. Fur with a thickness less than one centimetre tends to have a thermal conductivity lower than that of the surrounding air, while thicker fur has a thermal conductivity greater than that of air. Birkebak explained the low thermal conductivity of thin furs on the basis of very small air spaces within the fur layer. According to him, the smaller the air spaces the closer one approaches heat transfer by pure conduction. The mean thermal conductivity of animal furs was found by a number of workers to be higher than that of still air. According to Monteith (1973) this implies that the air trapped in the fur was not perfectly still and that free convection and radiation occurred simultaneously with conduction.

Insulation is a temperature difference per unit heat flux and per unit area and describes the resistance of the coat to the conduction of sensible heat (Monteith 1973). Monteith (1973) also advocates the use of the thermal resistance unit with dimensions of time per unit length, instead of the more conventional unit of insulation. Resistance is insulation multiplied by the volumetric heat capacity of air and the use of this system has the following advantages:

1. The transfer equations become analogous to Ohm's law (flux = $^{\text{potential}}/_{\text{resistance}}$) and complex systems can now be treated as electrical circuit analogues.
2. The mathematics of energy, mass and momentum transfer can be unified into a consistent system of equations.
3. Plant physiologists, ecologists and micrometeorologists have already adopted this terminology.

If thermal insulation depends on the air trapped in the fur and the boundary layer of still air above the fur, it follows that forced convection would decrease thermal resistance. If the wind penetrates the fur itself, the thermal conductivity of the fur and thus heat loss would increase even further. Lentz and Hart (1960) and Moote (1955) found that conductivity increased with an increasing windspeed. Nevertheless, Cena and Monteith (1975a) found that although thin fur is affected by forced convection, the conductivity of 'thicker' fur does not change appreciably. 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) stressed the importance of density in determining the resistance against wind penetration into the fur and concluded that the conductivity of fur with a density less than 1 000 hairs cm^{-2} is greatly affected by forced convection.

The pelage of mammals not only provides protection against heat loss but also influences the amount of radiant heat gained from the environment.

In cold environments, the warming effect of solar radiation can reduce the amount of metabolic heat needed to maintain a stable body temperature. In warm environments, however, solar radiation will increase the heat load of the animal and ultimately, evaporative water loss will have to be increased if the animal has to maintain a stable body temperature (Hutchinson *et al.* 1976).

The spectrum of incident solar radiation spans 0,3 to *ca.* 2,2 µm. This range is referred to as short-wave radiation. The solar spectrum can be divided into the ultraviolet from 0,3 - 0,4 µm, the visible spectrum from 0,4 - 0,7 µm and the infrared from 0,7 - 2,2 µm. Animal pelts reflect solar radiation both in the visible and the infrared regions of the spectrum (Monteith 1973). Riemerschmid and Elder (1945) measured the reflectance of different coloured cattle coats exposed to solar radiation and found that the lighter coats reflected more short-wave radiation than the darker coats. However, when evaluating an animal's heat balance, the heat load at the skin surface is a more important consideration. Hutchinson and Brown (1969) found that solar radiation is not only absorbed at the coat surface but it penetrates into the fur to a varying degree. Radiation penetrates deeper into white than into coloured coats and, as expected, dense coats offered greater resistance to penetrance than sparse coats. Despite the deeper penetration, they also found that white coats still had a lower heat load at the surface of the skin than similarly insulated dark coats. The difference, however, decreased with increasing windspeed. It would seem therefore, that lighter coats give better protection against solar heat gain but that the effect of density and wind speed should also be considered. Bonsma and Pretorius (1943) found that cattle with light-coloured coats were better adapted to hot conditions than similar animals with dark coloured coats. Similarly, Finch and Western (1977) found that the proportion of light-coloured cattle increased linearly with heat stress in a study on the distribution of differently coloured cattle in East Africa. The beneficial effect of a dark colour on the energy expenditure of animals has been demonstrated by Hamilton and Hepner (1967) on the Australian zebra finch. The energy expenditure of these birds, when dyed black, at an ambient temperature of 10°C averaged 23% less than the white birds. Finch *et al.* (1980) have demonstrated the same phenomenon while investigating the metabolic rate of black and white Bedouin goats, which are herded in the Negev Desert. The metabolic rates of the black goats during winter were 25% lower than that of white goats, when standing in full sunlight. No difference was recorded when these animals were in the shade.

The effect of pelage depth on minimising radiative heat gain must also be considered. For example, Schmidt-Nielsen (1959) found that the thick fur on a camel's back provides protection against solar heat gain. Shorn camels produced 60% more sweat than the unshorn animals, which indicates an increased heat load at skin level after shearing. The same phenomenon has been demonstrated for shorn sheep by Macfarlane *et al.* (1958). These results suggest that a thick pelage can have adaptive value under conditions of intense solar radiation. Nevertheless, the coats of most mammals that cannot avoid intense solar radiation in arid regions appear to be thin (Hutchinson *et al.* 1976). Turner and Schleger (1960) found a negative correlation between growth of beef cattle in a tropical environment and their coat scores, based largely on increasing hair length. Moreover, summer coats are in general thinner than winter coats and thus a thin coat appears to be associated with the facilitation of thermoregulation under hot conditions. The thin summer coat, however, usually has a higher bulk density than the winter coat (Allen *et al.* 1970) and this would alleviate heat load at the skin level, because penetrance is reduced. It seems, therefore, as if the advantage of a thin pelage in summer does not reside in its protection against heat gain but is rather related to the facilitation of heat loss. Sensible heat loss would be greater across a thin pelage than across a thick pelage. The effect of pelage thickness on the effectiveness of cutaneous evaporation is not entirely clear. Allen *et al.* (1970), for example, found no free moisture in the coats of sweating cattle, although the coats varied widely in depth and this suggests that a thick coat does not obstruct water vapour diffusion. However, Cena and Monteith (1975b) demonstrated that the resistance against water vapour diffusion in a sheep's fleece increased with increasing fleece thickness. Surprisingly, however, the resistance for a fleece, thicker than *ca.* 4 cm, increased more slowly than that of an equivalent layer of still air. The authors explained this phenomenon on the grounds of liquid movement between or along the fibres which assisted the diffusion of water vapour in the fleece. In my opinion this could imply that the water adsorbed by the wool fibres would not contribute towards heat loss from the animal's skin. Consequently, the efficacy of cutaneous evaporation would be reduced.

It is clear that an analysis of the adaptive value of different pelages is a complex task and involves more than a mere examination of the thermal qualities of the pelage. For example, the colour of the pelage is not only implicated in thermoregulation, but is also of importance in camouflage and social behaviour. Nevertheless, a deeper understanding of the animal's physiological ecology can be gained if more data on the physical properties of the pelage become available. To the best of my knowledge, little or no work has been done on the physical properties of the pelages of indigenous African ungulates. In this study my intention was to examine these physical properties in selected African ungulates. The properties studied included fur thickness, the effect of forced convection on the insulation of the pelages as well as the effect of solar radiation on heat flux through the pelages. It was hoped that this knowledge might contribute to a better understanding of the animals' ecology and their thermal physiology. A comparison of these data with those of Scholander's on arctic mammals was also considered to be worthwhile.

PROCEDURE

Pelage thickness

In the following series of experiments the pelts of 16 different ungulate species were used. The pelts were obtained from the South African Museum, the Transvaal Museum and from private collections. A total of 131 pelts were studied of which only six 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. The pelage depth of each pelt was measured at seven different positions with vernier calipers (Fig. 1). In each position, the mean was determined from five measurements. An average body weight for each species was obtained from the ranges in the literature (Zaloumis and Cross 1975; Burton 1962; Shortridge 1934 and Dorst and Dandelot 1970).

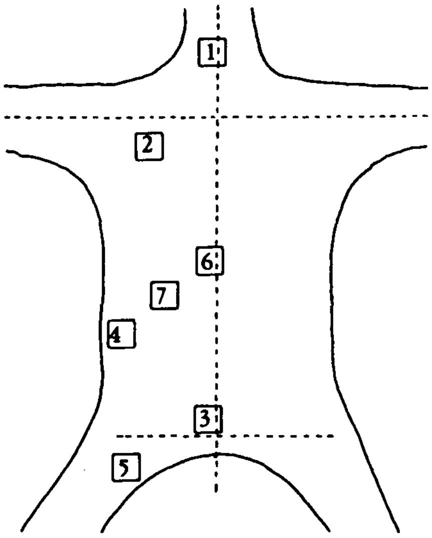


Figure 1 The positions at which pelage depths were measured

Insulation

The heat transfer through the pelage was determined by employing a guarded hot plate technique. The apparatus consisted of a small brass disc (D = 5,8 cm and H = 0,32 cm) which was fitted into a larger brass block (D = 9,2 cm and H = 6,0cm). 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 accurately 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). The digital thermometer reads accurately to the first decimal place, but this was regarded as insufficient for the equilibrium setting of the disc and block. The direct current output from the digital thermometer was therefore connected to a multimeter and a difference of 0,005°C could then be detected.

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 (Fig. 2a). The pelts were placed on top of the apparatus and maximum contact between the disc and undersurface of the pelt was effected by placing a layer of petroleum jelly

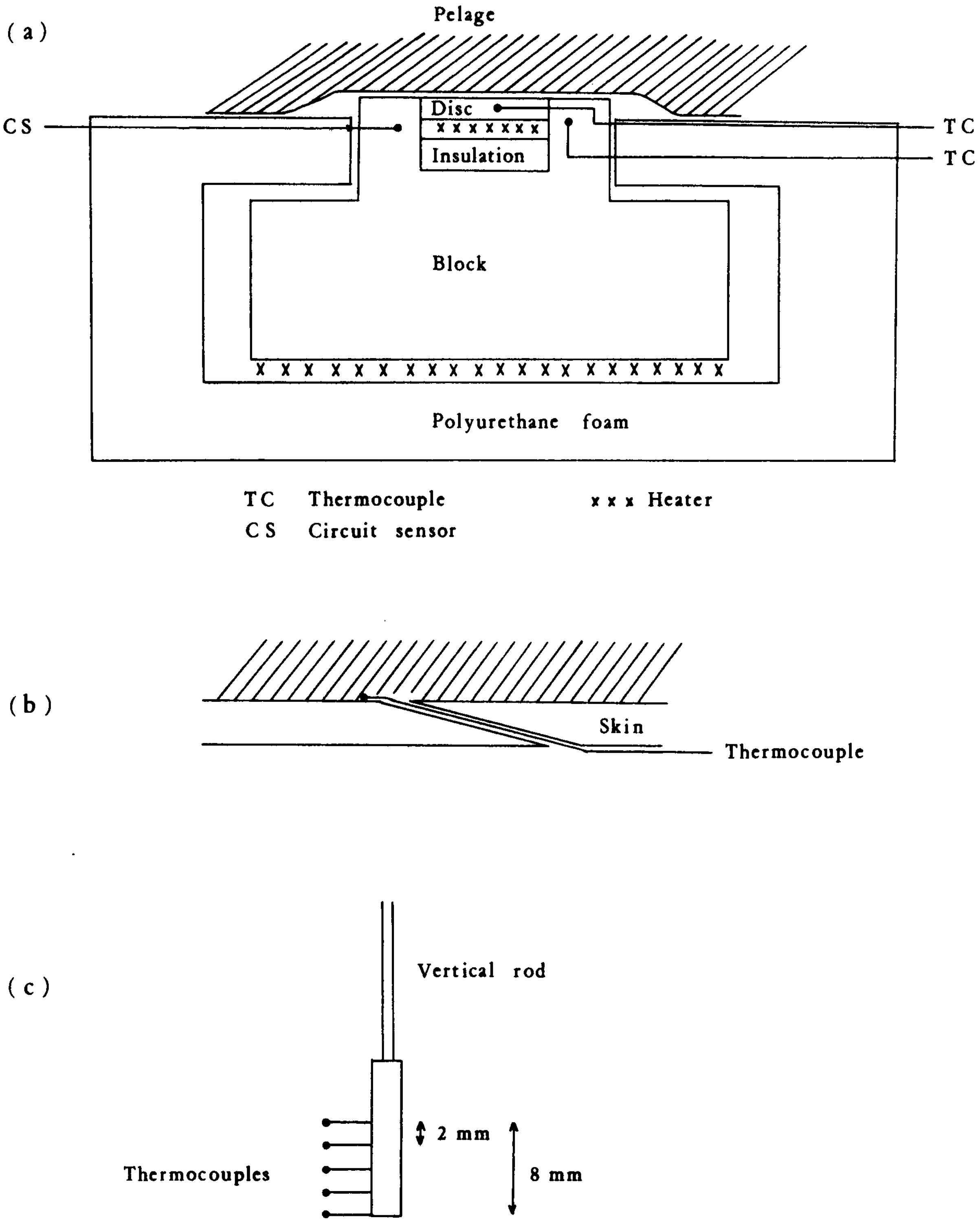


Figure 2 The guarded hot plate apparatus

between the two. The apparatus was kept in a temperature controlled room at 10°C (±1). Room temperature remained constant during each specific measurement.

A windtunnel (L = 100 cm, H = 26 cm and W = 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 windspeed was measured with a vane anemometer and measurements were made at 0, 1, 2, 3 and 4 m s^{-1}.

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 (Fig. 2b). The fur surface temperature and temperature gradient in the boundary layer of air were measured with a series of thermocouples (Fig. 2c), 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 the measurements were made on eight different types of pelts. 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. Due to circumstances beyond my control, the pelts of three klipspringers and Namaqua-Afrikaner sheep were only measured in still air.

The following equations were used in the calculations.

$$k = \frac{Q\ d}{A\ (Tsk - Ts)}$$

$$Cf = \frac{Q}{A\ (Tsk - Ts)}$$

$$Cf{+}A = \frac{Q}{A\ (Tsk - Ta)}$$

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

$$r = I\ \rho\ cp$$

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)

Tsk is the skin temperature (K)

Ts	is the fur surface temperature (K)
Cf	is the conductance of the fur ($W\ m^{-2}\ K^{-1}$)
Cf+A	is the conductance of fur and boundary layer of air
Ta	is the air temperature
I	is insulation ($K\ m^2\ W^{-1}$)
r	is resistance ($s\ m^{-1}$)
ρ cp	is volumetric specific heat of air at 20°C (1216 $Jm^{-3}{}^{\circ}C^{-1}$)

where

ρ	is the density of dry air at 20°C (1204 $g\ m^{-3}$), and
Cp	is the specific heat of air (1,01 $J\ g^{-1}\ {}^{\circ}C^{-1}$)

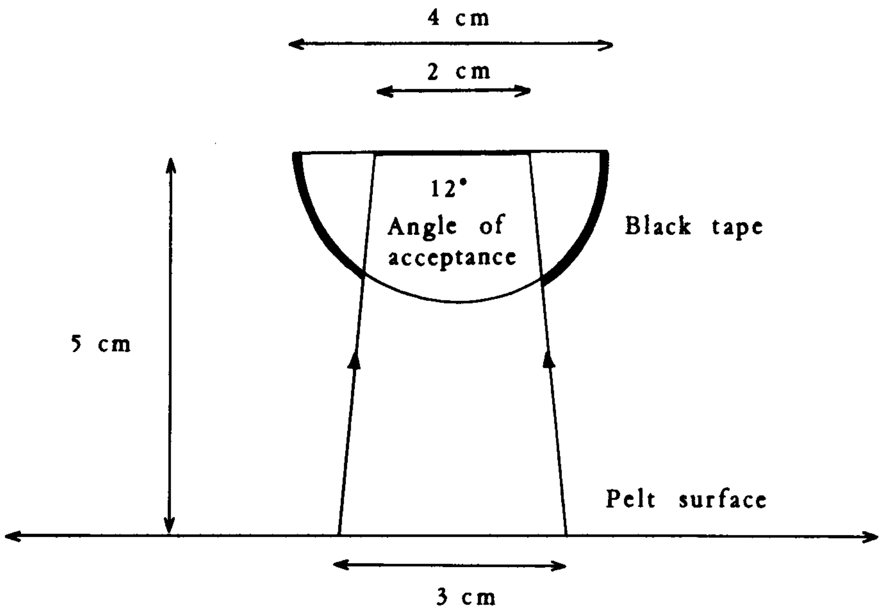
Reflectance

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 168,6°. According to Hutchinson *et al.* (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: $\% = 100 \sin^2\theta$ where 2θ is the angle of acceptance. Thus 99,01% 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.

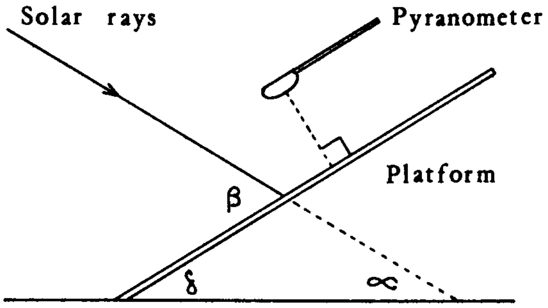
Most of the pelts, however, measured between 25 and 100 cm in width and a restricted pyranometer was needed. A strip of thick black tape (H = 4,5 mm) was fixed to the base of the glass dome. The angle of acceptance was then reduced to 122,6° and 100% of the radiation received was from the pelt, when the latter had a diameter greater than 25 cm. In certain instances, I was interested in the reflectance of specific areas on the pelts which measured less than 25 cm in diameter. For these measurements, I restricted the pyranometer to an angle of acceptance of 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 (Fig. 3a).

Reflectance measurements were taken at different angles of solar elevation. The pelts were mounted on a platform which could be adjusted from a horizontal to a vertical position when δ was changed (Fig. 3b). The solar elevation (α) during each measurement was calculated using standard equations. Thus the size of δ 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 (Figs. 3c and 3d).

In all the measurements I held the pyranometer 5 cm above the pelt surface

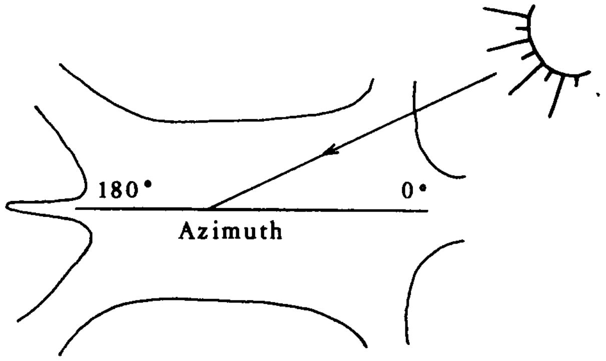


(a) A restricted pyranometer

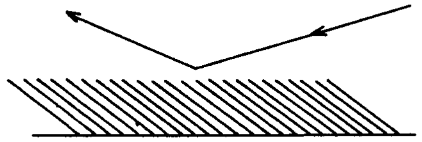


∝ Solar elevation
β Angle of incidence

(b) Adjustable platform



(c) Orientation of pelt towards sun



(d) Orientation of pelt towards sun

Figure 3 Technique used for reflectance measurements 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 (Fig. 4). I used a board coated with Vadec white matt paint as the standard. The paint was tested in the manufacturers' laboratories and was found to have a reflectance of 0,9 in the visible range.

During each measurement, I followed the following procedure. 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~~ was measured at that specific angle of incidence. I followed Riemerschmid and Elder's (1945) suggestion and measured the diffuse component of the total reflected radiation only at 30°, 15° and 5°. When the sun was at the higher elevations too large a part of diffuse sky radiation was obscured, when the pelt or standard was shaded. The mean reflectance for diffuse radiation was, therefore, 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 calculated in the following way.

$$\text{Reflectance} = \frac{\text{Reflected radiation from pelt}}{\text{Reflected radiation from standard}} \quad 0{,}9$$

In both springbok and bontebok, four different pelts were used and $\bar{x} \pm s$ were determined for every angle of incidence.

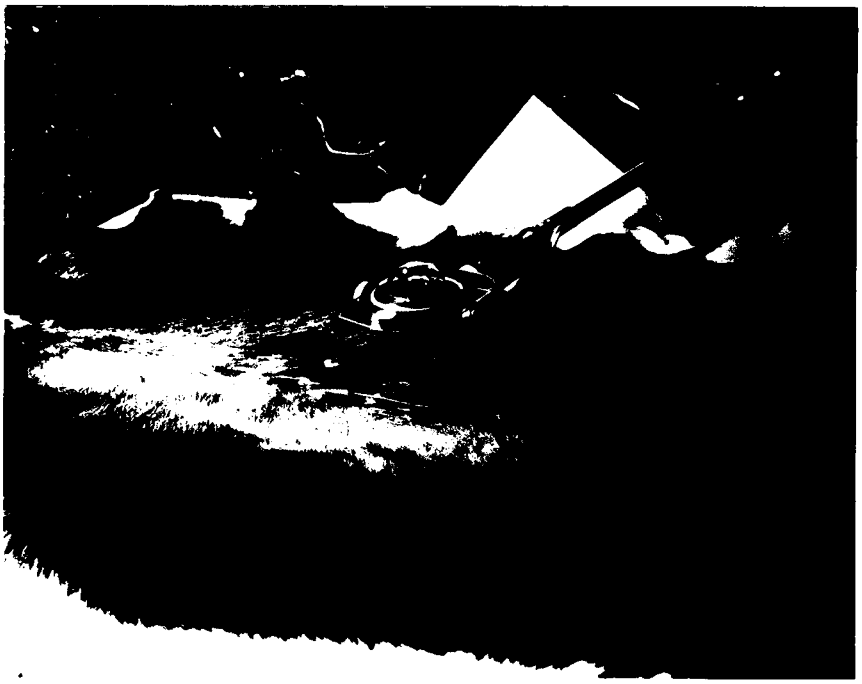


Figure 4 Apparatus for measuring reflectance of a pelage

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 and 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 varying 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 solarimeter.

RESULTS AND DISCUSSION

Pelage thickness

The pelage depth ranged from 1 - 28,2 mm and decreased with increasing body weight, which ranged from 12,5 - 727 kg (Fig. 5 and Table 1). A power curve describing the association between the two variables was calculated and the following regression equation was obtained.

$$y = 65{,}16\ X^{-0{,}60}$$

(where y = depth and X = body weight)

The coefficient of determination (r^2) was 0,83, consequently 83% of the total variation in depth can be accounted for by the fitted regression. The slope of the regression line is reasonably close to -0,67 which is generally used to indicate the relationship between body weight and surface area. Consequently, it would appear as if pelage depth is determined to a great extent by surface area and is therefore primarily involved in heat exchange processes.

In contrast to my 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 weight of *ca.* 5 kg and no further significant increase in thickness occurred. This apparent contradiction between the results of Scholander *et al.* and my own can be explained by the marked difference between the arctic environment and that of the African savanna as well as the relationship

TABLE 1 The relationship between mean body weight and mean pelage depth in selected African ungulates

Scientific name	Common name	Mean weight (kg)	Mean depth (mm) ± s	n
Raphicerus melanotis	grysbok	12,5	15,15 ± 3,61	2
Oreotragus oreotragus	klipspringer	13,4	21,65 ± 3,61	15
Raphicerus campestris	steenbok	14,5	7,50 ± 1,64	23
Pelea capreolus	vaal ribbok	20,5	17,8 ± 3,37	8
Antidorcas marsupialis	springbok	34,0	4,44 ± 1,18	17
Aepyceros melampus	impala	64,0	3,85 ± 0,54	10
Damaliscus dorcas phillipsi	blesbok	82,0	5,01 ± 0,75	4
Damaliscus dorcas dorcas	bontebok	91,0	3,28 ± 0,36	5
Connochaetes gnou	black wildebeest	135,0	5,03 ± 2,39	3
Damaliscus lunatus	tsessebe	148,0	2,85 ± 0,64	4
Oryx gazella	gemsbok	198,0	4,02 ± 1,45	5
Hippotragus niger	sable antelope	205,0	3,14 ± 0,86	5
Connochaetes taurinus	blue wildebeest	238,0	2,71 ± 0,56	10
Equus burchelli	zebra	272,0	2,10 ± 1,01	6
Tragelaphus strepsiceros	kudu	275,0	2,17 ± 0,65	12
Taurotragus oryx	eland	727,0	1,0	2

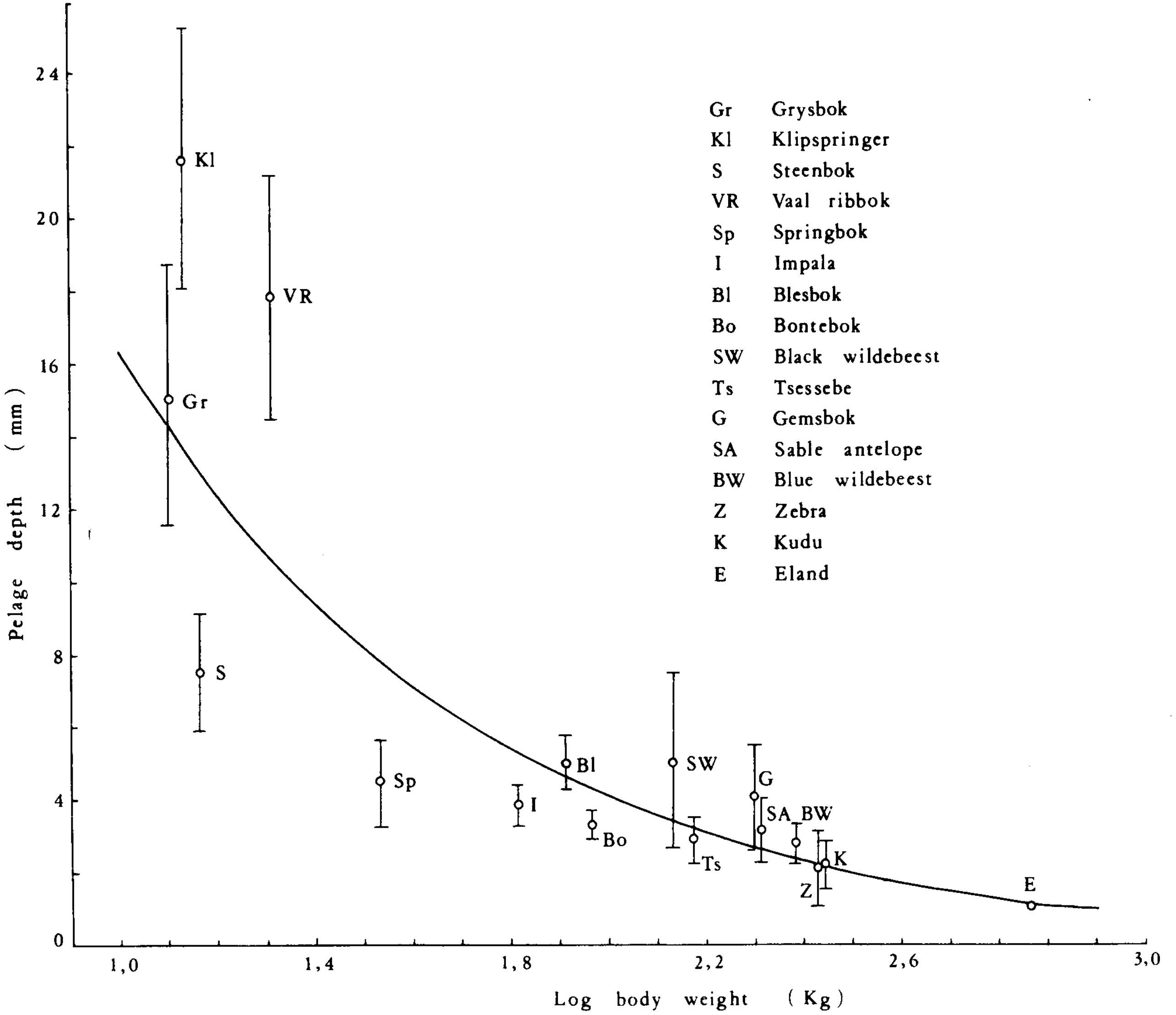


Figure 5 The relationship between pelage depth and body weight in selected African ungulates

between body weight and the surface area. It is well known that the ratio of surface area to volume decreases with an increasing body weight. Smaller animals have difficulty in reducing heat losses to the environment while larger animals in hot environments face the problem of dissipating enough heat to the environment (Richards 1973). In warm environments the gradient between body and air temperature would be relatively small and, in certain cases, ambient temperature could even exceed body temperature. In these circumstances the rate of heat gain or loss would be high in small mammals and because of the small volume and high thermal inertia, the body temperature could increase or decrease rapidly. 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, therefore, Scholander found that within the smaller range, pelage depth increased with increasing body size. Scholander's results 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 my 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 exponential decline in pelage depth which occurs with increasing body weight.

It is also of interest that a correlation between body size and cutaneous evaporative water loss has been established by Robertshaw and Taylor (1969). They found that smaller mammals rely to a greater extent on respiratory evaporation while cutaneous evaporation becomes more important with increasing body size. Whether this phenomenon is correlated with pelage depth is not yet clear. Cena and Monteith (1975b) have also found that in sheep the resistance against water vapour diffusion increased with increasing wool thickness. Furthermore, Hutchinson *et al.* (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 generally considered as a protective device against bruising in the rocky environment in which they live. Nevertheless, Norton (1980) 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, however, 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 recognised as being among the swiftest of the African antelope.

Insulation

Before the total insulative properties of the animals' coats are evaluated, I wish to report on and discuss the thermal conductivity values obtained for the various animal coats. In this investigation, I found that the conductivities for the furs ranged from 22,4 - 74,5 mW m^{-1} K^{-1} in still air. These values correspond well with the literature values. 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}. My results (Fig. 6 and Table 2) 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

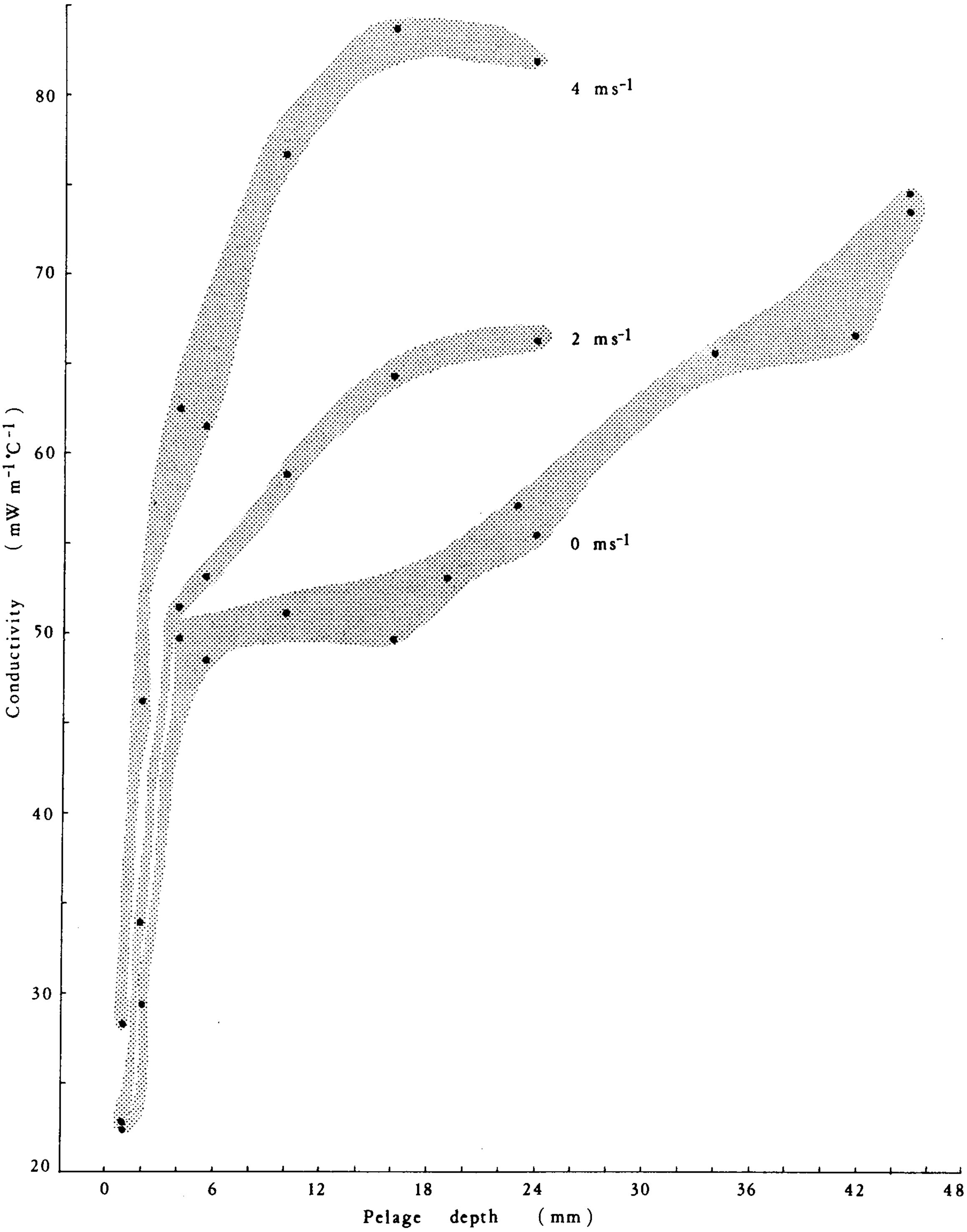


Figure 6 The effect of windspeed upon the relationship between conductivity and pelage depth

TABLE 2 The mean conductivities of selected ungulate pelages at different windspeeds

Name	Depth (mm)	Conductivity ± s (mW m^{-1} K^{-1}) 0 m s^{-1}	1 m s^{-1}	2 m s^{-1}	3 m s^{-1}	4 m s^{-1}
Eland	1,0	22,4 ± 1,1	19,0 ± 0,8	22,6 ± 0,7	25,5 ± 0,3	28,2 ± 0,3
Kudu	2,0	29,4 ± 1,2	28,7 ± 0,7	33,9 ± 0,8	40,5 ± 0,3	46,2 ± 0,4
Bontebok	4,0	49,8 ± 1,6	48,8 ± 0,9	51,6 ± 0,6	56,2 ± 0,7	62,6 ± 0,6
Springbok	5,5	48,4 ± 1,8	50,8 ± 2,2	53,2 ± 1,5	57,4 ± 1,7	61,6 ± 1,5
Steenbok	10,0	51,2 ± 2,6	53,0 ± 0,8	58,9 ± 1,6	66,9 ± 1,3	76,8 ± 1,8
Grysbok	16,0	49,7 ± 1,6	55,7 ± 1,6	64,3 ± 1,8	73,9 ± 1,1	83,7 ± 1,5
Klipspringer	19,0	53,0 ± 4,7				
	23,0	57,1 ± 5,0				
	24,0	55,3 ± 1,3	59,4 ± 2,5	66,2 ± 1,5	73,6 ± 1,0	81,8 ± 0,4
	34,0	65,6 ± 0,4				

(continued)

Table 2 continued

Name	Depth (mm)	Conductivity ± s ($mW\ m^{-1}\ K^{-1}$) $0\ m\ s^{-1}$	$1\ m\ s^{-1}$	$2\ m\ s^{-1}$	$3\ m\ s^{-1}$	$4\ m\ s^{-1}$
Sheep	42,0	66,5				
		± 2,1				
	45,0	73,5				
		± 3,3				
	45,0	74,5				
		± 4,1				

terms of thermal conductivity and expressed it as a function of fur thickness. Birkebak's examination, furthermore, yielded the same unexpected trend as mine, 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 recognised the fact that thickness measurements of thin furs are very difficult to make and that small errors can lead to highly erroneous conductivity values. Nevertheless, he accepted this general trend. He explained it on the basis of very small air spaces trapped within the fur which resulted in high resistance against heat transfer.

The relationship between thermal conductivity and pelt thickness is illustrated in Fig. 6. All the pelts, except for the eland's, had conductivity values higher than that of still air. Cena and Monteith (1975a) found that the high thermal conductivities of animal furs can be ascribed to (1) air conduction, (2) radiative transfer, and (3) 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 and Monteith (1975c) for instance, found that the interception function (p) for long-wave radiation depended on (1) the mean diameter of the hairs, (2) the density of the hair, and (3) 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 7 shows that although thermal conductivity increased with increasing pelage depth, conductance decreased exponentially with increasing depth (r^2 = 0,98). Thus the effect of the increase in pelage thickness was greater than the effect of the increasing conductivity. In Fig. 8 I have illustrated three linear relationships between thermal resistance 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 resistance values of the pelages plotted against the relevant depths. This shows that the relationship between thermal resistance and pelage depth was not strictly linear because the conductivity value increased with increasing depth. The power curve gave the best coefficient of determination (r^2 = 0,984) and shows an excellent correlation between thermal resistance and pelage depth.

Birkebak (1966) compared the values of Scholander *et al.* (1950) for insulation versus fur thickness with those of Hammel's (1955) and Hart's (1956) and found good agreement. In Fig. 9 I have again compared my

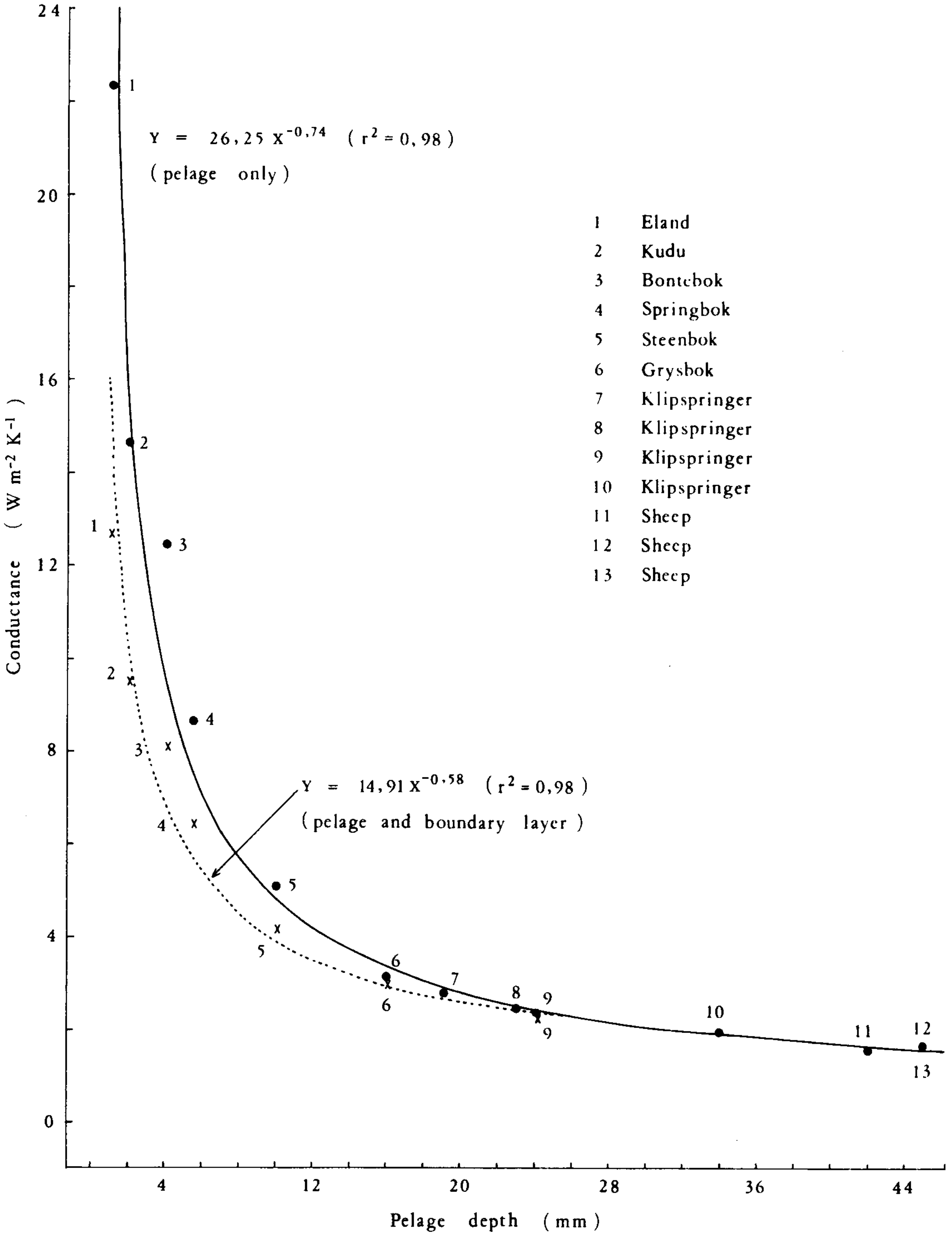


Figure 7 The relationship between thermal conductance and pelage depth of selected ungulates

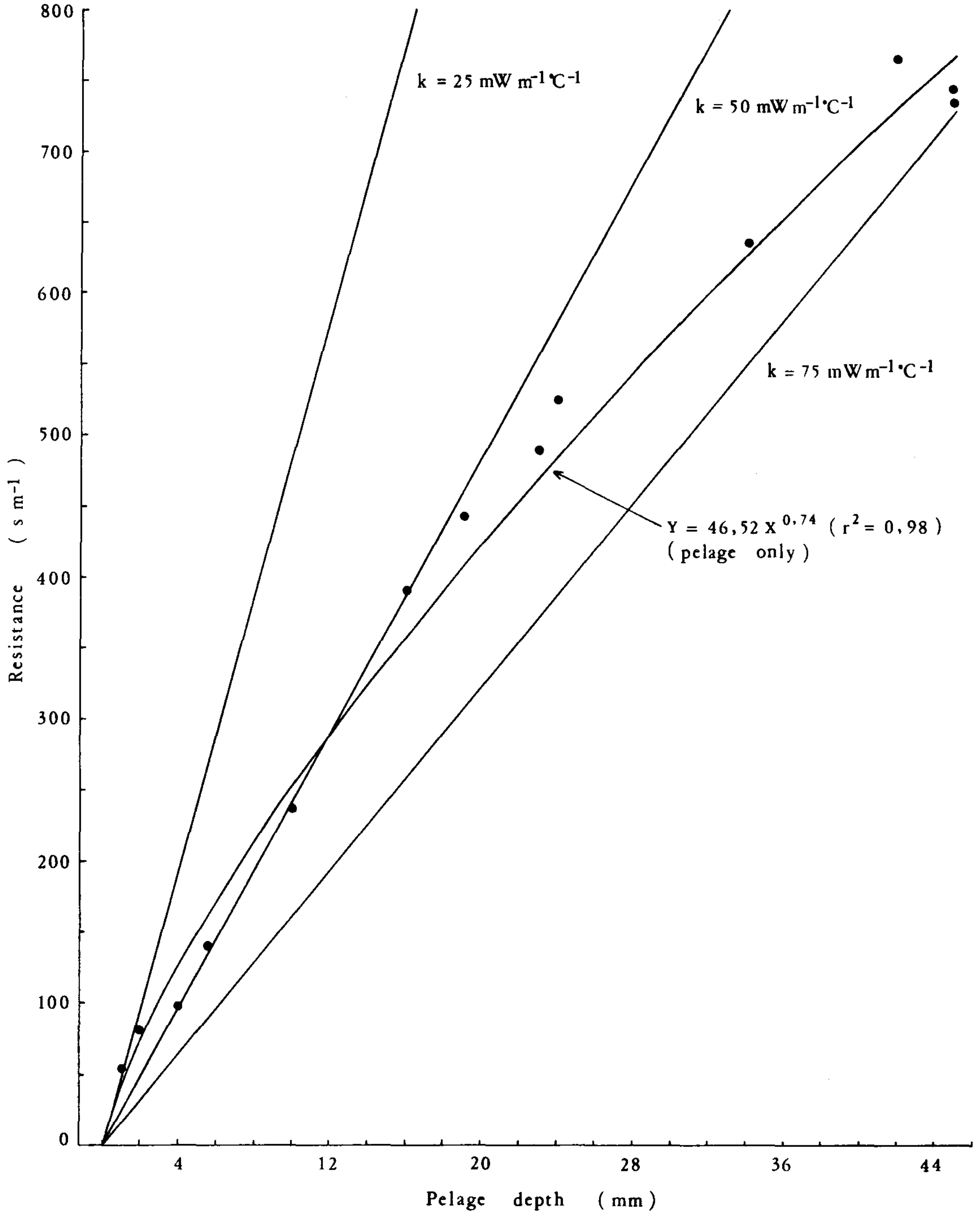


Figure 8 The effect of thermal conductivity upon the relationship between thermal resistance and pelage depth

results (total resistance = pelage and boundary layer) with those of Scholander *et al.* and my results in general showed a lower resistance at equal depths than his. This was expected, since he took the resistance of the skin also into account while I did not. Furthermore, one would expect arctic animals to have a denser pelage which would offer a higher resistance against heat transfer. Figure 9 also shows that the thicker pelages had lower resistances to heat transfer than an equal layer of still air. In contrast, the resistance to heat transfer of a thin pelage can be even higher than that of still air. This difference was caused by the different thermal conductivities of the pelages.

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 resistance was only determined on seven species, of which the thickest pelage was 24 mm. Previously, I showed that the best correlation between resistance 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. I have therefore illustrated the relationship between resistance and pelage depth in Fig. 10 as a linear function. Figure 10 shows that the importance of the boundary layer decreased with increasing pelage depth and windspeed.

In Table 3 I have summarised 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

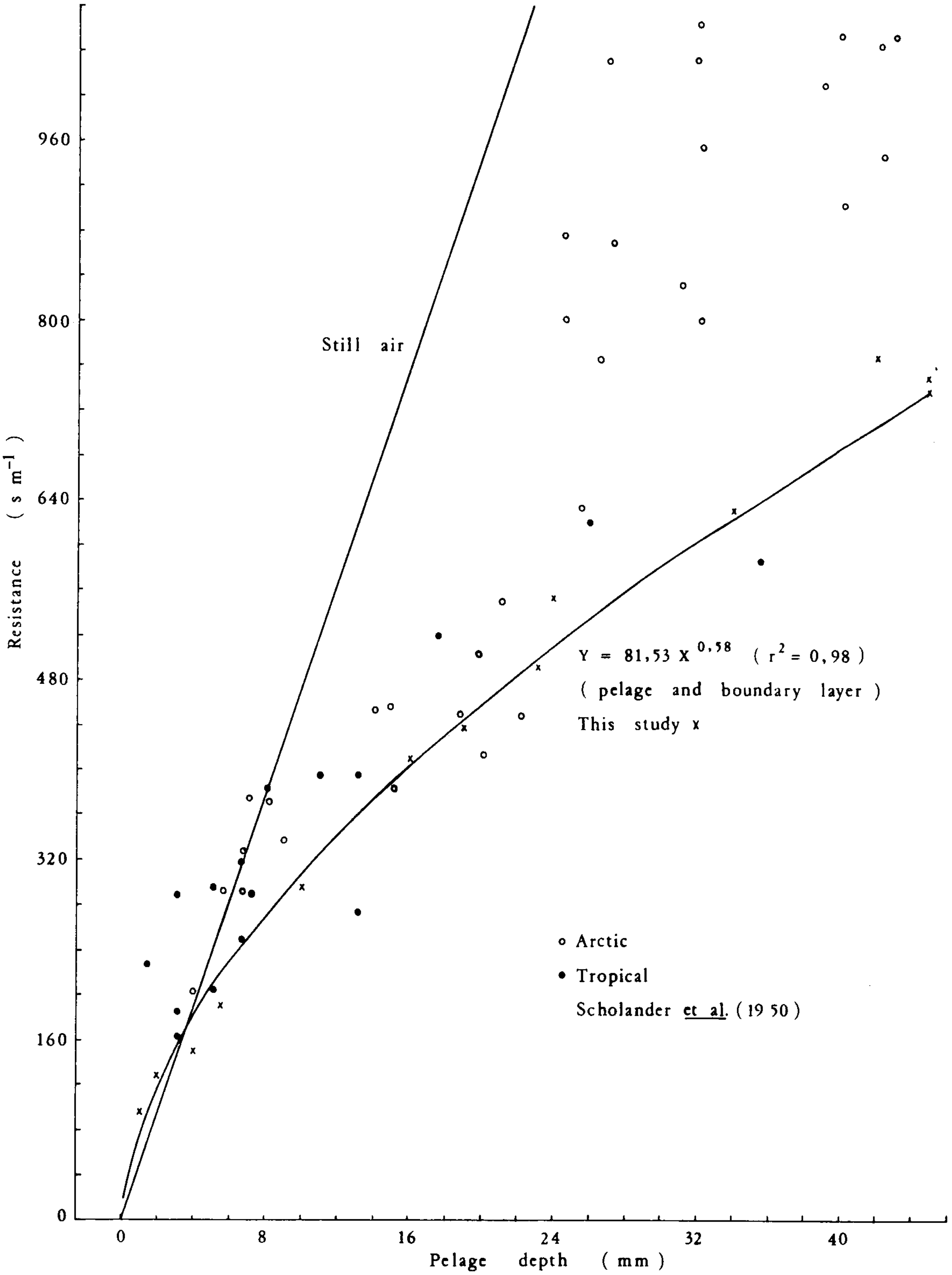


Figure 9 The relationship between total thermal resistance and pelage depth

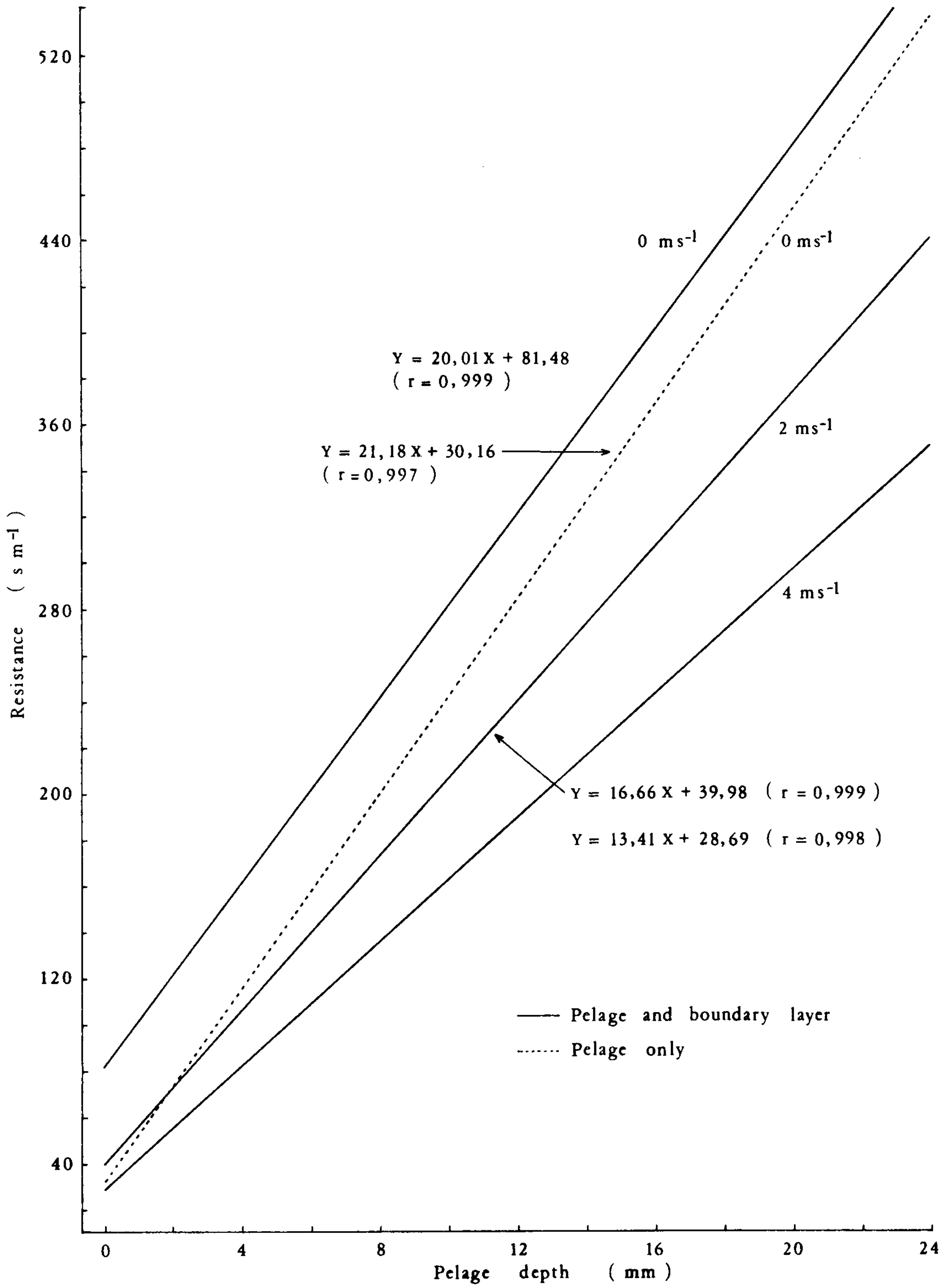


Figure 10 The effect of windspeed upon the relationship between thermal resistance and pelage depth

TABLE 3 The contribution of the boundary layer towards the total thermal resistance of various pelts at windspeeds of 0 and 2 m s^{-1}

Species	Pelage depth	Measured contribution		Calculated contribution	
	(mm)	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 4 Regression equations (pelage only) which show the relationship between pelage thickness (χ) and thermal resistance (y) at different windspeeds

Windspeed m s^{-1}		r^2
0	$y = 21,183\ X + 30,155$	0,994
1	$y = 18,986\ X + 38,767$	0,997
2	$y = 16,908\ X + 34,460$	0,999
3	$y = 15,079\ X + 30,221$	0,999
4	$y = 13,410\ X + 28,695$	0,997

equations. It is clear that at 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 resistance of the fur as well. This can be seen from the slopes of the regression lines which decreased with increasing windspeed (Table 4).

The effect of forced convection on the individual pelts is illustrated in Fig. 11. In the presentation of these dat~~e~~a, I have preferred to use conductance units rather than resistance, because the conductance values increased linearly with increasing windspeed. 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 - 8 m.p.h) had a greater effect than an increase from 3,58 to 8,05 m s^{-1} (8 - 18 m.p.h.). 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}. My data also shows 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.

Previously I demonstrated that the boundary layer had a much greater effect on total insulation in the thinner pelts than in the thicker pelts. Thus the difference between effective and actual thickness would be greater in the thinner pelts. I calculated effective thickness, as

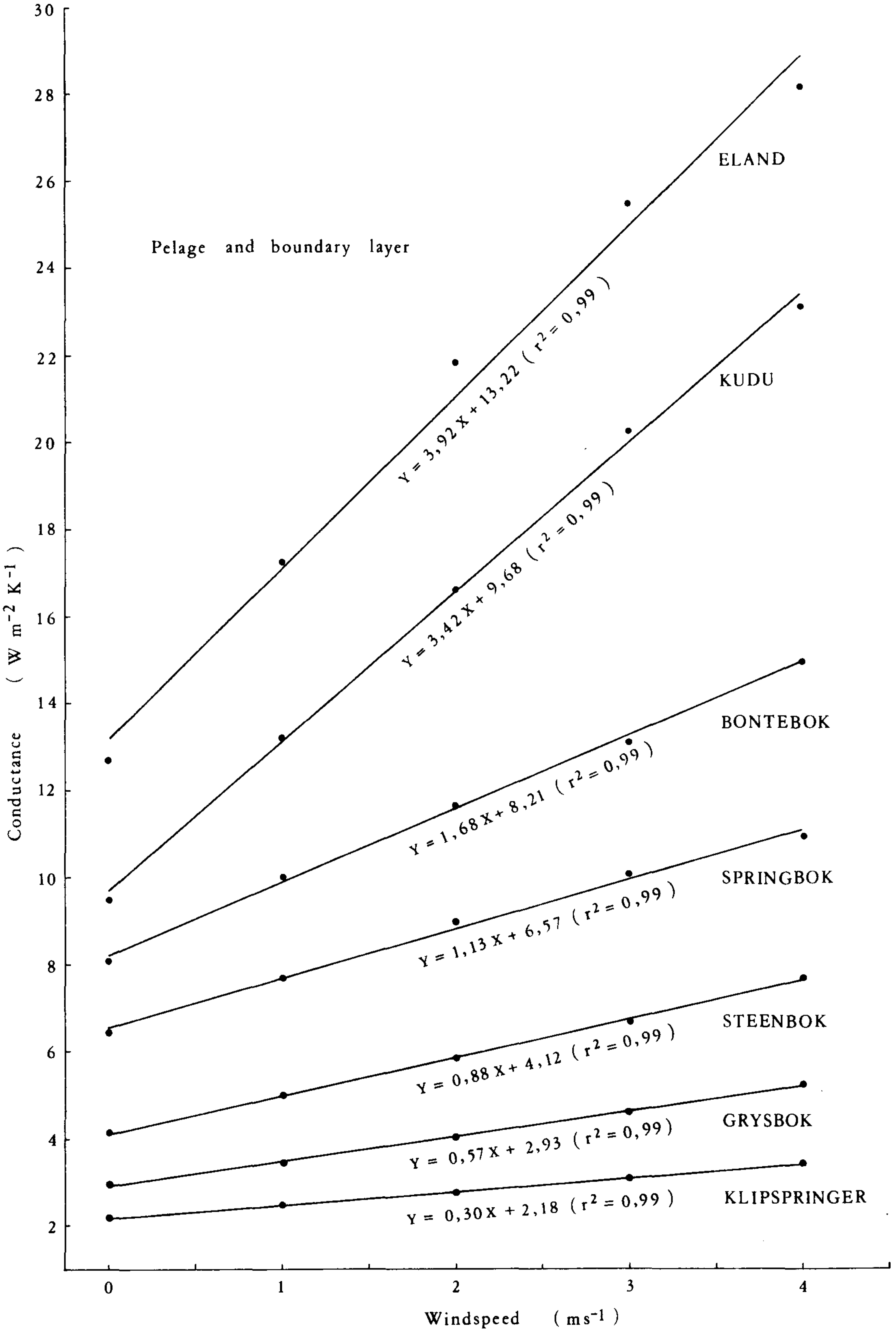


Figure 11 The relationship between thermal conductance and windspeed

the pelage thickness which would offer the same resistance to heat flow in still air as the resistance obtained for the pelage plus boundary layer of air. Forced convection eliminated or reduced the thickness of the boundary layer dramatically and consequently had a much greater effect on the insulation provided by thin pelages. Table 5 shows how forced convection reduced the effective thickness of the pelages. At a windspeed of 4 m s^{-1} the effective thickness of a klipspringer's pelage was 60% of the effective thickness at 0 m s^{-1} while that of the eland's pelage was only 18%.

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 is illustrated in Figs 12a, b, c, d and e. 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).

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} (18 m.p.h.) 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 and Monteith (1975a),

TABLE 5 The effect of forced convection on the effective thickness of various ungulate pelages

Species	A.t. Actual thickness (mm)	E.t.0 Effective thickness at 0 m s^{-1}	E.t.4 Effective thickness at 4 m s^{-1}	$\frac{\text{E.t.4}}{\text{E.t.0}}$ x 100 %	$\frac{\text{E.t.4}}{\text{A.t.}}$ x 100 %
Klipspringer	24,0	25,1	15,1	60	63
Grysbok	16,0	17,5	10,1	58	63
Steenbok	10,0	11,9	6,3	53	63
Springbok	5,5	7,6	3,4	45	62
Bontebok	4,0	6,2	2,5	40	63
Kudu	2,0	4,3	1,2	28	60
Eland	1,0	3,4	0,6	18	60

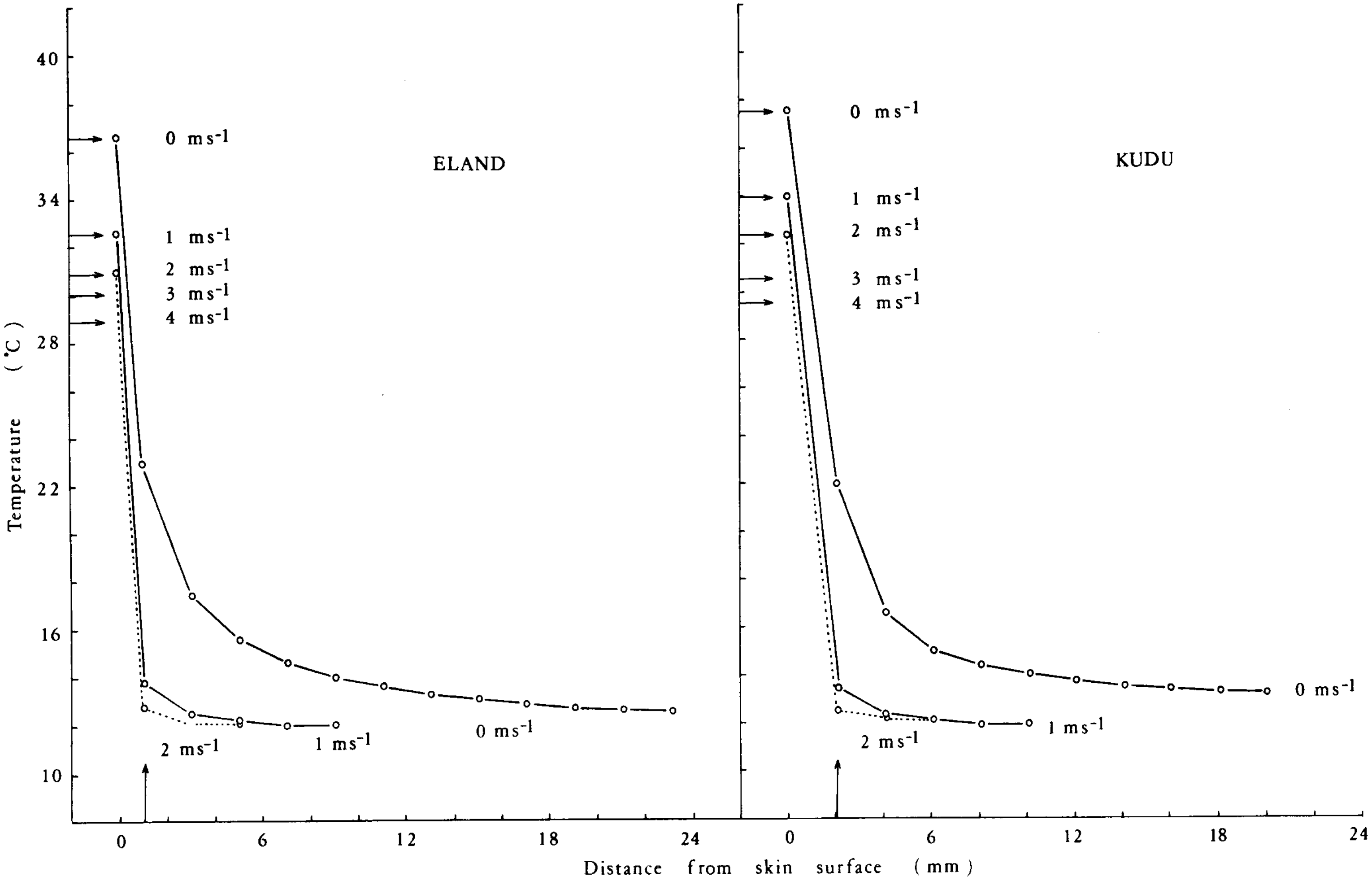


Figure 12a The effect of windspeed upon the temperature gradient across the pelage and boundary layer

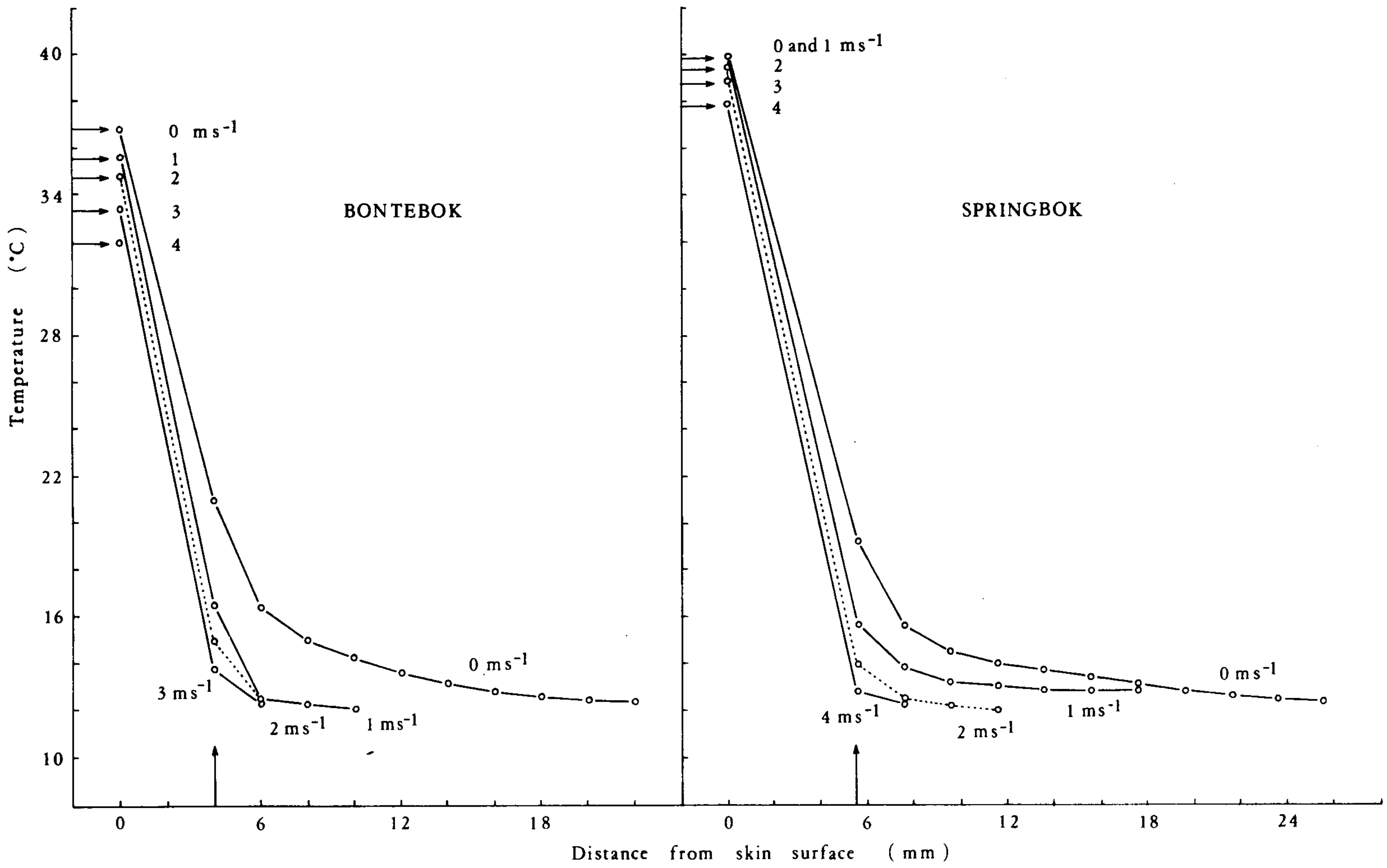


Figure 12b The effect of windspeed upon the temperature gradient across the pelage and boundary layer

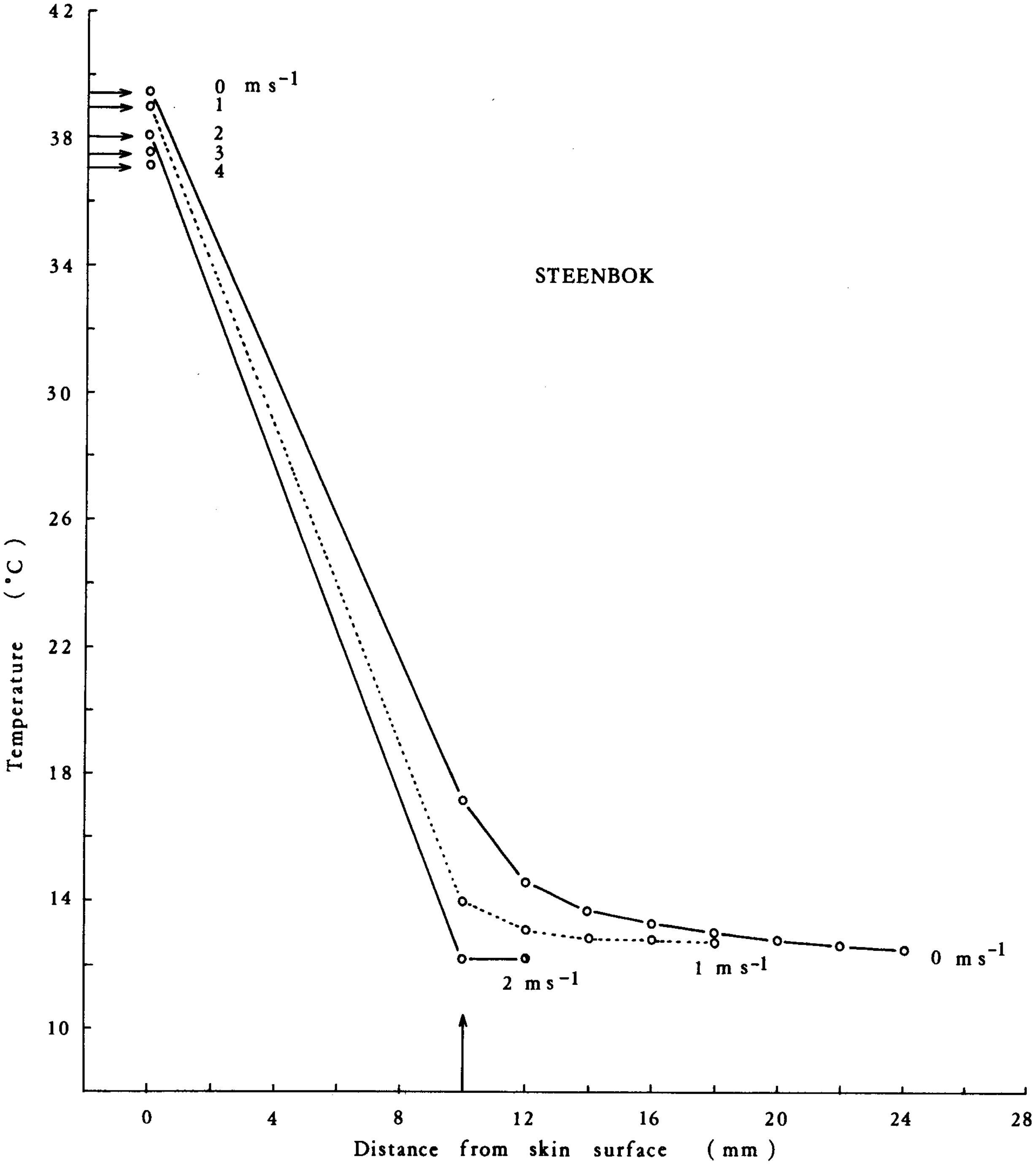


Figure 12c The effect of windspeed upon the temperature gradient across the pelage and boundary layer

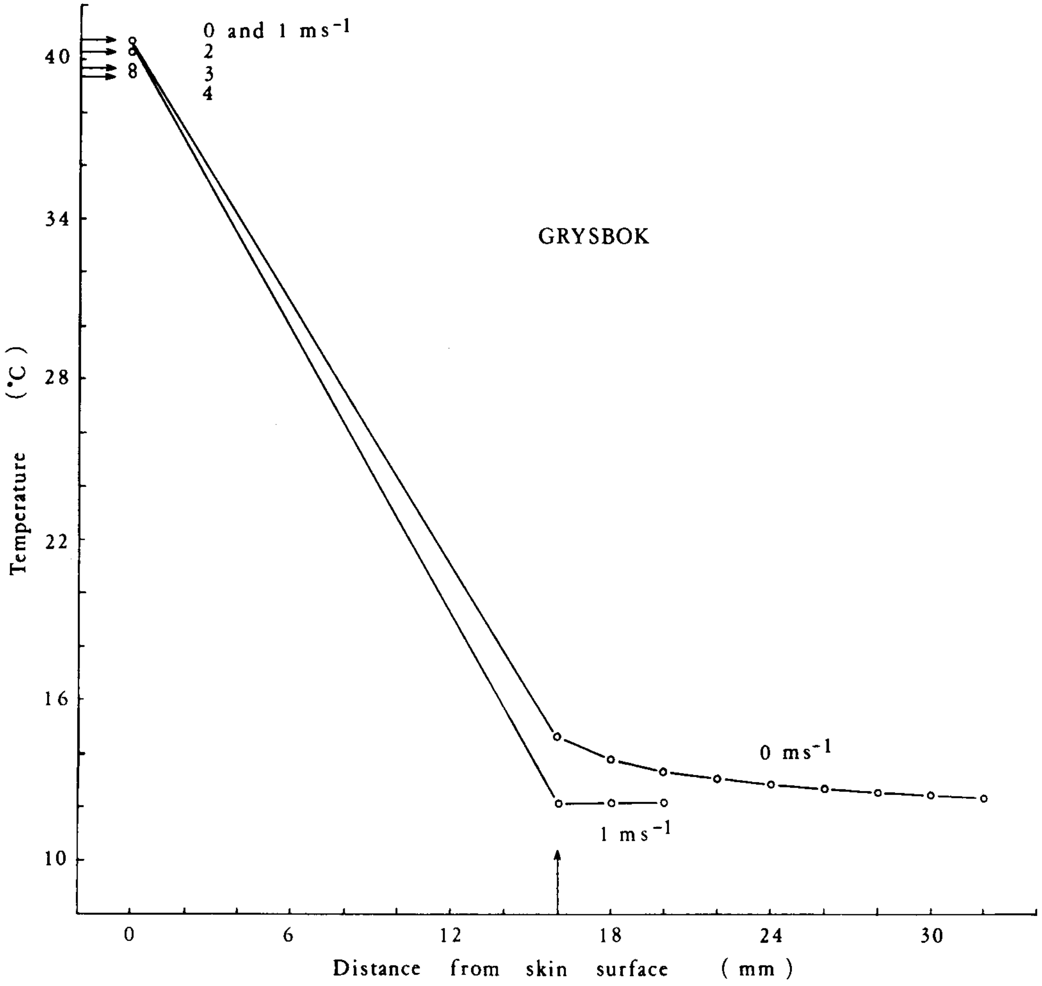


Figure 12d The effect of windspeed upon the temperature gradient across the pelage and boundary layer

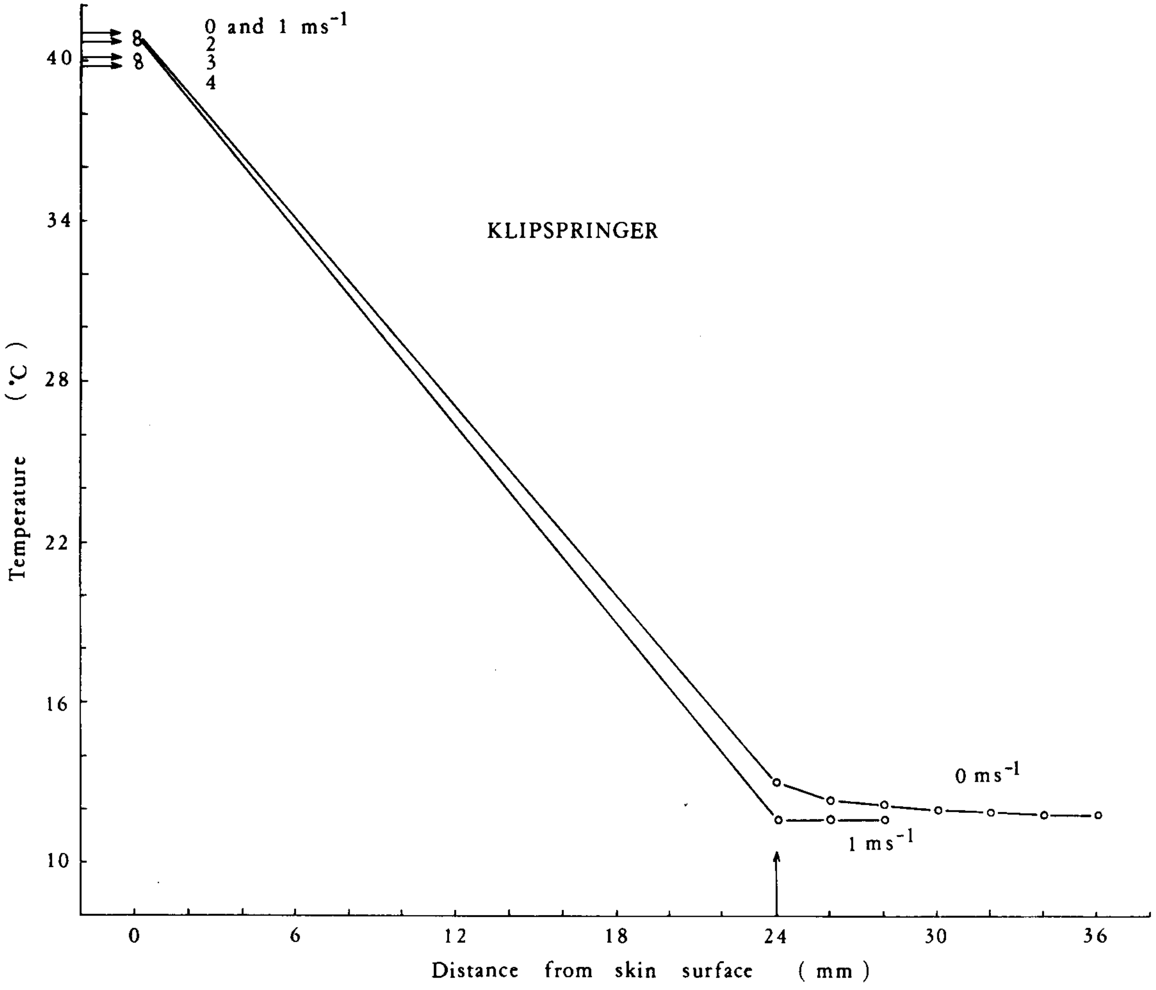


Figure 12e The effect of windspeed upon the temperature gradient across the pelage and boundary layer

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. My 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 and Monteith (1975a).

Reflectance

Figures 13a - j show the reflectances of the pelts at various angles of solar elevation. In all the pelts studied, reflectance values increased with a decreasing angle of incidence. Riemerschmid and Elder (1945) came to the same conclusion when studying cattle coats. Hutchinson *et al.* (1976) argued that the increasing reflectance found by Riemerschmid and Elder could be ascribed to an increase in gloss, which would result in an increase in specular as opposed to diffuse reflection. I found that 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; zebra, black stripes and springbok, brown lateral line. In contrast, the grysbok, for example, showed an increase in reflectance of only 0,15 units with a decreasing angle of

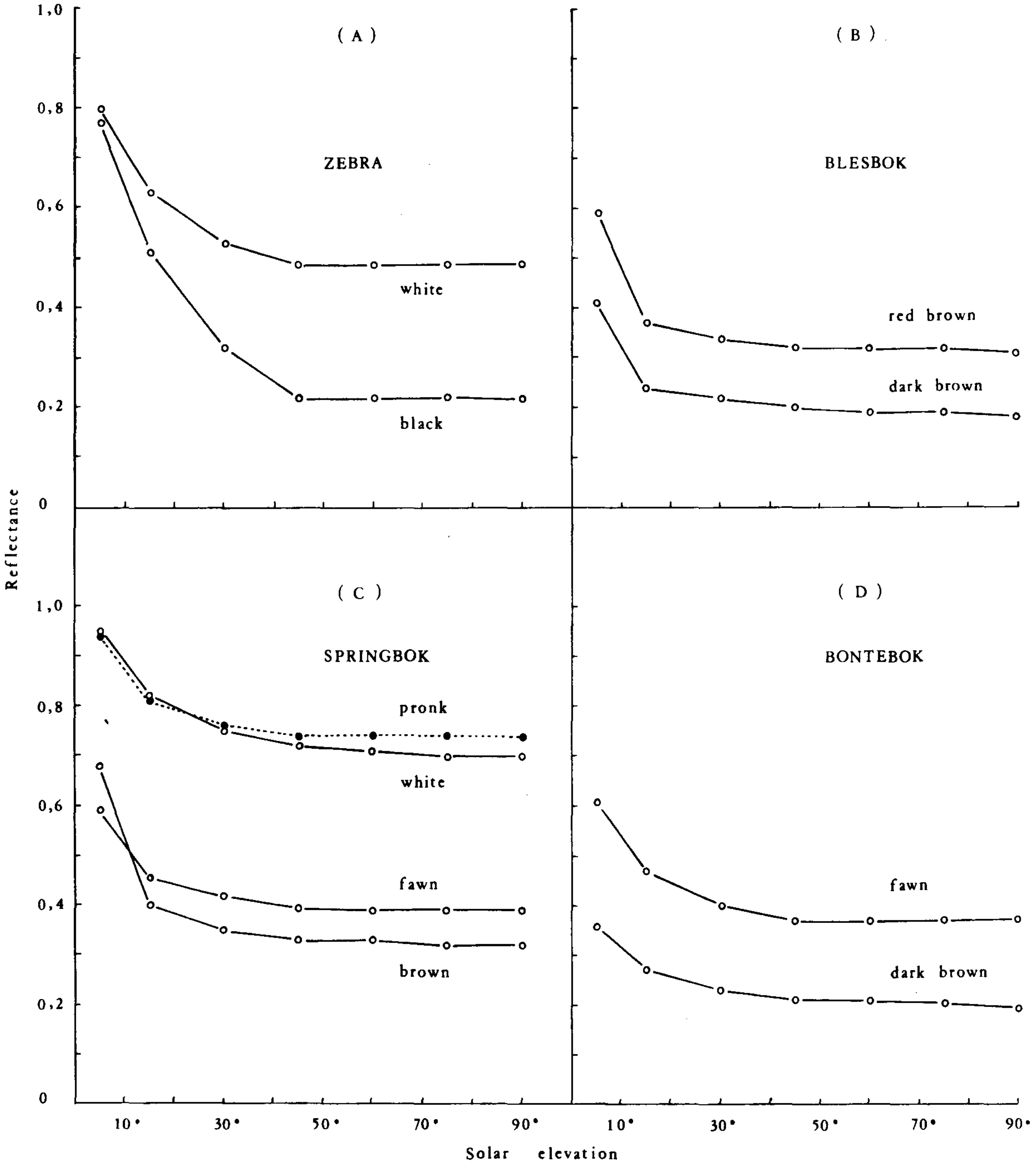


Figure 13 The effect of solar elevation upon the reflectance of various pelages

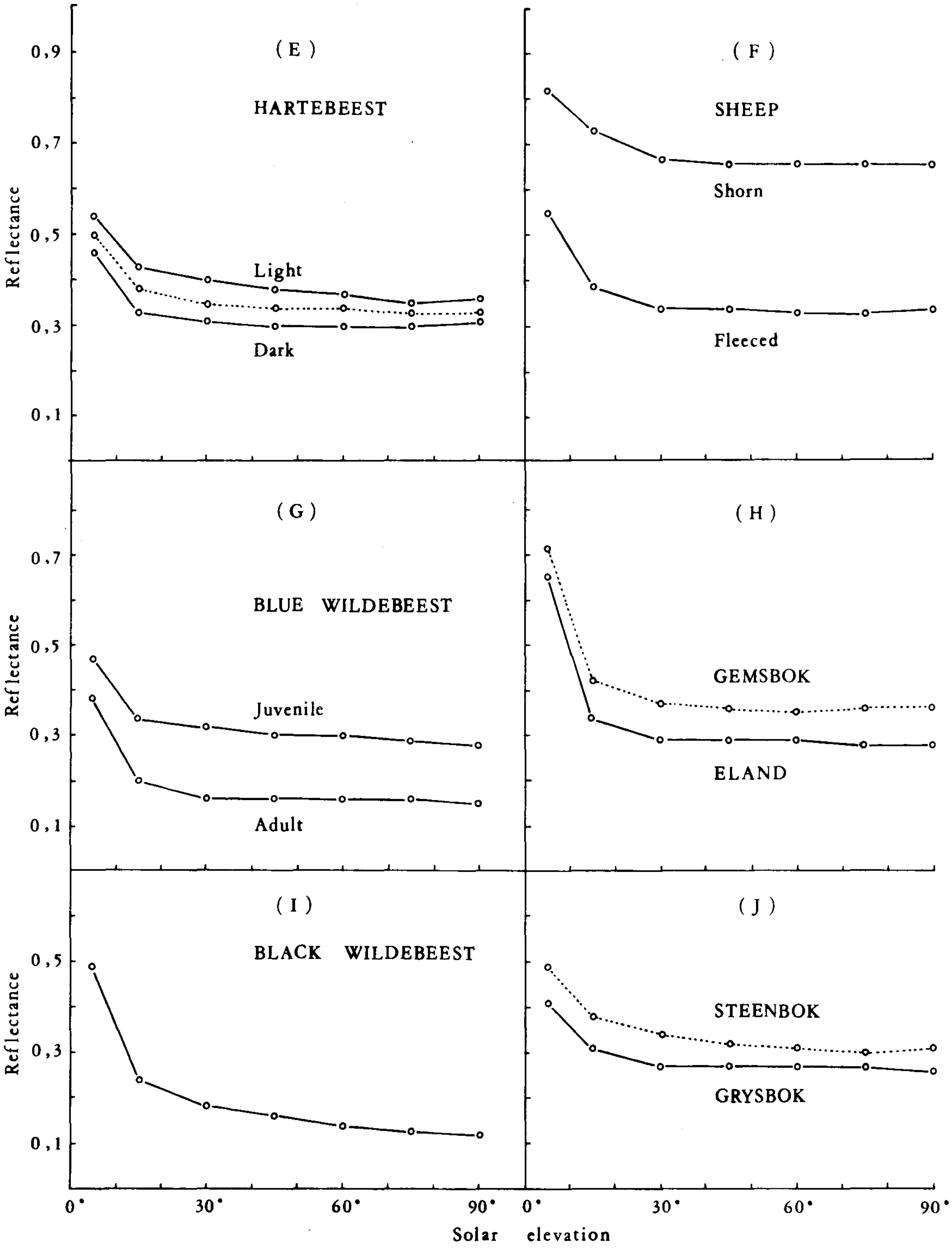


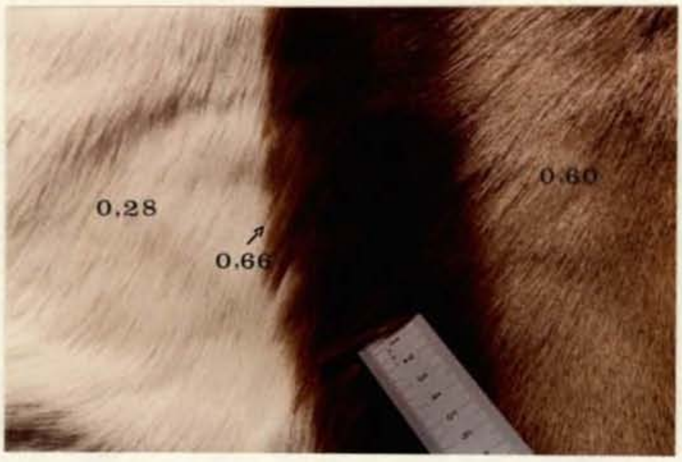
Figure 13 The effect of solar elevation upon the reflectance of various pelages

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 absorptances of the coats for direct solar radiation varied from 0,25 to 0,85 and are shown in Figures 14a - o. These photographs 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 the literature values. Finch (1972a) reported values of 0,75 and 0,64 respectively for the eland and hartebeest.

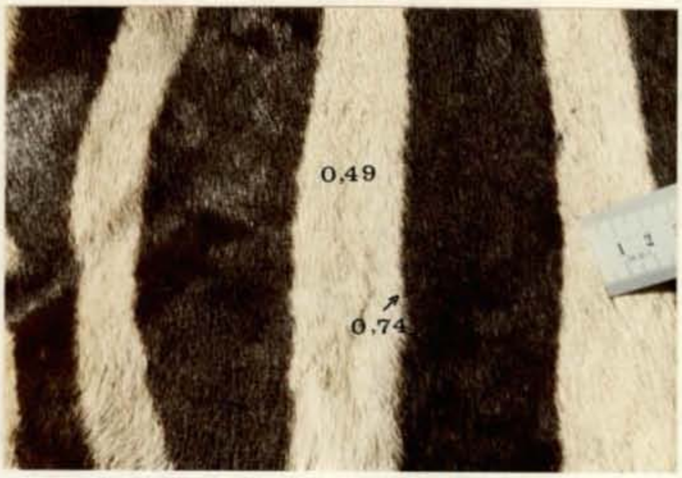
Surprisingly, the weighted mean absorptance for the four different white-coloured coats differed considerably. For example, the white areas on the springbok's pelt (belly and pronk) gave the lowest absorptance values (0,28 and 0,25 respectively). The shorn sheep had a dull, slightly yellowish-white colour 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 hair.

Figures 14h and i show that the juvenile blue wildebeest had a much lower



a) Springbok

b) Springbok pronk

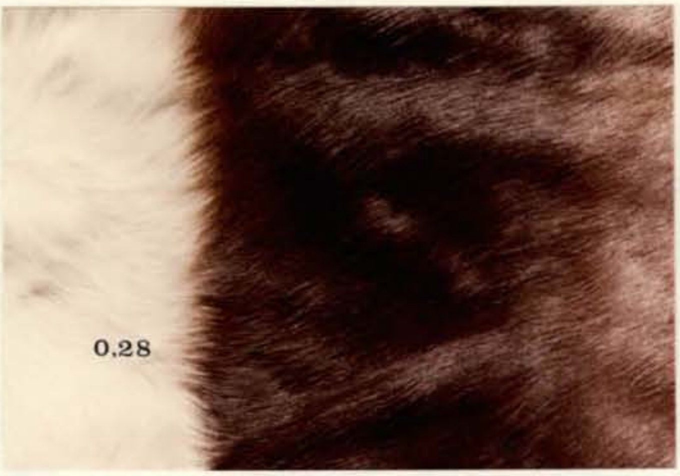


c) Zebra

Figure 14 Weighted mean absorptance of selected ungulate pelts

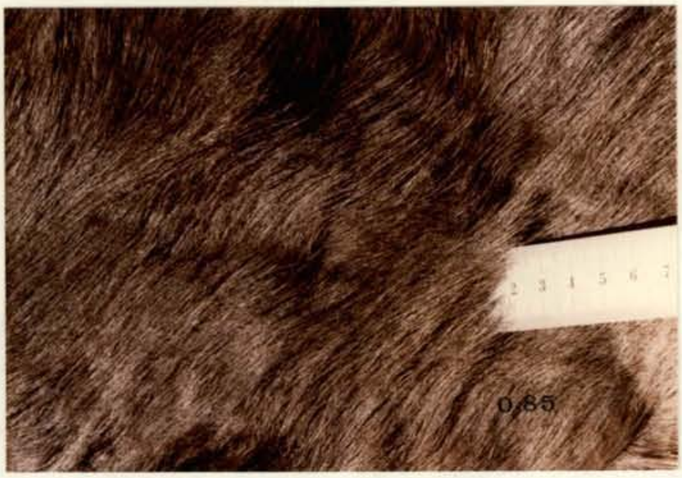
d) Blesbok

e) Bontebok

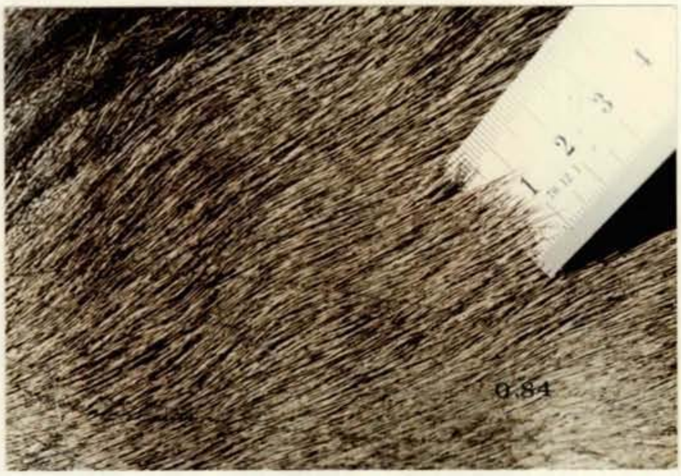


f) Bontebok

Figure 14 Weighted mean absorptance of selected ungulate pelts



g) Black wildebeest



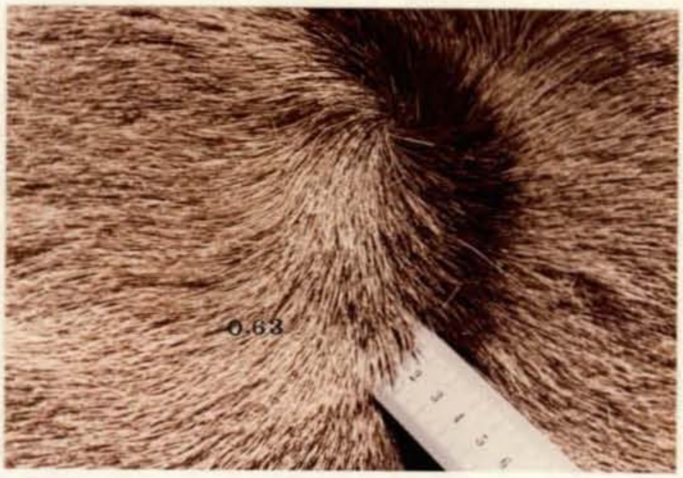
h) Blue wildebeest
adult

i) Blue wildebeest
juvenile

Figure 14 Weighted mean absorptance of selected ungulate pelts

j) Eland

k) Hartebeest

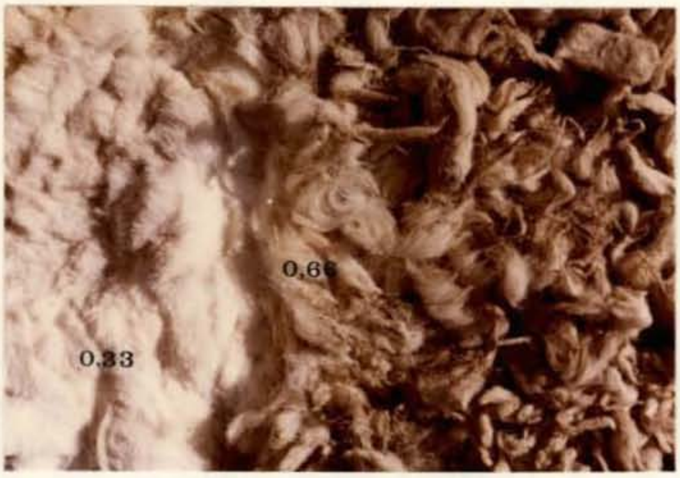


l) Gemsbok

Figure 14 Weighted mean absorptance of selected ungulate pelts

m) Steenbok

n) Grysbok



o) Namaqua-Afrikaner sheep

Figure 14 Weighted mean absorptance of selected ungulate pelts

absorptance value than the adult. Furthermore, 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 also 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 of 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 ~~all~~ 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 ~~allows~~ 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 ambient 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 and 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 sweating and would therefore 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 black 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 allows wide fluctuations in its body temperature (adaptive hyperthermia) and as a result, conserves water very efficiently. He has 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. To this I would like to add 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 (based on body size) pelage thickness. 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. Nevertheless, the thin pelage represents a serious disadvantage and the reasons for this adaptation are complex and, as stated previously, are probably involved in the superior sprinting ability of this species. These factors will be discussed in detail in Chapter 3.

As described previously, Hutchinson and Brown (1969) and Cena and Monteith (1975c) maintain that short-wave radiation is not absorbed on the surface but penetrates the fur to varying 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.

In Fig. 15 I have illustrated skin and surface temperatures, measured on three different areas of a bontebok's pelt. From 9h00 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 fawn fur exhibited a heat load between that of the white and dark-brown fur. The fawn fur, however, was slightly thicker than the white or dark-brown fur and this factor contributed towards a reduced heat load at skin-level. In contrast, Fig. 16 shows that the heat load on the skin covered by the white and fawn fur became approximately equal, when windspeed increased. During these measurements, windspeed fluctuated between 2-4 m s^{-1}. The penetrance of radiation was greater into the sparse, white fur than into the denser fawn fur. Nevertheless, at low windspeeds, the lower absorptance of the

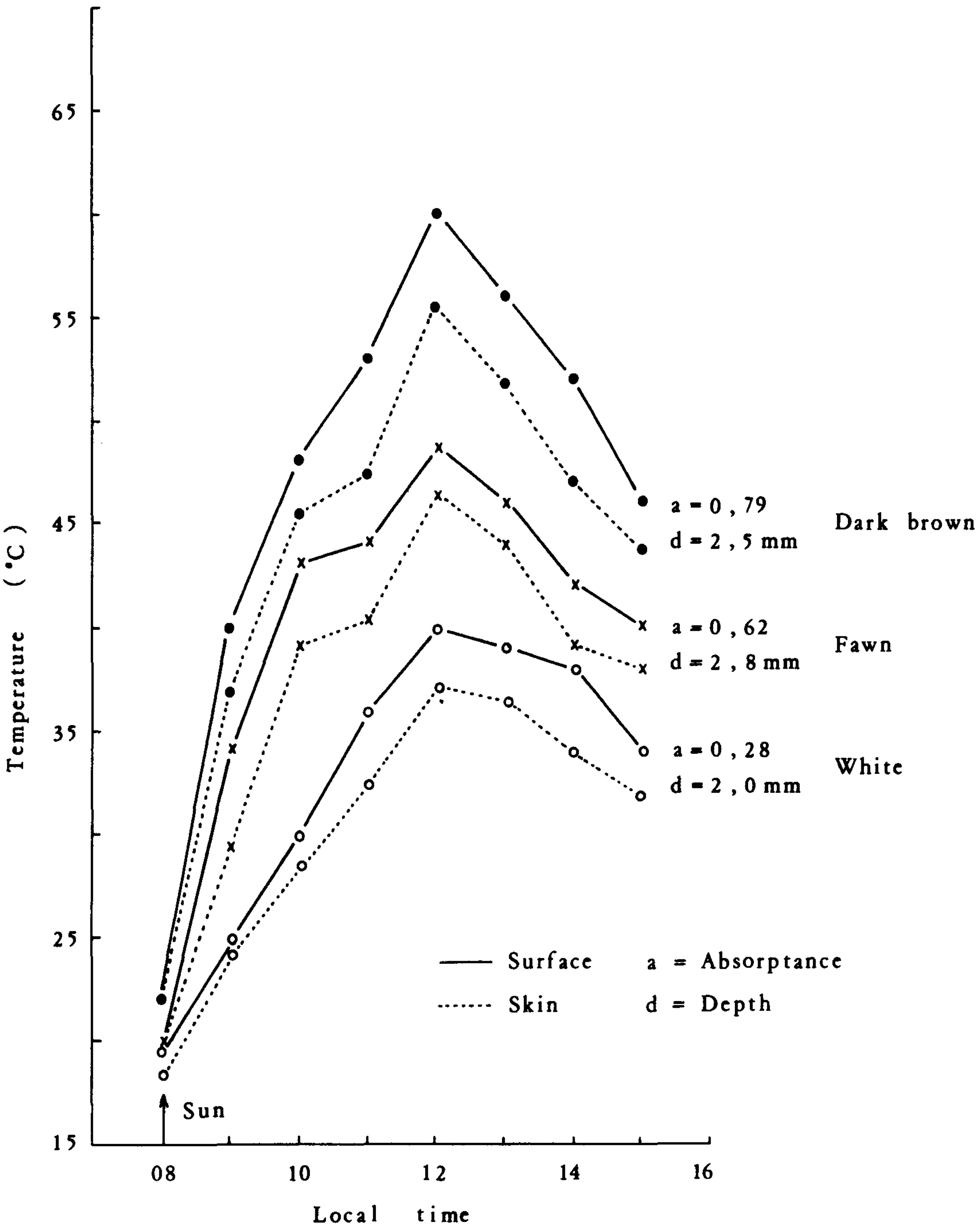


Figure 15 The heating effect of the sun upon the surface and skin of three differently coloured areas on the bontebok's pelt when windspeed was low

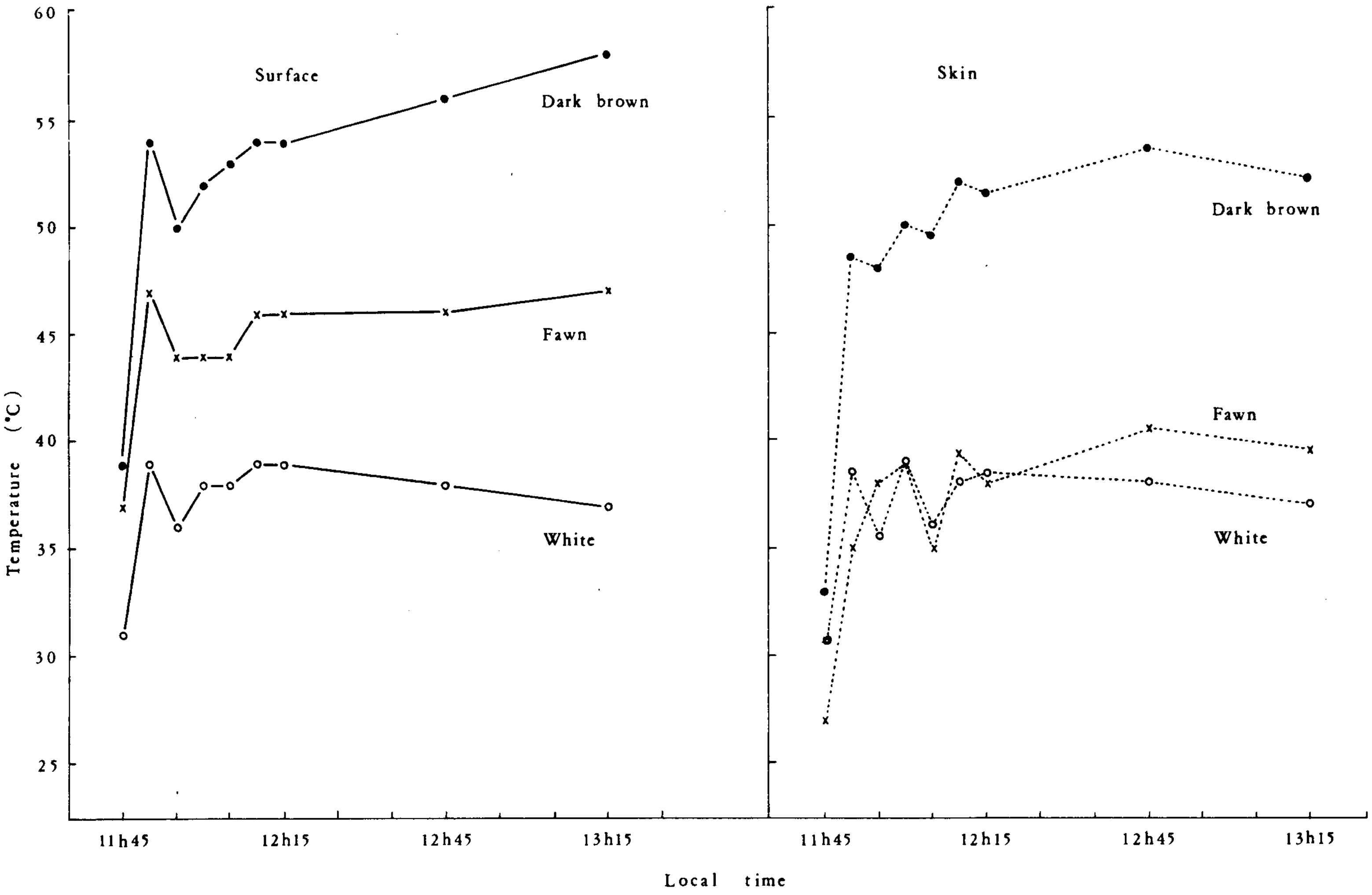


Figure 16 The heating effect of the sun upon the surface and skin of three differently coloured areas on the bontebok's pelt when windspeed was high

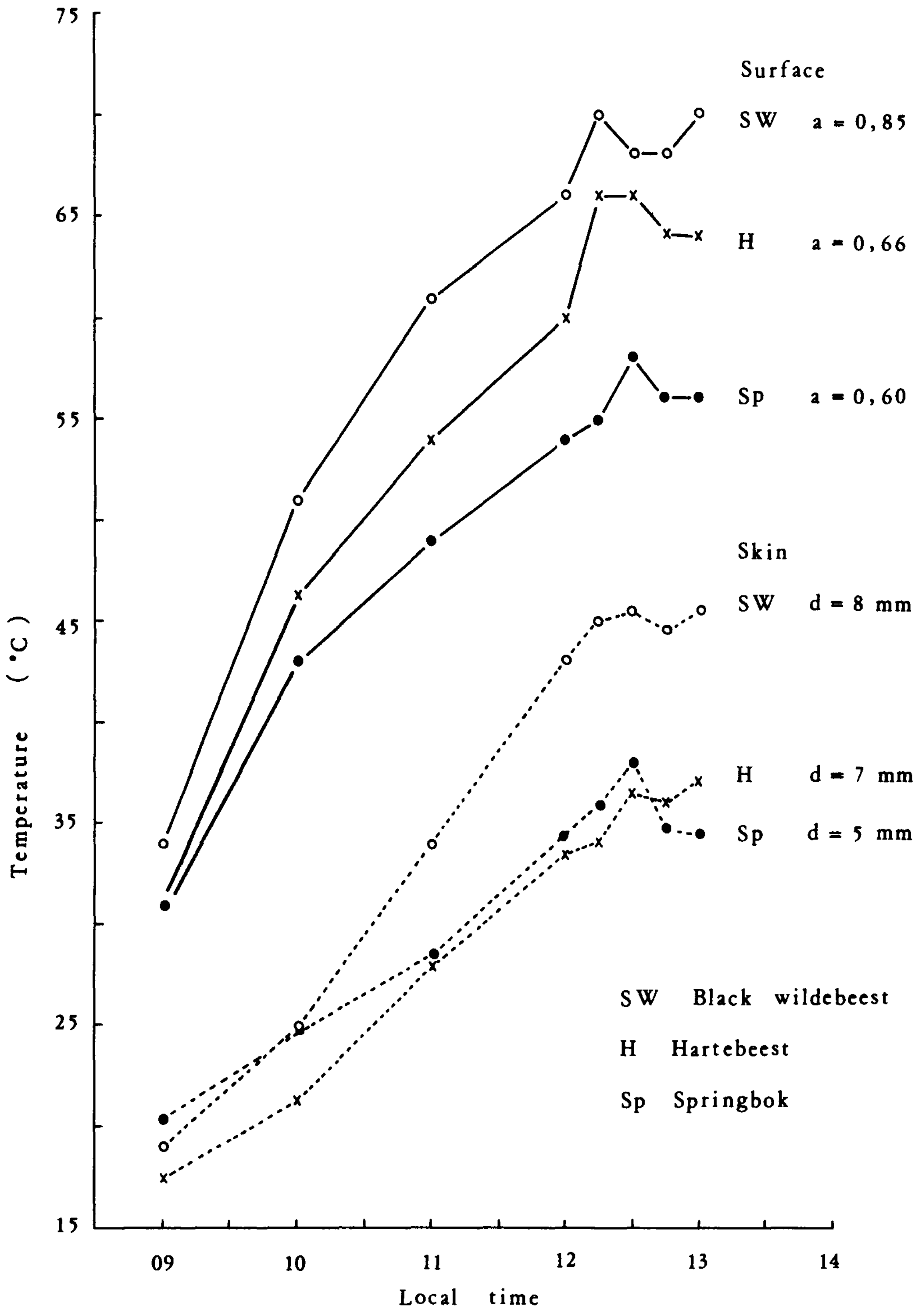


Figure 17 The effect of solar radiation on the surface and skin temperatures of three different pelts

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, fawn and white furs had approximately the same heat load. The same general phenomenon was reported by Hutchinson and Brown (1969). Finally, Fig. 17 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. In the wildebeest experiment, windspeed never exceeded 1 m s^{-1}.

CONCLUSIONS

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

2. Thermal conductivities of pelts which had a thickness between 1 and 45 mm, ranged from 22,4 - 74,5 mW m^{-1} K^{-1}. The very thin pelages had a conductivity lower than that of still air and the conductivities increased with increasing pelage thickness. Radiation and free convection contributed towards the increasing heat transfer in thicker pelts. This might be due to a lowered interception function for radiation which results when the angle between the hairs and the normal to the skin decreases.

3. Thermal conductance decreased with increasing pelage thickness. Thus the effect of a thicker insulation was greater than the increase in conductivity. The relationship between thermal resistance and pelage thickness was linear but when pelages thicker than *ca.*24 mm were included, a power curve gave a better coefficient of determination.

4. 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.

5. 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. The effective thickness of a 24 mm pelage at 4 m s^{-1} was 60% of the effective thickness at 0 m s^{-1}, while that of a 1 mm pelage was only 18%.

6. 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.

7. A knowledge of the physical 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.

CHAPTER 2

PHYSIOLOGICAL THERMOREGULATION AND PHYSICAL HEAT EXCHANGE IN NAMAQUA-AFRIKANER SHEEP IN A NATURAL ENVIRONMENT

INTRODUCTION

Thermoregulation in mammals has in the past been studied mainly under artificial conditions, created in the laboratory. In many of those experiments the effects of solar radiation and wind have been neglected and consequently, the results obtained in an outdoor environment have often differed from those obtained in the laboratory. For example, Taylor (1969) has shown in laboratory studies that respiration rate in the eland is positively correlated with body temperature. In contrast, Finch (1972a) found in a field situation that variations in skin rather than body temperature influenced evaporative cooling in the eland and hartebeest. Despite the fact that the thermal environment outdoors is very complex, certain aspects of thermoregulation can best be studied under such conditions.

Until recently only a few researchers have attempted to measure all the components of a heat balance for any specific animal. Porter and Gates (1969) have made a valuable contribution as they have described methods for determining the energy balance of animals in the field. However, their calculations, obviously based on incorrect assumptions, suggested that sheep cannot endure air temperatures greater than *ca.* 24°C for long, when they are subjected to solar radiation and a windspeed less than $1\ m\ s^{-1}$. Subsequently, other researchers suggested certain improved methods and Finch (1972 and 1976) successfully evaluated the various avenues of heat gain and loss in the eland, Coke's hartebeest and Boran cattle. She concluded that the heat absorbed at the fur surface can be more than nine times that produced by metabolic heat. However, most of the former heat load was reradiated back to the environment and lost by convective cooling. Therefore, in an outdoor environment, the primary compensation for a high heat load appears to be by physical processes which occur automatically on the external surface of the animal.

The purpose of this study was first of all to investigate basic physiological thermoregulatory responses in an outdoor environment and to compare these results with those obtained in the laboratory. Secondly, I wished to study the thermal interaction between the animal and the environment and to assess the importance of various avenues of heat loss and gain, both physical and physiological. Finally, I have attempted to calculate a total heat balance for the animals to test the practicability and accuracy of the various proposed methods. I decided to use Namaqua-Afrikaner sheep as experimental animals for the following reasons. This animal is indigenous to the drier areas of South and South West Africa and, therefore, represents a true semi-desert breed. Southern Africa contains a large proportion of semi-desert areas where the husbandry of such breeds can be of great importance. Furthermore, the pelage characteristics of sheep offer great potential for studying the physical properties involved in heat exchange. For example, the thickness and colour can be altered by shearing and, finally they are easy to handle and are therefore ideal experimental animals for the many delicate measurements which a heat balance study involves.

PROCEDURE

Experiment 1 - Physiological thermoregulation in sheep

Two Namaqua-Afrikaner sheep were used in this study which was conducted on the farm Vrolijkheid (19° 53'E, 33° 55'S), situated in the Little-Karroo region in South Africa. The animals were kept outdoors in crates constructed of thin steel piping, which restricted them to one position and provided a minimum amount of shade. The crates were erected on hard-packed soil and were orientated in a North-South direction, with their heads facing North. Both animals were subjected to a training period of several months and submitted calmly to all experimental procedures. The measurements were taken on nine different days, spread over a period of three months (February, March and April). During the study period, the animals received food and water *ad lib*.

The following environmental and physiological measurements were recorded on an hourly basis. Ambient temperature was measured in the shade with a S.A.B.S. approved mercury thermometer and I calibrated all the YSI thermister probes which were used, against this thermometer. The thermister probes were connected to a YSI telethermometer and were used to measure sun, ear and rectal temperatures. An air-temperature thermister probe No. 405 was attached to the crate to determine sun temperature while a general purpose probe No. 401 was inserted to a depth of 10 cm into the rectum to measure rectal temperature. Ear temperature was measured with a surface temperature thermister probe No. 409. This probe was attached with surgical tape to the inside of one ear, midway between the base and tip. A Barnes infrared thermometer was used to measure the surface temperature of the sheep's fleece. The average surface temperature was calculated from eight measurements, of which four were taken dorsally and two on each lateral surface. The respiration rate of the animals was recorded from visual counts of the movements of the thoracic cage with the help of a stop-watch. I checked the accuracy of this method with a pneumograph belt, connected to a Washington oscillograph. A wet and dry bulb swinging hygrometer was used to calculate relative humidity. The windspeed was determined with a three-cup anemometer which was erected at the same height above the ground as the sheep's dorsal surface. Finally, I made notes on the general sun and shade conditions and estimated the proportion of the sky covered by clouds (fractions of eight) during each reading.

Experiment 2 - Heat balance studies

The same two sheep were used in these experiments which were also conducted on the farm Vrolijkheid. The winter data were obtained during July (solar declination: + 21,8°) on three consecutive days. The sheep were fully fleeced and were used alternatively on each day. The experimental animal was given water *ad lib.*, but was not fed 16 hours prior to and during the experiment. The summer data were obtained on four consecutive days during December (solar declination: -23,22°). For this experiment, one of the sheep was shorn while the other one was left fully fleeced. Both animals were restrained in crates during the day but only one was subjected to the full spectrum of measurements. Certain of the measurements were also recorded simultaneously on the second sheep.

The equation describing the heat balance for an animal in the sun includes the following components; metabolic heat, net radiation, convection, conduction, evaporation and stored heat. I shall now discuss the various methods used to measure and calculate the contribution made by each of these components in the sheep's heat balance.

Radiative heat exchange:

The radiant heat which participates in the energy balance of animals covers a wavelength range of *ca.* 0,2 - 80 µm. It is customary in physiology to divide the spectrum into a short-wave region (wave lengths $< 2 - 3$ µm) and a long-wave region (wavelengths $>2 - 3$ µm). However, the division is based purely on a difference in the optical properties of animal coats in the two regions (Mitchell 1974). The short-wave radiation impinging on an animal can be divided into three components, namely direct solar radiation (S), diffuse radiation (s) from the sky and clouds and reflected radiation (rg (S + s)) from the ground and terrestrial objects. The long-wave radiation exchange includes thermal radiation from the atmosphere (La) and from the ground (Lg) as well as the amount of radiation emitted by the animal's surface (Ls). However, the radiative exchange of the animal with its surroundings depends not only on the radiation intensity but also on the surface area (A) involved in the exchange and the absorptance (a) of the surface for short- and long-wave radiation. Therefore, the portion of the potential radiation actually absorbed by the animal, can be described as the effective radiative heat load (R abs). In this experiment the equations used to calculate radiative heat exchange are similar to those described by Porter and Gates (1969), Finch (1972 and 1976) and Hutchinson *et al.* (1976).

$$R\ abs = a1\ Ap\ {}^{S}/_{\sin\theta} + a1\ Aa\ s + a1\ Ag\ rg\ (S+s) + a2\ Aa\ La + a2\ Ag\ Lg$$

where

a1 = absorptance for short-wave radiation

a2 = absorptance for long-wave radiation

Ap = profile area directed towards direct solar radiation

Aa = surface area exposed to diffuse atmospheric radiation

Ag = surface area exposed to diffuse ground radiation

rg = reflectance of ground for short-wave radiation

θ = solar elevation

The total incident short-wave radiation from the upper hemisphere was measured with a Kipp's solarimeter which was mounted 0,75 m above the ground. A small black shield was used to obscure the direct rays from the sun and in this way, diffuse radiation from the sky was measured. Thus by subtracting the diffuse component from the total radiation, the intensity of direct solar radiation was obtained. The solarimeter was rotated through 180° to measure the short-wave radiation reflected from the ground. The intensity of long-wave radiation from the ground and atmosphere, was calculated by empirical formulae. According to Monteith

(1973) most natural surfaces can be treated as 'full radiators' and thus the Stefan-Boltzmann law was used to calculate the intensity of long-wave radiation from the ground.

$$Lg = \sigma \bar{T}g^4$$

where

$\bar{T}g$ = mean ground surface temperature (K)

σ = Stefan-Boltzmann constant ($5{,}6697 \times 10^{-8}$ Wm^{-2} K^{-1})

A Barnes infrared thermometer was used to measure the ground surface temperature. The mean temperature was calculated from six measurements of which two were taken underneath the animal and the rest at a two-metre distance from the animal in front, behind and on both sides. The sky does not function as a 'full radiator' but atmospheric radiation can be expressed as a fraction of full radiation at 'screen temperature (σ Ta^4)' (Monteith 1973).

$$La = Ea \sigma Ta^4$$

where

Ta = air temperature

Ea = emissivity of the atmosphere.

The emissivity of the atmosphere is affected by the cloud cover and therefore, different empirical formulae should be used for clear and cloudy skies. I used the following formulae proposed by Monteith (1973) to calculate long-wave atmospheric radiation.

Clear skies:

$$Ea\ (0) = 0{,}53 + 0{,}06\ \sqrt{e}$$

Cloudy skies:

$$Ea\ (c) = Ea(0)\ (1 + nc^2)$$

where

e = vapour pressure (mbar)

c = the fraction of the sky covered by cloud and n ranges from 0,04 - 0,2 depending on the cloud type.

The vapour pressure was obtained by multiplying relative humidity with the saturation pressure at the relevant ambient temperature. The latter was measured with a S.A.B.S. approved mercury thermometer and the saturation pressure was obtained from tables. A wet and dry bulb swinging hygrometer was used to determine relative humidity.

The mean absorptance for short-wave radiation for the shorn and unshorn sheep was measured by the method described in the previous chapter. Although the direct solar beam, diffuse sky radiation and radiation reflected from the ground have different spectra (Hutchinson *et al.* 1976) and thus the absorptance of a pelt would differ for the three short-wave components, I used the same mean absorptance in all three cases. Also, I followed the example of Porter and Gates (1969) and Finch (1972 and 1976) and assumed that the absorptance for long-wave radiation is equal to 1,0.

The total skin (Ask) and pelage surface (As) areas of the animals were calculated by means of a method described by Moen (1973). Each animal was regarded as a series of cylinders and the measured length and circumference of each cylinder were used to calculate the appropriate surface area (Fig. 18). In each instance, the circumference was measured over the skin and over the wool and therefore, total skin and total wool surface area could be determined.

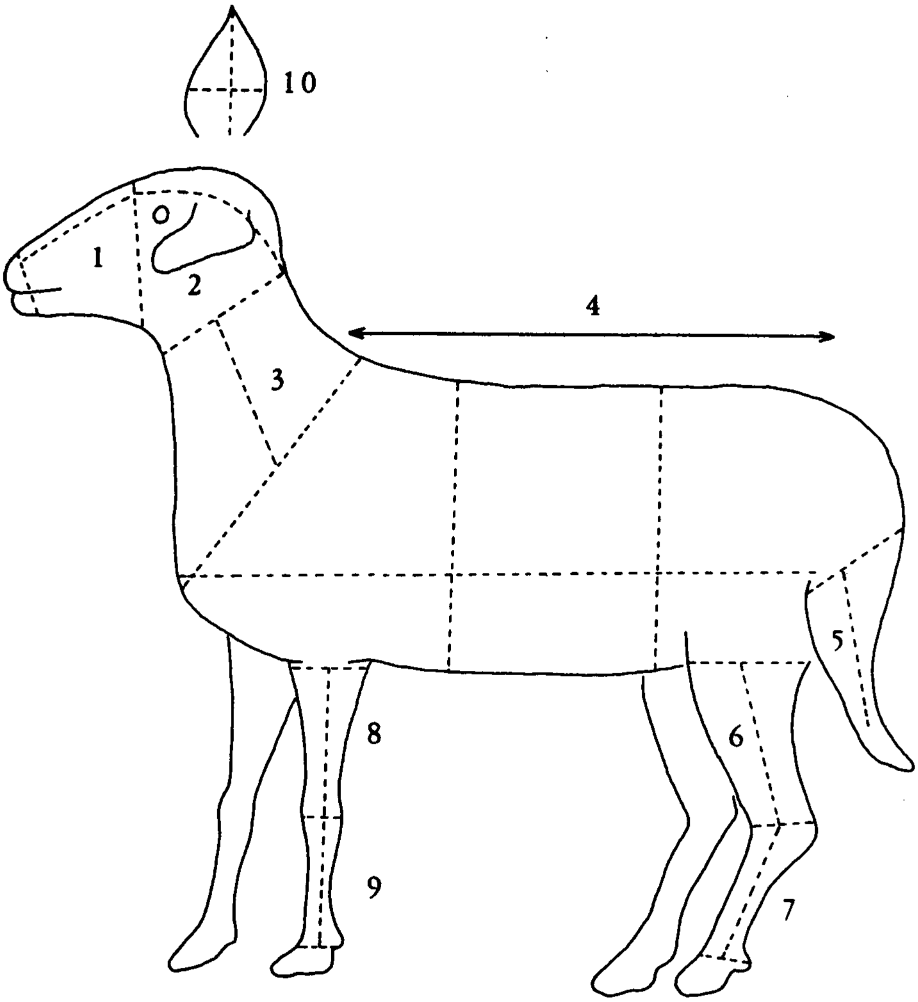


Figure 18. The division of the sheep's body into series of cylinders to determine total surface area

Clapperton *et al.* (1965) calculated the surface area exposed to diffuse radiation for sheep and expressed it as a percentage of the total skin area, calculated from Mitchell's (1927) formula $A = 0{,}09\ W^{2/3}$ (where W = animal's weight in kg). They found that the exposed area of shorn sheep was 85% whereas it was 119% for fleeced sheep. Furthermore, according to Porter and Gates (1969) diffuse radiation from the sky involves the upper half of the animal's body while diffuse radiation from the ground, involves the lower half of the animal's body. Therefore, all types of diffuse radiation are only involved with half the exposed surface area of the animal. In this experiment, I calculated Aa and Ag as

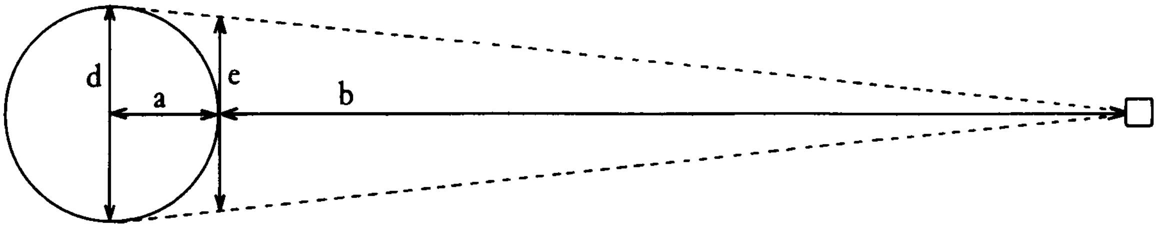
$$Aa = Ag = \frac{0{,}85\ As}{2}$$

The surface area exposed to direct solar radiation was measured and calculated in the following ways

1. The horizontal shadow area (Ah) of the sheep was outlined on a large sheet of paper at each relevant solar azimuth and angle of elevation. The shadow area was then cut out and measured on a planimeter. Finally, Ah was multiplied with the sine of the solar elevation, to convert it to the profile area normal to the sun.

2. Radiation profiles (Ap) were determined by photographing the sheep at different azimuth and elevation angles. A piece of cardboard of fixed dimensions was placed next to the sheep at an equal distance from the camera. The photographs were then enlarged and subsequently, the surface areas of the sheep and reference surface (cardboard)

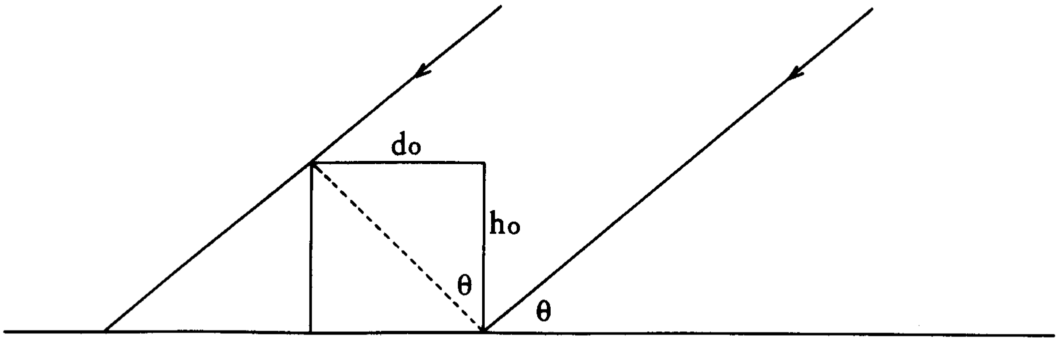
were determined on a planimeter. The ratio of the true surface area of the reference surface and the measured value from the photograph provided an enlargement factor with which the surface area of the sheep on the photograph could be multiplied. Furthermore, to make allowance for parallax, I followed the example of Clapperton *et al.* (1965) and determined a parallax correction factor (Fig. 19).



Parallax correction factor (PCF) = $\left(\frac{a + b}{b} \right)^2$

Figure 19. Determination of the parallax correction factor.

The PCF was then multiplied with the computed surface area of the sheep to obtain Ap. When taking the photographs, I made use of trigonometric calculations to determine the appropriate elevation angle and later used the technique of Clapperton *et al.* (1965) to determine the exact elevation angle from which the photograph was taken. For each photograph, a cylinder with its height equal to its diameter was placed next to the sheep. The apparent height (ho) and diameter (do) were subsequently measured on the photograph and the simulated solar elevation (θ) was determined determined from these measurements (Fig. 20).



$$\tan \theta = {}^{do}/ho$$

Figure 20. Determination of the solar elevation on photographs

The last component in the animal's radiative heat exchange with the environment, is the reradiation from the animal's surface. The following equation was used to calculate the amount of radiant energy involved.

$$Ls = Ar \ E\sigma \ \bar{T}_s^{\ 4}$$

where

Ar = o,85 As

$\bar{T}s$ = mean surface temperature

The surface temperatures were measured with a Barnes infrared thermometer and the mean was averaged from six readings taken around the circumference of the animal's body.

Convective heat loss:

Air is a very good thermal insulator and therefore, conduction was considered negligible. However, convection can be an important mode of heat loss, although the basic transfer process remains one of conduction. A fundamental analysis of convective transport can be extremely complicated and for this reason many researchers have used an empirical approach. Convective heat loss is a function of windspeed, the size of the animal, the temperature difference between the pelage surface and the air and certain properties of air. All these variables have been incorporated into dimensionless groups which can be used to calculate convective heat transfer (Monteith 1973 and Campbell 1977). In this experiment, convective heat loss was calculated in the following way. The windspeed was measured with a three-cup anemometer which was erected at the same height above the ground as the animal's body. The meterage was recorded over a 20 minute period to get an average windspeed. In addition, mean surface temperature and ambient temperature were recorded during each observation. Subsequently, the Grashof number (Gr) and the Reynolds number (Re) were calculated and I used the criteria proposed by Monteith (1973) to determine whether free or forced convection dominated. If free convection dominated, I used the following equations to determine Nusselt number (Nu).

$$\mathrm{Nu} = 0{,}48\ \mathrm{Gr}^{0{,}25} \quad \text{when } 10^4 < \mathrm{Gr} < 10^9$$

or

$$\mathrm{Nu} = 0{,}09\ \mathrm{Gr}^{0.33} \quad \text{when } \mathrm{Gr} > 10^9 \quad \text{(Monteith 1973)}$$

However, when forced convection dominated, I used the relationship $\mathrm{Nu} = 0{,}65\ \mathrm{Re}^{0{,}5}$ which Monteith (1973) calculated from measurements on sheep. Finally, convective heat flux density (C) was determined from the equation

$$C = \frac{Nu \ \rho cp \ DH}{d} \ (\bar{T}s - Ta)$$

where

ρcp = volumetric heat capacity of air ($J \, m^{-3} \, K^{-1}$)

DH = thermal diffusivity of air ($m^2 \, s^{-1}$) and

d = diameter of animal's body (m)

Metabolic rate and evaporative water loss:

The oxygen consumption and respiratory water loss were measured using an open flow-through system (Fig. 21). Ambient air was sucked through the system using a high-speed vacuum pump and a Rotameter (Series 1100 flow-meter) to measure and set the required flow rate. A series of cylindrical containers, filled with drierite (Calcium sulphate) or silica gel were connected into the system and the dried air was collected in a meteorological balloon. During each determination, the procedure was as follows. First of all, ambient air was pumped through the system so that ambient water was absorbed in the tubes and dried ambient air was collected in the first balloon. Thereafter, the procedure was repeated with the animal in the system and in this instance both ambient and expired water were collected in the tubes while the dried air in the second balloon was a mixture of ambient and expired air. During the winter experiments, I maintained a flow rate of *ca.* 15 l min^{-1} and the sampling period lasted 10 minutes. However, during the summer experiments the flow rate had to be increased to *ca.* 25 l min^{-1} to accommodate the higher respiration rate and therefore, the sampling period was reduced to four minutes. The air collected in the meteorological balloon was then pumped through a volume meter and the air temperature and total volume were recorded. The barometric pressure was obtained from a calibrated aneroid barometer and consequently, flow rate at STP could be calculated. Subsamples of the ambient air and mixed air, collected in the meteorological balloons were collected in 50 ml syringes before injection into an Oxygen Analyser.

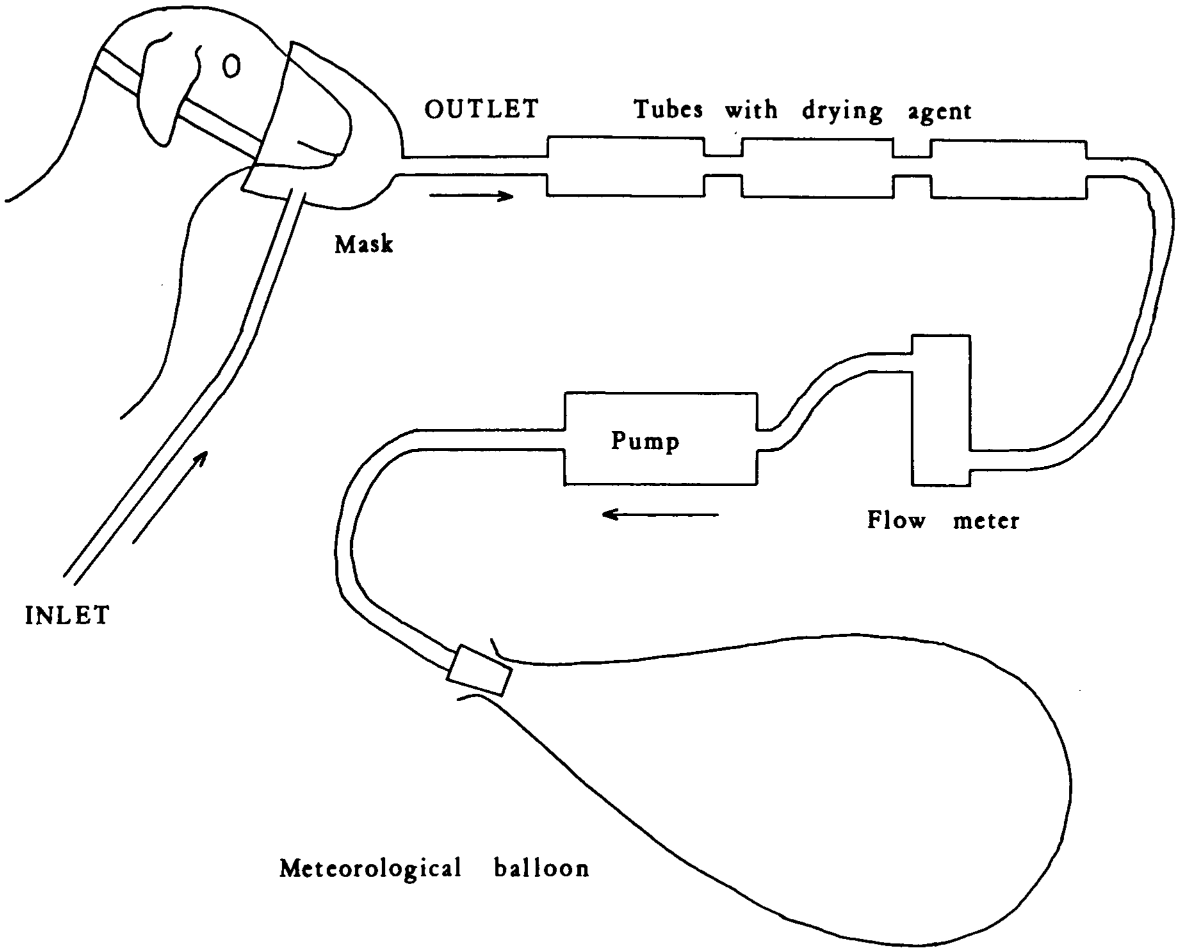


Figure 21 The open flow-through system for determination of oxygen consumption and respiratory water loss.

By weighing the drierite tubes before and after the above procedure, the water content of the ambient and expired air could be calculated. However, I suspected that all the water in the air was not being absorbed by the drying agent. I therefore decided to use a method described by Withers (1977) to determine both the water and oxygen content of the balloon air.

The syringes, filled with ambient and mixed air from the meteorological balloons, were analysed in a Beckman Oxygen Analyser (OM 13). The air was injected into the analyser through various filter combinations which either absorbed CO_2 (soda asbestos) or H_2O (drierite), or both. Consequently, the following measurements could be obtained.

O_2% amb. $(-CO_2 - H_2O)$
O_2% amb. $(+CO_2 + H_2O)$
O_2% mix. $(-CO_2 - H_2O)$
O_2% mix. $(+CO_2 - H_2O)$
O_2% mix. $(+CO_2 + H_2O)$

where

amb. = ambient air, and
mix. = mixed air.

The measured flow rate (FR meas) of the ambient air indicates the flow rate of a volume of air which contained O_2, CO_2, N_2 and H_2O (not absorbed in the drierite tubes). Furthermore, the O_2% of this volume of air is indicated by O_2% amb. $(+CO_2 + H_2O)$. However, the CO_2 content of ambient air is negligible. Therefore,

$$0_2\% \text{ amb. } (+CO_2 + H_2O) = \frac{0_2 \cdot 100}{0_2 + N_2 + H_2O}$$

$$\text{Therefore} \quad 0_2 + N_2 + H_2O = \frac{0_2 \cdot 100}{0_2\%} = FR \ (+ H_2O)$$

$$= FR \ (\text{meas.})$$

The $0_2\%$ in the volume of air where H_2O and CO_2 were removed, is given by $0_2\%$ amb. $(-CO_2 - H_2O)$.

$$\text{Therefore,} \quad 0_2\% \text{ amb. } (-CO_2 - H_2O) = \frac{0_2 \cdot 100}{0_2 + N_2}$$

$$\text{Therefore} \quad 0_2 + N_2 = \frac{0_2 \cdot 100}{0_2\%} = FR \ (-H_2O)$$

Furthermore,

$$\frac{FR\ (-H_2O)}{FR\ (+H_2O)} = \frac{0_2 \cdot 100}{0_2\% \text{ amb. } (-CO_2 - H_2O)} \times \frac{0_2\% \text{ amb. } (+CO_2 + H_2O)}{0_2 \cdot 100}$$

Therefore

$$FR\ (-H_2O) = \frac{0_2\% \text{ amb. } (+CO_2 + H20)}{0_2\% \text{ amb. } (-CO_2 - H_2O)} \times FR\ (+H_2O)$$

Therefore, the amount of water in ambient air still present in the balloon air is:

$$FR\ (+H_2O) - FR\ (-H_2O) = H_2O \text{ in balloon (STP)}$$

This volume of water was in each instance converted to mass, by multiplying by $^{18}/22,4$.

The same procedure was followed to calculate the volume of water in the balloon containing the mixed air. Consequently, the volume of water in the balloon, derived from the expired air, can be calculated by difference. Therefore, the total volume of expired water consists of the sum of the expired water absorbed in the drierite tubes and the expired water which was collected in the meteorological balloon. Unfortunately, however, during the summer experiments the water content of the air in the balloons was not determined. I therefore decided to bring in a correction factor, which was based on the results of the winter experiments. For all the winter determinations I calculated the water absorbed by the drierite tubes as a percentage of the total water and then determined the mean percentage. Subsequently, this mean percentage was used to correct the summer values obtained from the drierite tubes. However, the question then arose as to whether the drierite used in the summer experiments at the higher flow rate had the same drying potential as the drierite used in the winter experiments. I therefore decided to check the effectiveness of the drierite in the following manner. According to Monteith (1973) water vapour pressure and water vapour concentration can be related:

$$\chi = \frac{217e}{T}$$

where

χ = water vapour concentration (mg l^{-1})

e = water vapour pressure (mbar) and

T = ambient temperature (K)

With this equation, I was able to calculate a theoretical ambient water vapour concentration for each sampling period. During the winter experiments, the ambient water absorbed in the drierite tubes was 84%

(mean) of the theoretical ambient water, while it was 81% (mean) for the summer experiments. Therefore, I concluded that the drierite had the same efficacy during the winter and summer experiments. The respiratory water loss was converted to heat loss (Hex) by multiplying by 2416 J g^{-1}.

The O_2 consumption and CO_2 production of the animals were calculated by the methods described by Withers (1977). The amount of metabolic heat produced for each litre of oxygen consumed, was taken as 19,88 kJ $l\ O_2^{-1}$ (based on an RQ of 0,76).

The cutaneous water loss was measured with non-ventilated sweat capsules using drierite as the desiccant. The sweat capsule was applied to a shaved area on the skin in the midflank region. During each sampling period, the sweat capsule was applied to the skin surface for a period of *ca.* 10 - 15 minutes. Subsequently, the cutaneous water loss was calculated from the increase in drierite weight and expressed as heat loss (H cut) in W m^{-2}. In each instance, I used a conversion factor, based on the mean skin temperature. The mean skin temperature was averaged from four measurements which were taken round the circumference of the animal's trunk. I used a Bailey surface thermocouple connected to a Bat-8 thermometer, to measure skin temperatures.

Heat storage:

The amount of heat stored (Hst) was calculated by the equation

$$Hst = W \Delta \bar{T} c \quad \text{(Mount 1979)}$$

where

W = animal's weight (g)

c = mean specific heat of the body ($3{,}5\ J\ °C^{-1}\ g^{-1}$) and

$\Delta\bar{T}$ = change in the mean body temperature of the animal

Furthermore, the mean body temperature of the animal was calculated from measurements of rectal (Tr) and mean skin temperature ($\bar{T}sk$).

$$\bar{T} = 0{,}7\ Tr + 0{,}3\ \bar{T}sk \quad \text{(Mount 1979)}$$

The rectal temperature was measured with a Bailey rectal thermocouple which was inserted to a depth of 10 cm into the rectum, and connected to a Bat 8 thermometer.

Heat balance equation:

The following heat balance equation was used in this experiment.

$$M + Rabs = Ls + C + Hex + Hcut + Hst$$

All the components were expressed in $W\ m^{-2}$. However, Rabs, Ls and C are involved with the pelage surface area, whereas the rest are expressed as heat flux per m^2 skin surface area. Therefore, in the final balancing of the equation, I calculated the heat flux for all the components in Watts, to bear relation to the total animal.

Hourly measurements:

The following environmental parameters were recorded at intervals of one hour during the summer and winter experiments; incident short-wave radiation, ground and ambient temperature, windspeed, relative humidity, cloud cover (fractions of eight) and cloud type. In addition, the following physiological parameters were recorded hourly for the shorn and unshorn sheep during the summer experiments and for the fleeced sheep during the winter experiments; respiration rate and skin, rectal and pelage surface temperatures. Cutaneous water loss was also recorded hourly, but in the summer experiments, this parameter was only recorded for the one animal on which the whole heat balance was being conducted. The metabolic rate and respiratory evaporative water loss were measured during the morning, midday and early afternoon.

RESULTS AND DISCUSSION

Rectal temperature

Sheep are not limited in their distribution to one climatic zone and occur under widely different environmental conditions. In spite of this, many researchers have reported that sheep maintain a very stable deep-body temperature. Bligh and Harthoorn (1965) recorded the deep-body temperature of a variety of East-African ungulates using radiotelemetry and found that of all the animals tested, the sheep displayed the smallest daily fluctuations in body temperature. The sheep with the widest range had a mean body temperature of 39,2°C (38,5 - 40,0°C) while ambient temperature fluctuated between 19 and 27,5°C. As environmental temperature increases, the heat load on an animal obviously increases as well and several authors have reported an increase in rectal temperature with increasing environmental temperature. For example, Lee *et al.* (1941) found that the rectal temperature of sheep rose above normal when air temperature exceeded 32°C. The rectal temperatures of the sheep in their experiment increased by 3,2°C after a seven hour exposure to an environmental temperature of 43,3°C and a relative humidity of 65%. Hofman and Riegle (1977a) exposed shorn and unshorn Dorset ewes for 120 minute periods to air temperatures (Ta) of 25, 30, 35 and 40°C respectively. They found that the shorn sheep had a higher rectal temperature at Ta = 40°C than at all the lower air temperatures, whereas the rectal temperature of the unshorn sheep at Ta = 40°C was only significantly higher than the rectal temperature at Ta = 25°C. Moreover, they found that at all air temperatures, the unshorn sheep had a higher rectal temperature than the shorn sheep.

In the present study, the Namaqua-Afrikaner sheep maintained a fairly stable rectal temperature. Table 6 illustrates the mean rectal temperatures with ranges under various conditions. The minimum and maximum rectal temperatures recorded were 37,6°C and 40,8°C respectively. However, in contrast with the results of other authors recorded in climatic chambers, no significant correlation could be found between the ambient and rectal temperature. Table 7 shows that the rectal temperature of fully-fed sheep A increased significantly with increasing environmental temperature, whereas no significant increase was measured for sheep B. Table 8 shows that in the case of summer starved sheep the rectal temperature of sheep B (fleeced) decreased significantly with increasing environmental temperatures while that of sheep A (shorn) remained at the same level. Thus both shorn and fleeced sheep were able to maintain a stable body temperature in a very hot environment.

Table 6 The mean rectal temperatures (Tr) of the Namaqua-Afrikaner sheep in the various experiments.

Animal	n	$\bar{T}r \pm s$	Tr range	$\bar{T}a \pm s$	Ta range
Fully fed					
Sheep A (F)	44	39,51 ± 0,69	38,50 - 40,80	25,00 ± 6,51	15,0 - 38,9
Sheep B (F)	34	39,45 ± 0,41	38,70 - 40,35	22,12 ± 5,18	12,0 - 31,8
Winter-starved					
Sheep A (F)	11	39,71 ± 0,17	39,4 - 40,0	15,33 ± 4,66	5,5 - 22,0
Sheep B (F)	7	40,16 ± 0,24	39,8 - 40,5	16,89 ± 2,64	11,5 - 19,8
Summer-starved					
Sheep A (S)	32	38,35 ± 0,37	37,6 - 39,2	27,61 ± 4,16	20,2 - 34,5
Sheep B (F)	32	38,08 ± 0,38	37,6 - 38,8	27,61 ± 4,16	20,2 - 34,5

F = Fleeced

S = Shorn

Table 7 The mean rectal temperature (Tr) of fully fed sheep within various ambient temperature ranges (Ta)

	Ta = 10 - 20°C		Ta = 20 - 30°C		Ta = 30 - 40°C	
	Sheep A	Sheep B	Sheep A	Sheep B	Sheep A	Sheep B
$\bar{T}r \pm s$	38,92 ± 0,27	39,37 ± 0,42	39,36 ± 0,54	39,47 ± 0,44	40,44 ± 0,29	39,67 ± 0,12
$\bar{T}a \pm s$	17,47 ± 1,77	17,19 ± 2,38	24,03 ± 2,42	24,46 ± 2,71	35,42 ± 2,92	31,57 ± 0,21
n	10	14	24	17	9	3

Ta = 10 - 20°C vs Ta = 20 - 30°C : Sheep A - $p < 0{,}0025$ H.S.
Sheep B - $p > 0{,}05$ N.S.

Ta = 20 - 30°C vs Ta = 30 - 40°C : Sheep A - $p < 0{,}0005$ H.S.
Sheep B - $p > 0{,}05$ N.S.

Table 8 The mean rectal temperature (Tr) of shorn and fleeced sheep within various ambient temperature ranges (Ta)

	Ta = 20 - 24,9°C		Ta = 25 - 29,9°C		Ta = 30 - 34,9°C	
	Sheep A (S)	Sheep B (F)	Sheep A (S)	Sheep B (F)	Sheep A (S)	Sheep B (F)
$\bar{Tr} \pm s$	38,36 ± 0,44	38,44 ± 0,32	38,40 ± 0,42	38,05 ± 0,30	38,28 ± 0,23	37,79 ± 0,19
$\bar{Ta} \pm s$	22,99 ± 1,21		26,80 ± 1,15		32,63 ± 1,17	
n	10		11		11	

Ta = 20 - 24,9°C vs Ta = 25 - 29,9°C : Sheep A - $p > 0,05$ N.S.

Sheep B - $p < 0,01$ S

Ta = 25 - 29,9°C vs Ta = 30 - 34,9°C : Sheep A - $p > 0,05$ N.S.

Sheep B - $p < 0,025$ S

Pelage surface temperature

In Chapter 1 I demonstrated that the pelage of the Namaqua-Afrikaner sheep provides very good thermal insulation. This is also illustrated in Fig. 22 in the case of two unshorn sheep exposed to either shade or sun. The surface temperature of these animals was always very close to ambient temperature when the animals were in the shade. Therefore, very little body heat was conducted across the pelage to the environment. However, when the animals were exposed to solar radiation, the pelage surface temperature increased to as much as 30°C above ambient temperature. Moreover in the presence of sunlight, the difference between pelage surface temperature and ambient temperature varied considerably. This was due to the changing intensity and angle of solar radiation and fluctuating windspeed, which all influence surface temperatures profoundly.

Figure 23 shows the surface temperatures of the shorn and fleeced sheep which were measured under the same changing environmental conditions. When windspeed was less than 2 m s^{-1}, the fleeced sheep always had a higher pelage surface temperature than the shorn sheep. This was expected, since the absorptance for solar radiation was 0,66 for the fleeced sheep and only 0,33 for the shorn sheep (see Chapter 1). Figure 23 also shows that this difference in pelage surface temperature increased with increasing ambient temperature. The regression coefficients of ambient vs. surface temperature for the fleeced and shorn sheep were 1,21 and 0,79, respectively. This phenomenon can be explained by the difference in pelage thickness. The surface temperature of the fleeced

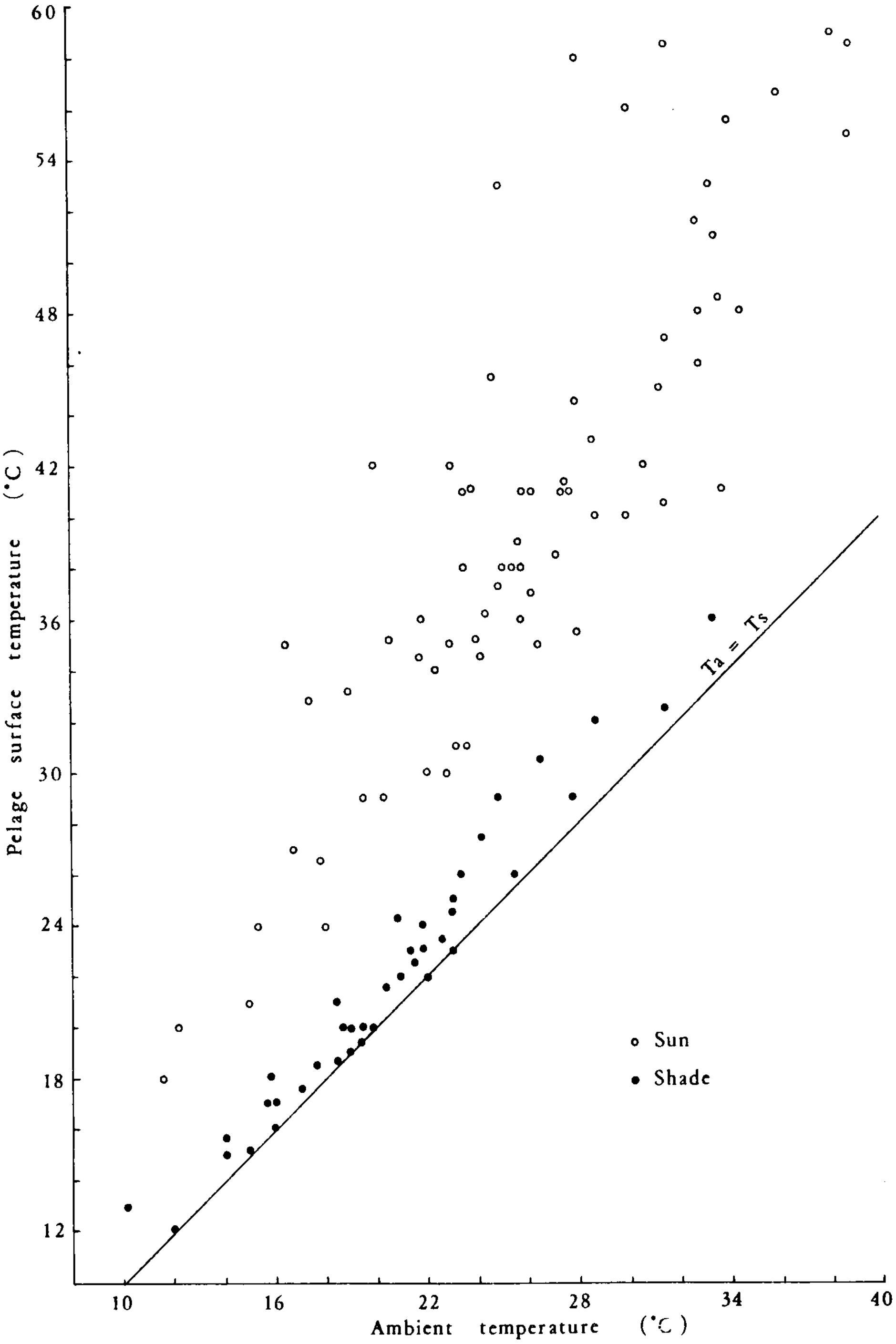


Figure 22 The surface temperatures of two fleeced sheep plotted against ambient temperature while exposed to shade and sun

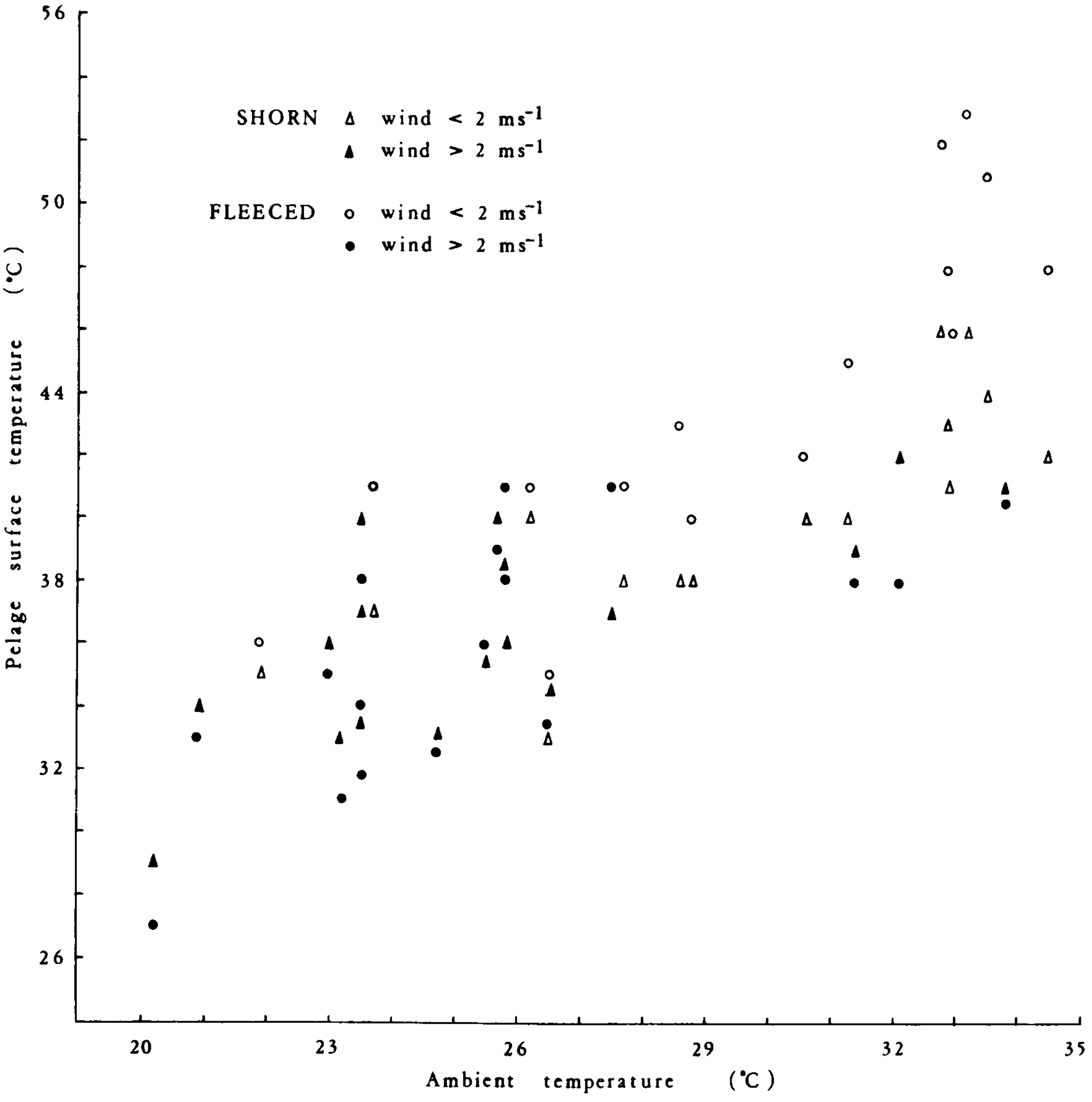


Figure 23 The surface temperatures of a shorn and fleeced sheep measured under identical outdoor conditions

sheep was predominantly determined by environmental factors, whereas the thin pelage of the shorn sheep allowed body heat to be conducted to the environment when the gradient was in that direction. At windspeeds greater than 2 m s^{-1}, the effect of pelage colour became of minor importance and in general the shorn sheep had a slightly higher pelage surface temperature than the fleeced sheep.

Skin and ear temperature

In Table 9 I have presented the mean skin temperature of the fleeced and shorn sheep, measured within different ambient temperature ranges. At Ta = 20 - 24,9°C, the fleeced sheep had a significantly higher skin temperature than the shorn sheep. In this same temperature range both the fleeced and shorn sheep had a higher mean skin temperature than mean surface temperature. The thermal gradient was therefore away from the skin and because of the difference in pelage thickness, heat loss from the skin was greater for the shorn than for the fleeced sheep. Moreover, the cutaneous evaporation for the shorn sheep in this ambient temperature range, was about double that of the fleeced sheep. Therefore, both cutaneous evaporation and sensible heat loss were greater for the shorn sheep and resulted in the lower skin temperature. In the Ta = 25 - 29,9°C range, there was no significant difference between the skin temperature of the fleeced and shorn sheep. Both respiration rate and cutaneous evaporation for the two animals were approximately equal. The latter result suggests that the animals had more or less the

Table 9 The mean skin temperature of the fleeced and shorn sheep within various ambient temperature ranges (Ta)

Animal	Ta = 20 - 24,9°C	Ta = 25 - 29,9°C	Ta = 30 - 34,9°C
Fleeced	37,39 ± 0,62	37,45 ± 0,52	38,20 ± 0,75
Shorn	36,58 ± 0,73	37,71 ± 0,35	39,00 ± 0,68
n	10	9	11

Ta = 20 - 24,9°C	: Fleeced vs. Shorn		$p < 0{,}01$	S
Ta = 25 - 29,9°C	: Fleeced vs. Shorn		$p > 0{,}05$	N.S.
Ta = 30 - 34,9°C	: Fleeced vs. Shorn		$p < 0{,}01$	S
Ta = 20 - 24,9°C	vs. Ta = 25 - 29,9°C :	Fleeced	$p > 0{,}05$	N.S.
		Shorn	$p < 0{,}0005$	H.S.
Ta = 25 - 29,9°C	vs. Ta = 30 - 34,9°C :	Fleeced	$p < 0{,}025$	S
		Shorn	$p < 0{,}0005$	H.S.

same heat load at skin level despite the difference in absorptance and pelage thickness. However, at higher ambient temperatures the fleeced sheep probably had a lower heat load at skin level than the shorn sheep. At Ta = 30 - 34,9°C the skin temperature of the shorn sheep was significantly higher than the skin temperature of the fleeced sheep and for both animals, mean surface temperature was higher than mean skin temperature. Nevertheless, the shorn sheep had a lower cutaneous water loss than the fleeced sheep and, despite the fact that the shorn sheep had the higher respiratory evaporative water loss, total evaporation was slightly lower for the shorn sheep. It seems, therefore, that even at ambient temperatures above 30°C, there was no dramatic difference between the heat load and thermal status of the fleeced and shorn sheep.

Table 9 shows that in the shorn sheep skin temperatures increased significantly at each ambient temperature range, while the increase was only significant between Ta = 24 - 29,9°C and Ta = 30 - 34,9°C for the fleeced sheep. Consequently, ambient temperature and other environmental factors, had a more pronounced effect on the skin temperature of the shorn sheep. Similarly, Precht *et al.* (1973) observed that a good thermal insulation renders skin temperature more independent of ambient temperature.

Skin temperature is not only affected by environmental heat load and cutaneous evaporation, but also by the rate of blood flow through the skin capillary beds. Blaxter (1961) stated that the skin capillaries can either be in a constricted or a dilated condition and that adjustments occur in a restricted range of environmental temperature. He also found that the effect was more pronounced in the animals' extremeties for instance in the ears. This change in vasomotor tone represents one of the more important physiological responses available to an animal to cope with changes in the heat balance within the thermoneutral zone. Blaxter (1961), for example, reported that in sheep the ears were maintained at temperatures slightly above that of the environment, when the environmental temperature was low. With increasing environmental temperature, the temperature of the ears suddenly rose by several degrees and then continued to rise at a slower rate. In his study, this sudden vasodilation occurred when environmental temperature was between *ca.* 21 and 24°C. Blaxter's studies were, however, performed in a climatic chamber in the absence of solar radiation. In my experiments with Namaqua-Afrikaner sheep I was able to discriminate between the effect of ambient temperature and solar radiation (Fig. 24). The results show clearly that the blood vessels were in a dilated condition at much lower ambient temperatures when the animals were exposed to solar radiation. In the case of sheep A, in the absence of solar radiation, the ear temperature was very close to ambient temperature until the latter increased to *ca.* 20°C. A further increase in ambient temperature then resulted in vasodilation. However, for the same animal, the vasomotor reaction had already occurred at an ambient temperature of 15°C, when the animal was subjected to solar radiation. This effect will be discussed in greater detail in the following chapter.

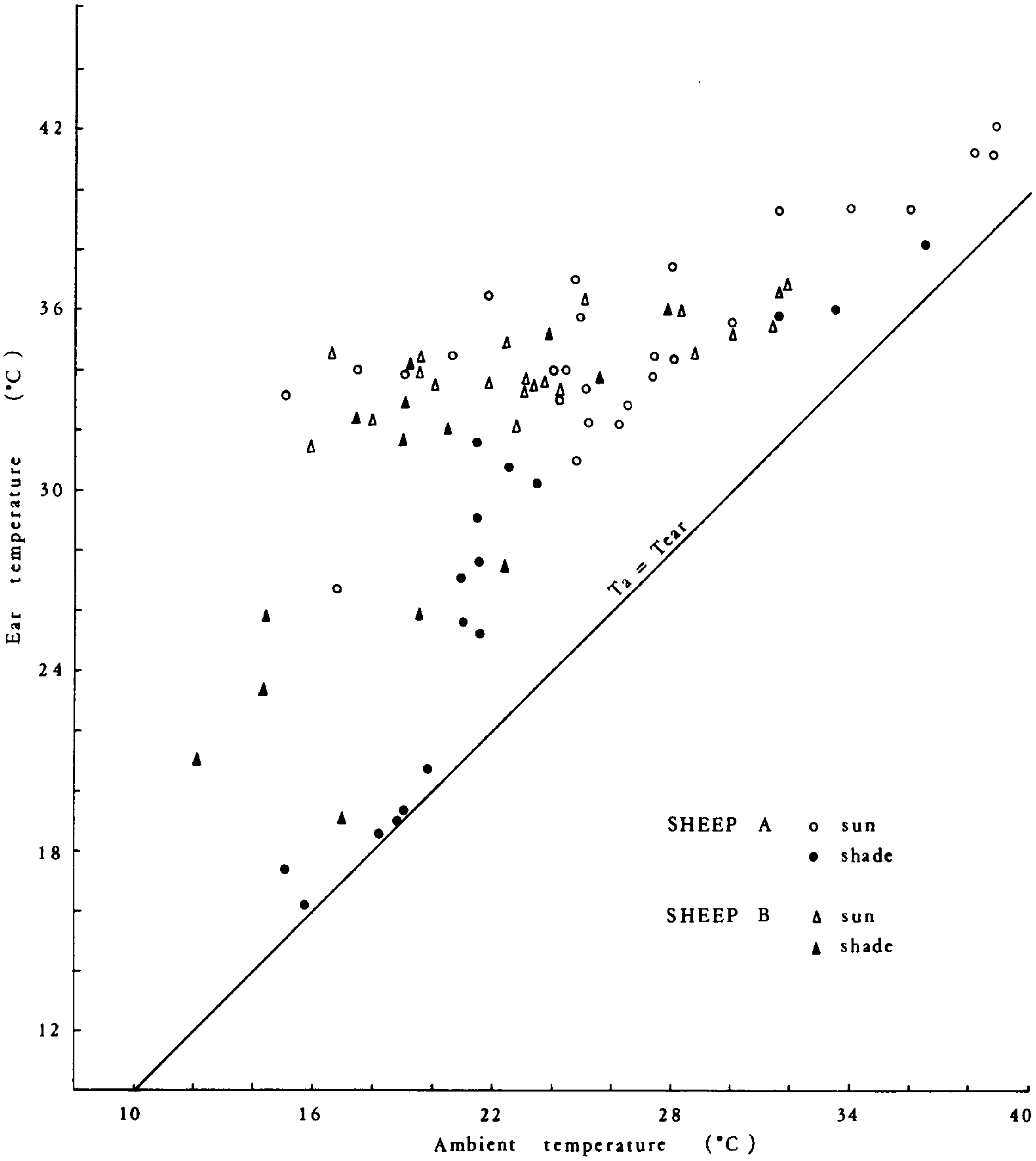


Figure 24 The ear temperatures of two sheep, recorded in the sun and shade at various ambient temperatures

Respiration rate

Sheep are generally regarded as efficient thermal panters and their respiration rate and thus respiratory evaporative water loss (REWL) is closely coupled with environmental heat load. Bligh (1972) is of the opinion that sheep start panting immediately upon exposure to excessive heat and are able to maintain a stable body temperature by evaporative heat loss even when the ambient temperature is equal to or slightly greater than body temperature. The normal respiration rate in a thermoneutral environment for sheep at rest is between 12 and 20 r. min^{-1} (Dukes 1964 and Hales 1973). However, when environmental heat load increases, respiration rate increases as well and two different 'phases' of respiration can be distinguished at high environmental temperatures. Hales (1976) described the two phases as rapid shallow panting (RSP) which is followed by a slower deeper panting (SDP). According to him, RSP is the initial response to high heat load and has a peak value that is on average seventeen times greater than the basal level. This is followed by a decline to *ca.* 70% of the peak rate with excessively high heat loads.

In an outdoor experiment, the heat load on an animal can be much higher than is indicated by ambient temperature alone because of intense solar radiation. On the other hand, convective cooling can alleviate the heat load dramatically. It is thus important to keep the complexity of an outdoor environment in mind when climatic room results and outdoor results are compared. In the present experiment the Namaqua-Afrikaner sheep had a minimum respiration rate of 18 r. min^{-1} and a maximum of

350 r.min^{-1}. The relationship between respiration rate and ambient temperature is indicated in Figs 25 and 26. In all the examples, respiration rate increased with increasing ambient temperature. However, Fig. 25 shows that at any particular ambient temperature, sheep B displayed a greater variation in respiration rate than did sheep A. In fact, for sheep A 85% of the variation in respiration rate can be accounted for by the fitted regression whereas in the case of sheep B only 39% of the variation can be explained by the fitted regression. Furthermore, the regression coefficients were 13,71 and 5,61 for sheep A and B, respectively. Consequently, it is clear that there were individual differences between the two animals and that ambient temperature had a much more pronounced effect on sheep A than on sheep B.

Figure 26 shows the relationship between respiration rate and ambient temperature for the same sheep in a different experiment, when sheep A was shorn and sheep B unshorn. They are referred to as Sheep A'(shorn) and sheep B'(fleeced). In this experiment, respiration rate was recorded for both sheep under identical environmental conditions. It was found that 79% of the total variation in respiration rate could be explained by the fitted regression for sheep A'(shorn) while the figure was only 42% for sheep B'(fleeced). Furthermore, the regression coefficients for sheep A' and B' were 18,04 and 7,64 respectively. It would seem, therefore, that variations in ambient temperature had a more pronounced effect on the respiration rate of the shorn than on the fleeced sheep. However, when the individual differences recorded in the previous experiment with the same sheep are taken into consideration, the importance of fleece

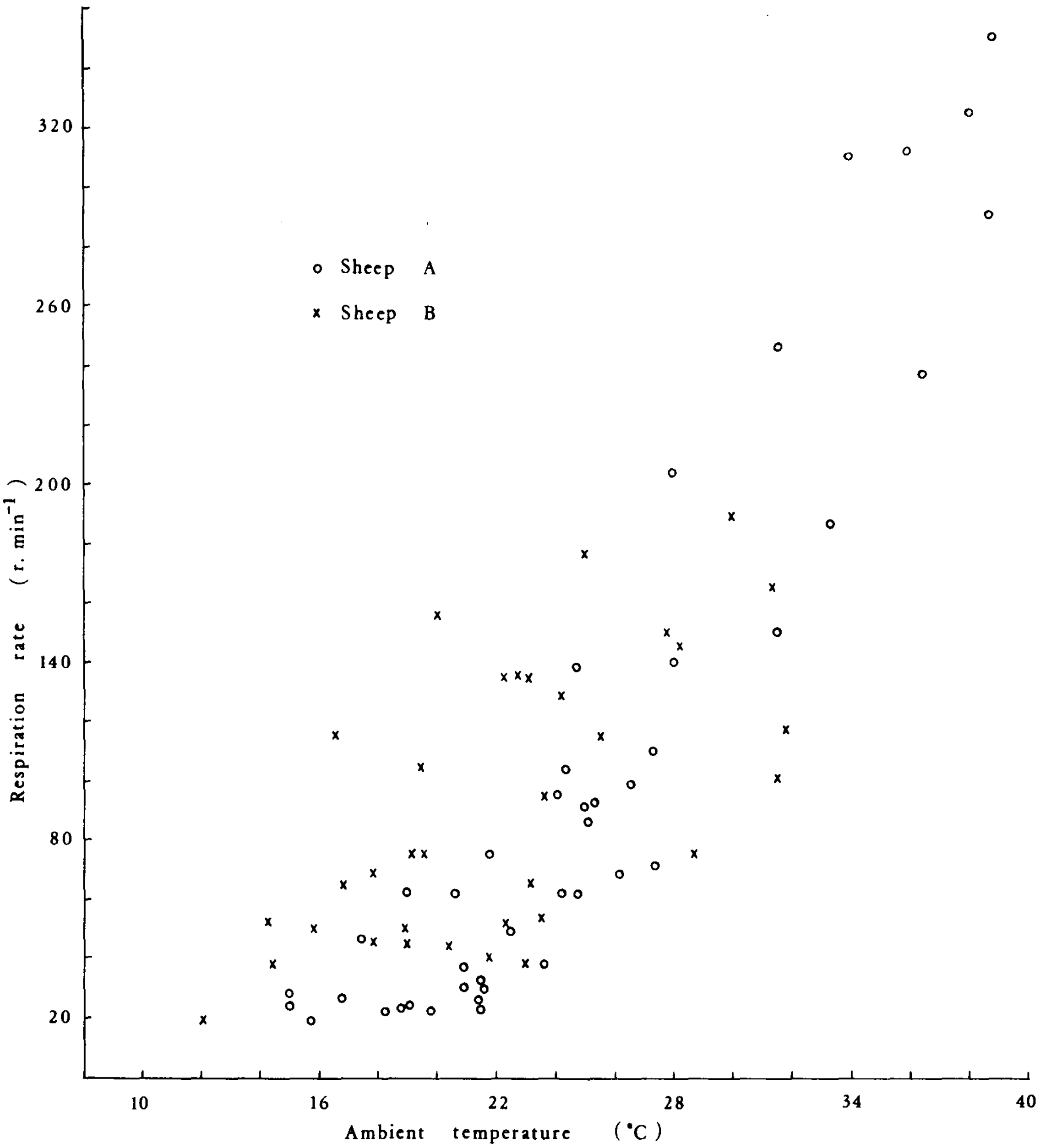


Figure 25 The relationship between respiration rate and ambient temperature for two fleeced sheep

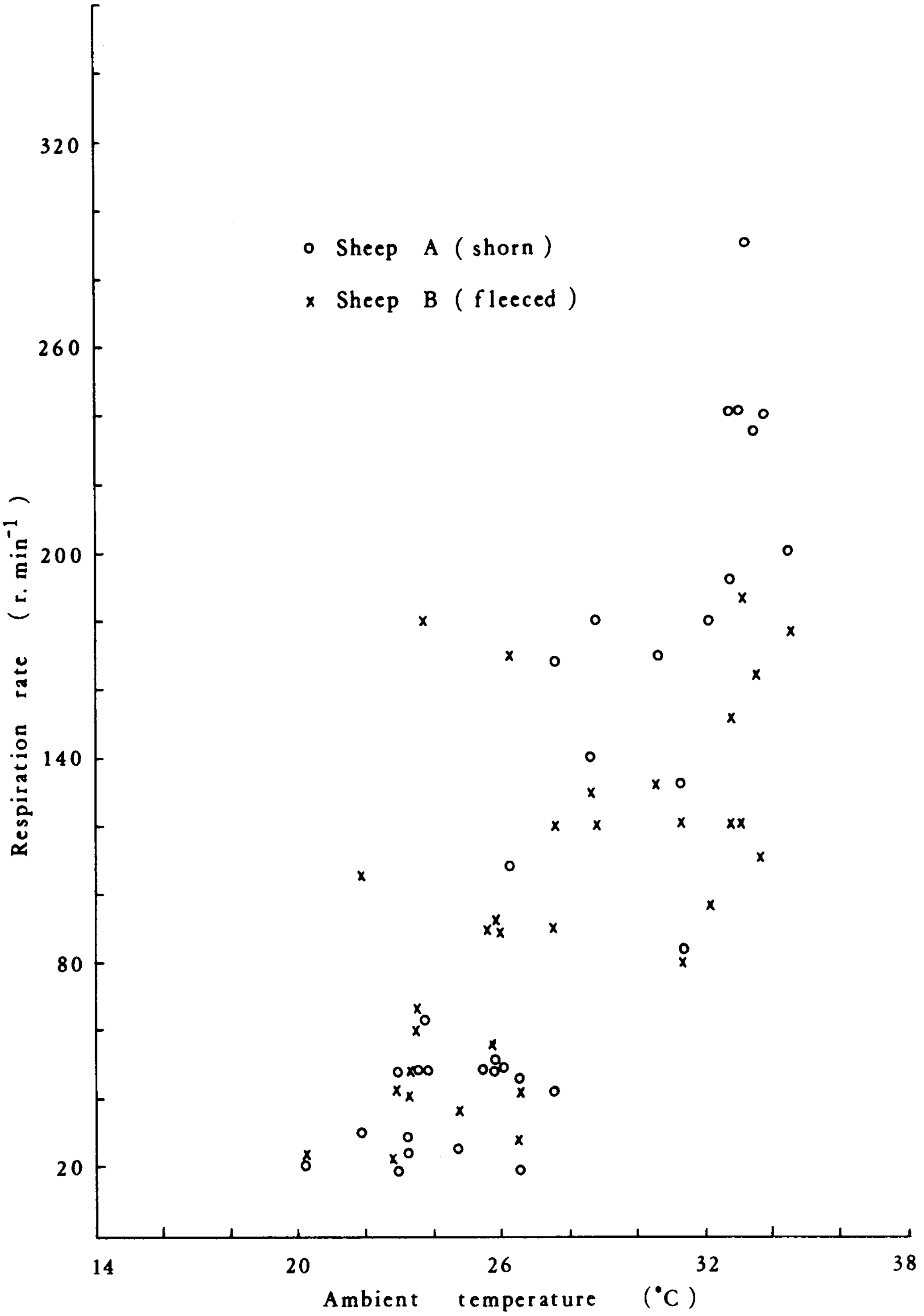


Figure 26 The relationship between respiration rate and ambient temperature for a fleeced and shorn sheep

thickness must be questioned. Therefore, it seems as if the individual differences between sheep A and sheep B, rather than the difference in fleece thickness, may explain the different regression coefficients in Fig. 26. Nevertheless, Table 10 shows that in the two lower Ta ranges, the fleeced sheep always had a higher respiration rate than the shorn sheep. Hofman and Riegle (1977a) reported that in their study in a climatic chamber, the fleeced sheep maintained a higher respiration rate than the shorn sheep at Ta = 25, 30, 35 and 40°C. However, this difference was only significant at Ta = 25 and 30°C. It seems therefore, that at a Ta < *ca.* 30°C, respiratory evaporation is of less importance to the shorn than to the fleeced sheep. At a Ta > *ca.* 30°C, respiratory evaporation becomes of increasing importance to the shorn sheep because the thin pelage provides very little protection against the increasing environmental heat load.

The question now arises whether deep body temperature, as indicated by rectal temperature, is related to the respiration rate of the Namaqua-Afrikaner sheep. Figs 27 and 28 show that with a rectal temperature less than *ca.* 40°C, the correlation between respiration rate and rectal temperature was very poor. However, the results obtained from sheep A indicate that when rectal temperature exceeded *ca.* 40°C, 60% of the variation in respiration rate can be accounted for by the fitted regression.

Ingram and Mount (1975) pointed out that stimuli from a number of regions (both peripheral and central) interact in the control of respiration

Table 10 The mean respiration rate (f) of fleeced and shorn sheep within different ambient temperature ranges (Ta)

	Fleeced Sheep A	Fleeced Sheep B	Shorn Sheep A'	Fleeced Sheep B'
Ta = 20 - 24,9°C				
f ± s	59,6 ± 33,7*	89,8 ± 45,6	35,2* ± 15,3	62,1 ± 48,0
f range	22 - 138	38 - 177	18 - 63	22 - 180
n	16	12	10	10
Ta = 25 - 29,9°C				
f ± s	108,8 ± 44,7	132,8 ± 38,7	81,3 ± 57,1	93,3 ± 41,5
f range	69 - 204	75 - 190	19 - 180	27 - 170
n	8	5	11	11
Ta = 30 - 34,9°C				
f ± s	223,0 ± 70,2	143,0 ± 41,7	200,2 ± 58,1	132,6 ± 33,0
f range	150 - 310	100 - 190	83 - 290	80 - 186
n	4	4	11	11

* Significantly different at $p < 0,01$

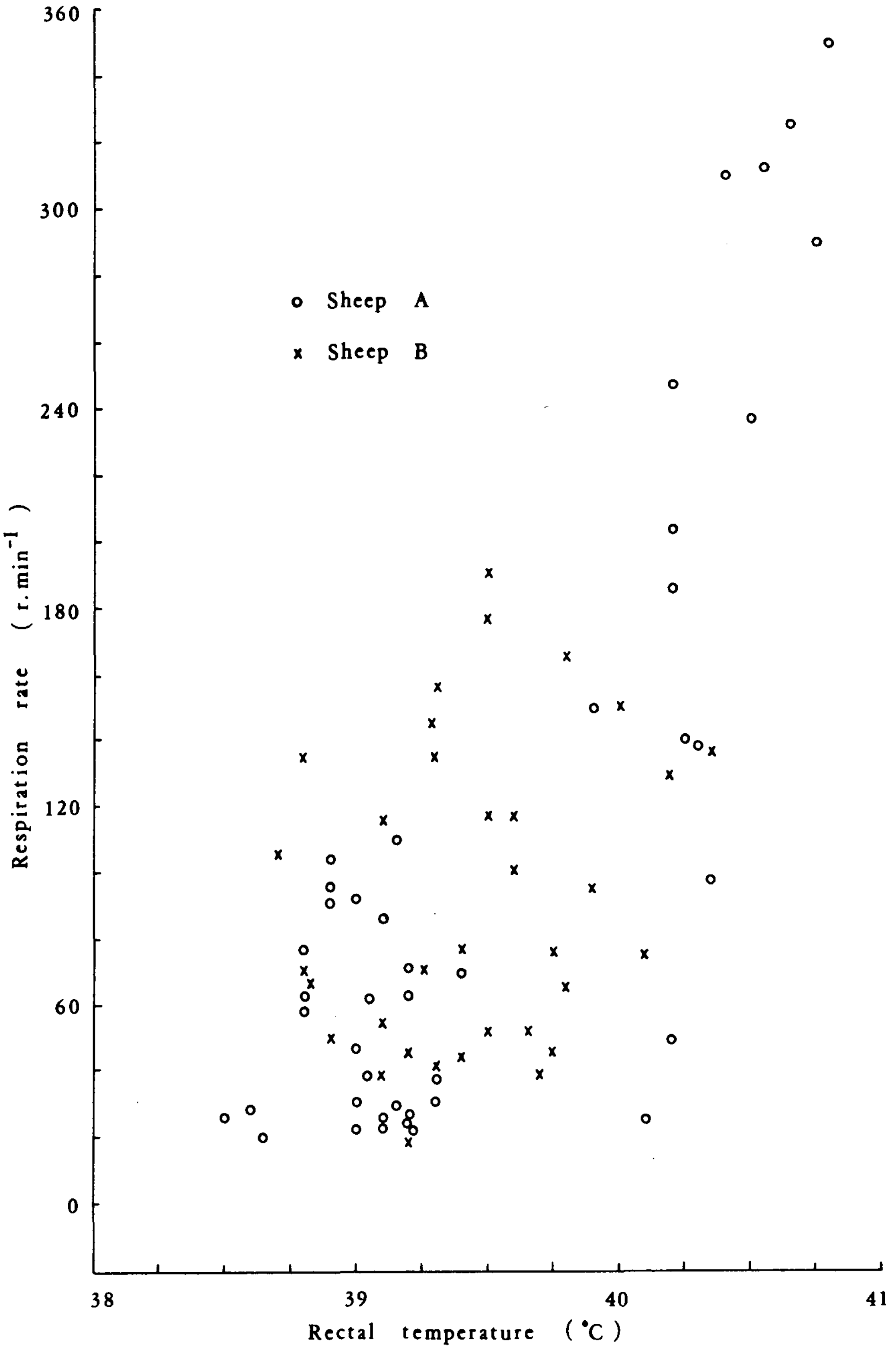


Figure 27 The relationship between respiration rate and rectal temperature for two fleeced sheep

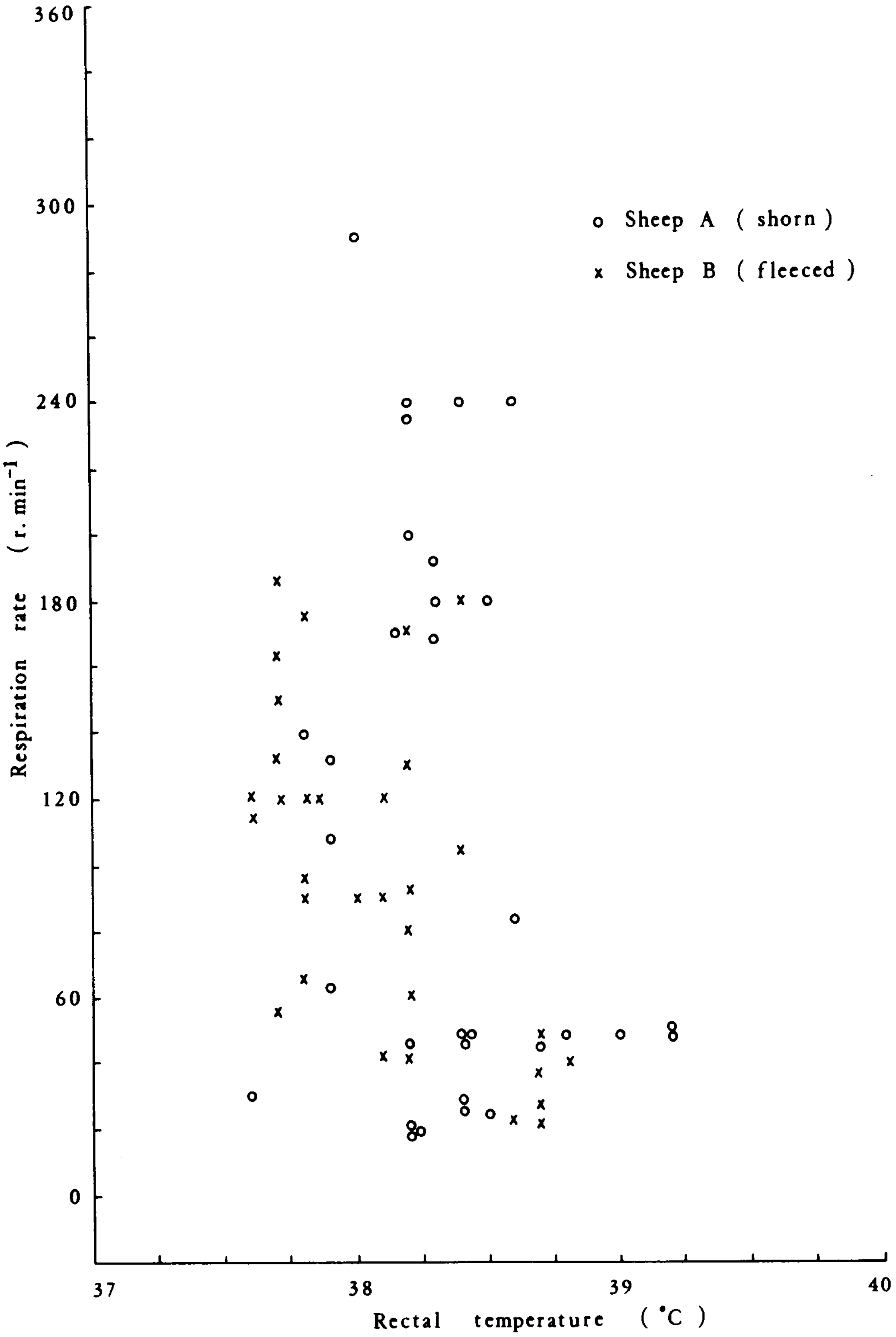


Figure 28 The relationship between respiration rate and rectal temperature in a fleeced and a shorn sheep

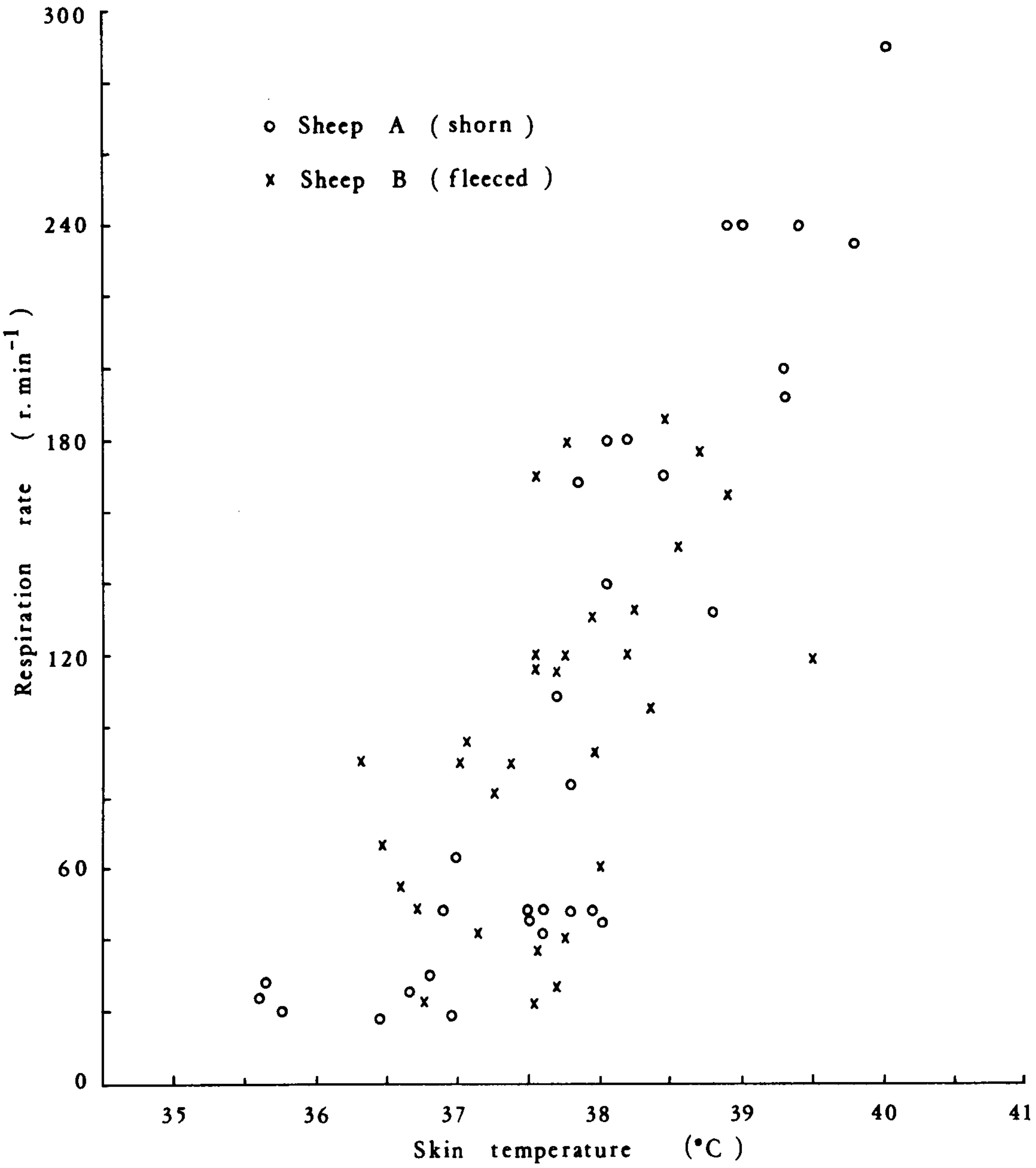


Figure 29 The relationship between respiration rate and skin temperature in a fleeced and a shorn sheep

rate. The relationship between respiration rate and skin temperature in the Namaqua-Afrikaner sheep was therefore examined (Fig. 29). The results show that variation in respiration rate, accounted for by the fitted regression between skin temperature and respiration rate, was 76% in the case of the shorn sheep (A') and 32% for the fleeced sheep (B'). Furthermore, the regression coefficient was 63,53 and 37,04 respectively for the shorn and fleeced sheep. Similarly, Hofman and Riegle (1977b) have reported that in the relationship they obtained between respiratory evaporative heat loss and trunk skin temperature, the regression coefficient for shorn sheep was larger than that obtained from fleeced sheep. Thus it is clear that an increasing skin temperature both in an outdoor environment and in a climatic chamber had a greater effect on the respiration rate of shorn than unshorn sheep. My results, therefore, strongly suggest that skin temperature (the peripheral sensors) affected respiration rate to a greater extent than did rectal temperature.

Finally, I have presented certain results in Fig. 30 obtained for sheep A during a summer's day, when this animal resorted to open-mouth panting. On this day solar radiation was intense with no wind and a low relative humidity. The ambient temperature increased steadily during the day to reach a maximum of 38,9°C between 15h00 and 17h00. Respiration rate increased to 310 r. min^{-1} at 12h30 (Ta = 35°C) and thereafter, the animal resorted to open-mouth panting. At this stage, rectal temperature exceeded 40,5°C and the respiration rate increased even further to reach a maximum of 350 r. min^{-1} at 15h30. When the respiration rate was

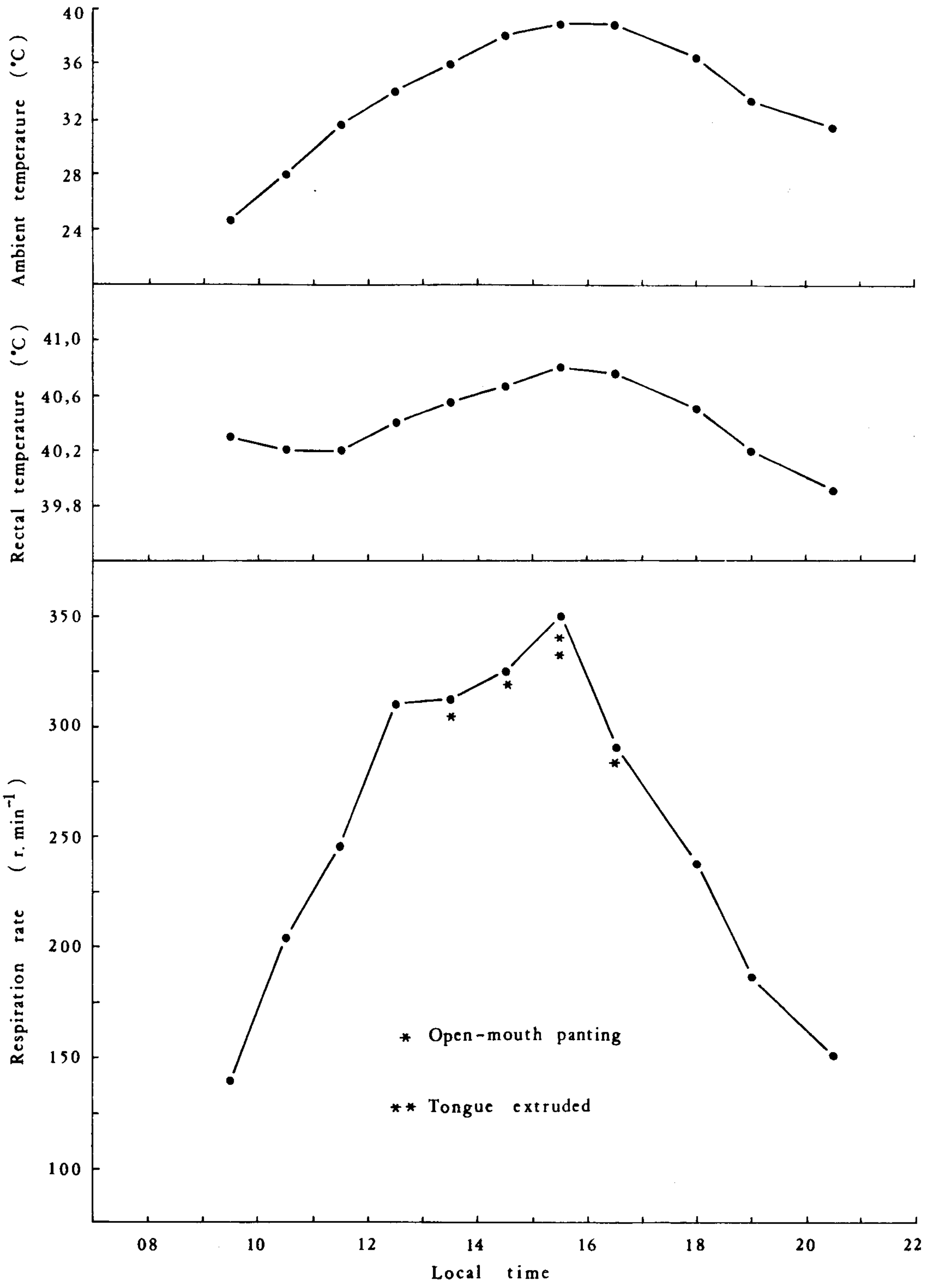


Figure 30 The respiration rate and rectal temperature of a fleeced sheep during an exceptionally hot day

at this maximum value, the animal panted with its mouth wide open and with the tongue extruded. At 16h30, ambient temperature was still at 38,8°C, but open-mouth panting had decreased to a rate of 290 r. min^{-1} (83% of the previous level). It is not possible to say if the animal changed to slower deeper panting (SDP) at this stage. However, the maximum values for ear, skin and surface temperature were recorded at 15h30. This suggests that the heat load on the animal was already decreasing at 16h30.

Because of the high respiration rate recorded, the open-mouth panting observed during this day apparently did not represent the typical slower deeper panting (SDP) described by Hales (1976). Nevertheless, the opening of the mouth can have an additional advantage in increasing the efficacy of respiratory evaporative heat loss. Schmidt-Nielsen *et al.* (1970), for example, demonstrated in the panting dog that the air expired through the mouth was very close to body temperature. In contrast, during normal breathing, the temperature of the air expired through the nostrils was well below body temperature and consequently, evaporative heat loss was less effective. This phenomenon has not as yet been demonstrated in sheep, but in theory the same phenomenon could occur.

Radiative heat load

Figure 31 shows examples of incident short- and long-wave radiation recorded during a cloudless and a cloudy day at the experimental site (19° 53'E, 33° 55'S) during December. Maximum short-wave radiation was recorded at 13h00 and coincided with the maximum solar elevation (79°) which occurred at 12h40. The ratio of diffuse to total sky radiation is predominantly influenced by the presence of clouds. When clouds are present the diffuse component increases and when dense clouds obscure the sun the direct component can disappear altogether. In the present examples, direct solar radiation averaged 88% of the total sky radiation during the cloudless day, whereas it only decreased to 77% during the cloudy day (cirrus clouds). The ratio of reflected to total radiation was constant at 0,30 and is a measure of the albedo of the ground for short-wave radiation.

Long-wave radiation from the atmosphere and ground reached their maximum intensities after maximum solar radiation was recorded. Furthermore, the fluctuation in long-wave radiation intensity during the day was less than the change in short-wave radiation intensity. Therefore, in the heat balance of an animal, short-wave radiation is only of critical importance for a few hours during the day, whereas long-wave radiation exchange remains important throughout the day and night.

Although direct solar radiation is the major component of incident short-wave radiation, this component is directional and would therefore fluctuate, depending upon the portion of the animal's total surface area exposed to the solar-beam. In order to calculate the profile area exposed to direct solar radiation, the body of the animal has often been regarded as a horizontal cylinder. However, Finch (1976) pointed out that the cylindrical model overestimated the amount of direct solar radiation

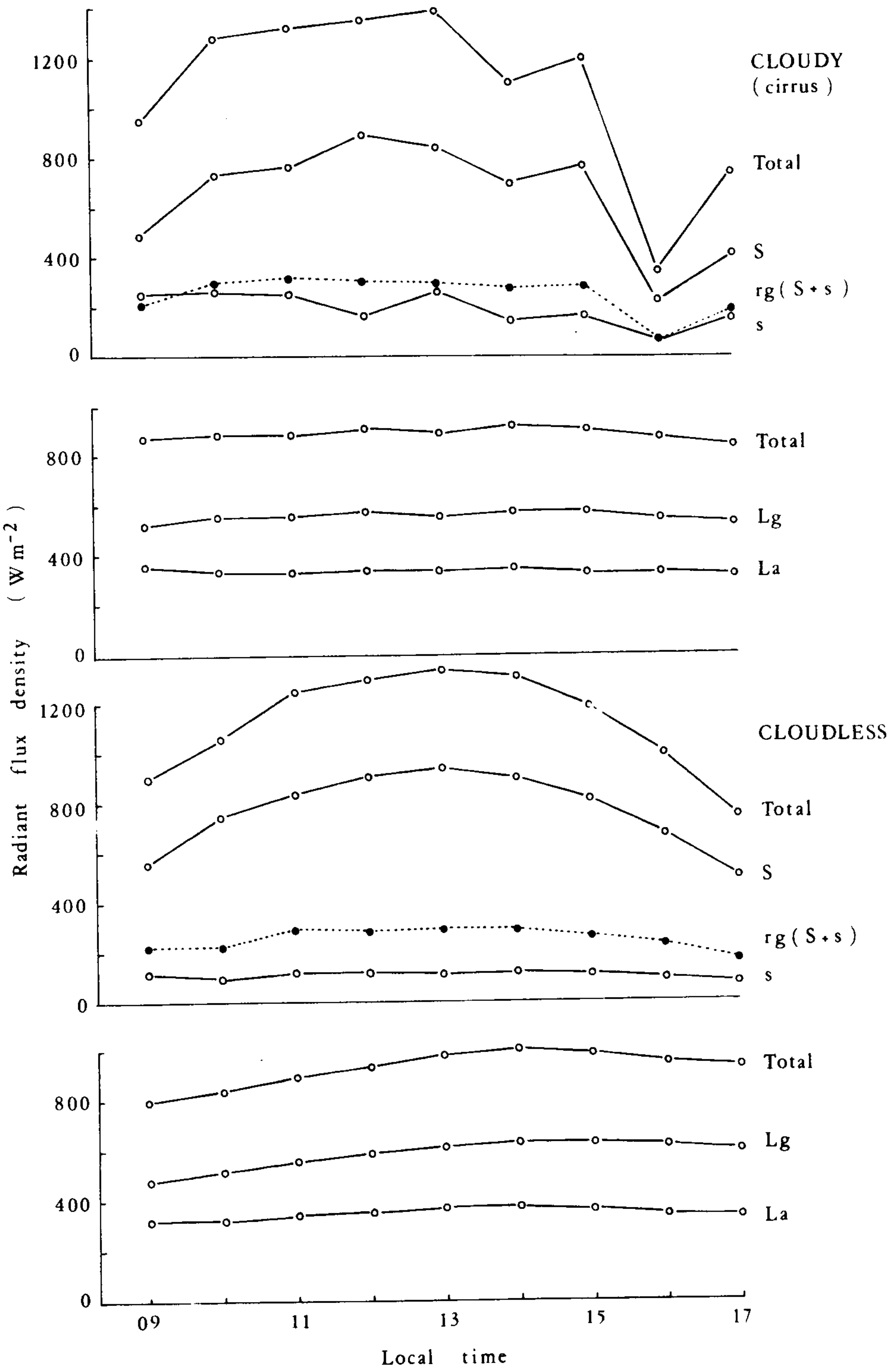


Figure 31 Incident short- and long-wave radiation recorded during a cloudy and cloudless day. (S is direct solar radiation; rg (S + s) is radiation reflected from the ground; s is diffuse radiation; Lg is long-wave radiation from ground and La is long-wave radiation from sky.)

absorbed (at higher solar elevations) when the long body axis of a Sussex bull was perpendicular to the solar rays. Clapperton *et al.* (1965) have attempted to overcome this problem by measuring the solar profiles of a number of sheep using a photographic method. In Fig. 32 I have compared the profile areas of Namaqua-Afrikaner sheep at various solar elevations with the mean profile area of six fleeced sheep obtained by Clapperton *et al.* (1965). Figure 32 shows that when the animals faced the sun, $^{Ap}/A$ increased with increasing solar elevation to reach a maximum when the sun was directly above the animals (elevation = 90°). In contrast, when the solar beam was at right angles to the animals' bodies, $^{Ap}/A$ was at its highest at the lower solar elevations and started to decrease when the solar elevation exceeded *ca.* 40°. In Fig. 32 I have also shown the solar profile calculated for a horizontal cylinder with dimensions similar to the body of the Namaqua-Afrikaner sheep. I used the formula proposed by Monteith (1973) and calculated $^{A\bar{p}}/A$ for seven different elevation angles (β) with the azimuth (θ) = 0° and = 90° respectively.

$$\frac{Ap}{A} = \frac{\operatorname{cosec}\beta \left\{ ^{2}/_{\pi} \; X \left(1 - \cos^{2}\beta \, \cos^{2}\theta\right)^{\frac{1}{2}} \cos\beta \, \cos\theta \right\}}{2\,(X + 1)} \; X \; \sin\beta$$

where $X = {}^{h}/r$ and

h = the length of the cylinder and

r = the radius of the cylinder

When the solar beam was parallel with the long body axis, $^{Ap}/A$ ratios for the cylindrical model and the photographic method employed on Namaqua-

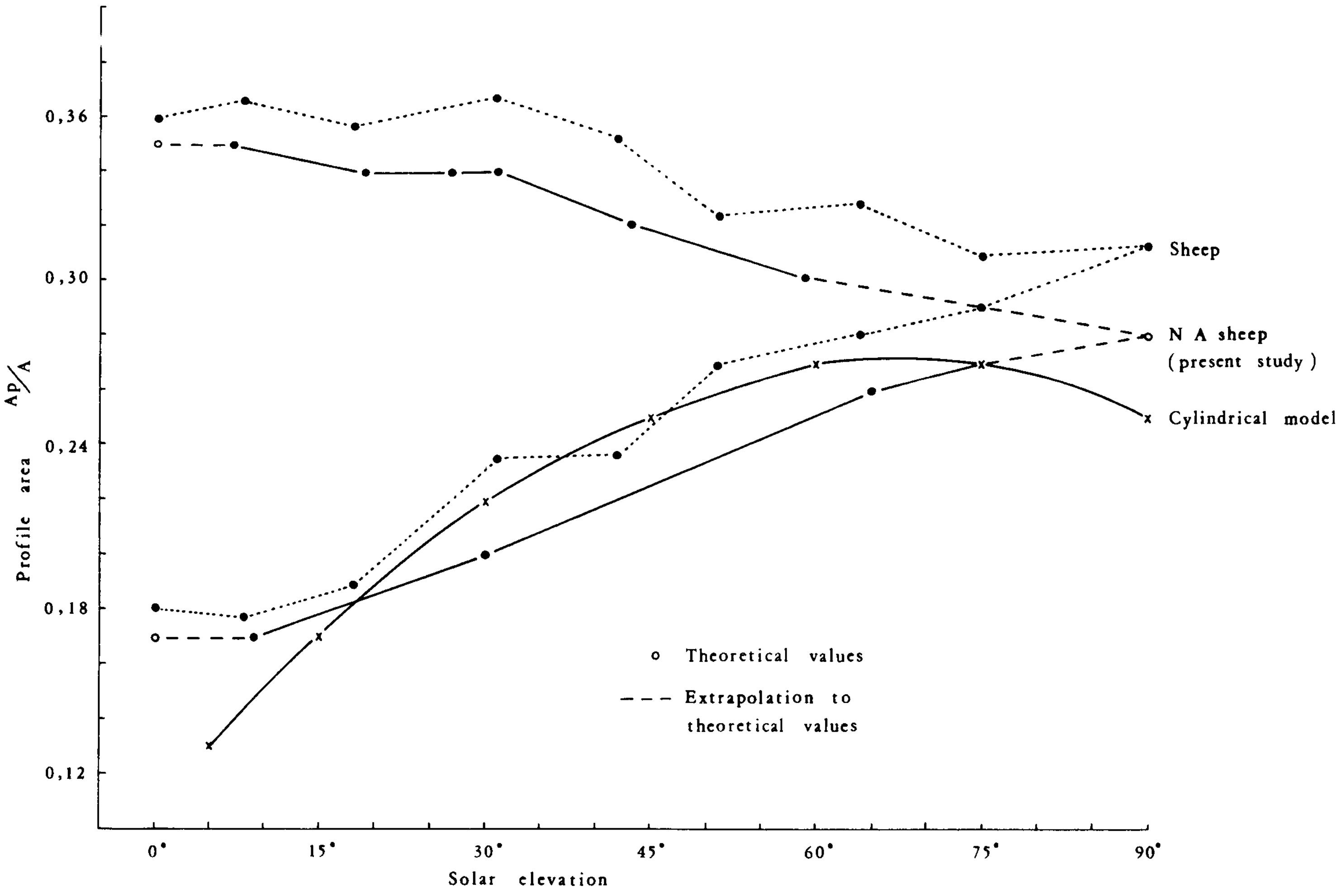


Figure 32 The relationship between the profile area exposed to direct solar radiation and solar elevation for a side and head presentation of sheep.
Cylindrical model from Monteith (1973) and sheep from Clapperton *et al.* (1965).

Afrikaner sheep were very similar, with $^{Ap}/A$ for the cylindrical model generally slightly higher. However, when the solar beam was perpendicular to the long body axis, $^{Ap}/A$ for the cylindrical model remained constant at 0,25 and was therefore always less than the $^{Ap}/A$ recorded by the photographic method. This contradicts Finch's (1976) conclusions, but she used a different formula $(\frac{1}{\pi})$ which estimated $^{Ap}/A$ at 0,32. When this value is applied in the present study, the cylindrical model would also overestimate the amount of direct solar radiation absorbed at the higher solar elevations. These calculations therefore, show the limitations of the cylindrical model and emphasize the need to measure the true profile area for any animal under investigation.

The short- and long-wave radiation absorbed by the sheep's pelage surface depend on the radiation intensity, the absorptance of the pelage surface and the proportion of the total surface area involved in the radiation exchange. The absorptance for short-wave radiation was established in the previous chapter as 0,66 for the fleeced sheep and 0,33 for the shorn sheep while the absorptance for long-wave radiation was regarded as 1,0. I calculated the amount of radiation absorbed from each of the five radiation components and determined the average value for each day's measurements. It can be seen from Table 11 that the lower absorptance of the shorn sheep resulted in a much lower short-wave radiative heat load. Consequently, the net radiative heat gain was lower for the shorn than for the fleeced sheep. However, one should keep in mind that the penetrance factor which was discussed in the previous chapter, was not taken into consideration. Therefore, the net

Table 11 Net radiation exchanges (W m^{-2}) for fleeced and shorn sheep during the summer and fleeced sheep during the winter (+ = net gain; - = net loss).

Radiation exchanges	WINTER				SUMMER									
	Fleeced Sheep				Fleeced Sheep					Shorn Sheep				
	1	2	3	Mean	1	2	3	4	Mean	1	2	3	4	Mean
S.w. rad. abs.														
Direct	125	129	115	123	148	181	161	8	125	74	90	81	4	62
Diffuse	18	17	30	22	53	30	48	99	58	26	15	24	50	29
Reflected	26	24	21	24	68	70	75	33	62	34	35	39	17	31
L.w. rad. abs.														
Ground	167	169	164	167	234	243	248	212	234	232	248	249	210	235
Sky	124	125	120	123	142	147	160	175	156	142	147	160	175	156
L.w. emitted														
by pelage	350	363	365	359	448	496	473	414	458	446	468	464	423	450
Net l.w. exchange	-59	-69	-81	-69	-72	-106	-65	-27	-68	-72	-73	-55	-38	-59
Total net rad.														
exchange	110	101	85	100	197	175	219	113	177	62	67	89	33	63

s.w. rad. abs. = short-wave radiation absorbed

l.w. rad. abs. = long-wave radiation absorbed.

radiative heat gain cannot give a true indication of the heat load at skin level. Furthermore, the thin pelage of the shorn sheep would have offered a much lower resistance against heat flow than the thick pelage of the fleeced sheep. These factors will be discussed in relation to the sheep's total heat balance at a later stage in this chapter.

Table 11 also shows that direct radiation was generally the largest component of the total short-wave radiative heat load in the study. The exception was on day 4 (summer) when cumulus clouds obscured direct solar radiation. Nevertheless, long-wave radiation from the ground was always the largest single component of the total radiative heat load on the animal. The same phenomenon was reported by Finch (1972) for the eland and hartebeest at midday in Kenya. In a field situation an animal can minimize the importance of direct solar radiation by orientation behaviour whereas the importance of long-wave radiation from the ground can only be reduced if the animal lies down or stands in the shade. Nevertheless, even on day 4 (summer) when the sheep were in shade and direct solar radiation was negligible, the net radiation exchange indicates a net heat gain for both the shorn and fleeced sheep. Therefore, radiation exchange with the environment resulted in a net gain during winter and summer conditions and for both fleeced and shorn sheep.

Heat balance

The following heat balance studies allowed comparisons to be made between winter and summer data as well as between fleeced and shorn sheep. The mean daily heat exchanges between the sheep and the environment are shown in Table 12. The mean contributions made by the various components towards total heat gain and loss are presented in Table 13.

Short- and long-wave radiation absorbed at the pelage surface (Rabs) contributed between 88% and 94% of the total heat gain. In the winter experiments, Rabs was on average 8,2 times greater than the metabolic heat (M). During the summer experiments, Rabs was on average 15,3 and 10,0 times greater than M in the fleeced and shorn sheep respectively. These results were expected, since summer conditions are characterised by high radiation intensities and the fleeced sheep had a much higher absorptance for short-wave radiation than the shorn sheep. Finch (1976) reported that in Boran cattle, long-wave radiation comprised on average 61% of the total absorbed radiation. In the present study, long-wave radiation comprised *ca.* 61% of Rabs in the fleeced sheep and *ca.* 76% in the shorn sheep. The similarity between the fleeced sheep and Boran cattle can be explained by a similar absorptance for short-wave radiation. Finch (1976) reported that Boran cattle had an absorptance of 0,67 while I found an absorptance of 0,66 for the fleeced sheep. For both the Boran cattle and Namaqua-Afrikaner sheep, the net long-wave radiation exchange was negative. However, the additional contribution from short-wave sources resulted in a net radiative heat flow towards the animals' bodies. This net radiative heat flow represented 71% of the heat load in the Boran cattle (Finch 1976) whereas it was 62% in the winter fleeced sheep, 81% in the summer fleeced sheep and 47% in the summer shorn sheep. The rest of the heat load was represented by the metabolic heat.

Table 12 Mean daily heat exchanges between 9h00 and 17h00 during summer and winter in fleeced and shorn sheep

Energy balance	WINTER			SUMMER							
	Fleeced Sheep			Fleeced Sheep				Shorn Sheep			
	Day* 1	2	3*	Day 1	2	3	4	Day 1	2	3	4
M (Wm^{-2})	68	56	59	51		47			49		58
† Rabs. (Wm^{-2})	460	464	450	645	671	692	527	508	535	553	456
† Ls (Wm^{-2})	350	363	365	448	496	473	414	446	468	464	423
† C (Wm^{-2})	37	40	46	151	125	124	97	160	95	113	124
Hex (Wm^{-2})	8	9	8	22		27			26		7
Hcut (Wm^{-2})	96	26	69	31		38			34		41
Hst (Wm^{-2})	− 7	+ 8	+13	+ 5	− 2	+ 1	− 1	+ 1	+ 5	+ 1	+ 1
Total gain (W)	752	713	725	957		1017			834		733
Total loss (W)	686	612	711	902		909			896		851
% error	9%	15%	2%	6%		11%			7%		15%
† Hs_1=Rabs−Ls−C	+73	+61	+39	+46	+50	+95	+16	−98	−28	−24	−91
Hs_2=Hcut+Hex+Hst−M	+29	−13	+31	+ 7		+19			+16		− 9

* This sheep was shorn during the summer experiment

† Expressed as $W m^{-2}$ pelage surface area while the others were expressed as Wm^{-2} skin surface area

$$\% \text{ error} = (\text{Total gain} - \text{Total loss}) \div \frac{\text{Total gain} + \text{Total loss}}{2}$$

M is metabolic heat; Rabs is effective radiative heat load;
Ls is reradiation; C is convective heat loss; Hex is respiratory evaporative heat loss; Hcut is cutaneous evaporative heat loss; Hst is stored heat and Hs is the sensible heat flow from the environment into the animal

Table 13 Mean contributions (%) made by the various components towards total heat gain and total heat loss

	WINTER			SUMMER			
	Fleeced Sheep			Fleeced		Shorn	
	Day 1	2	3	Day 1	3	Day 2	4
Heat gain							
M	12	10	11	7	6	8	11
Rabs	88	90	89	93	94	92	89
Heat loss							
Ls	73	82	74	69	72	75	71
C	8	9	9	23	19	15	21
Hex	2	2	2	3	4	4	1
Hcut	19	5	13	4	5	5	6
Hst	1	2	2	1	0	1	0

M is metabolic heat; Rabs is effective radiative heat load; Ls is reradiation; C is convective heat loss; Hex is respiratory evaporative heat loss; Hcut is cutaneous evaporative heat loss and Hst is stored heat.

The mean fasting metabolic rates of the sheep recorded under summer and winter conditions, are presented in Table 14. As expected the mean metabolic rate recorded during the winter, was significantly higher than the mean metabolic rate recorded during the summer. Although there was no significant difference between the summer fleeced and shorn values, the shorn sheep displayed greater variation than the fleeced sheep. This was also to be expected, since shorn sheep have a higher 'lower critical temperature' than fleeced sheep. These results, however, cannot be considered fasting metabolic rates in the true sense of the term. Blaxter (1961) explained that the feeding level before the fast, influences the time it takes to reach a minimum metabolic heat production. Moreover, he regarded a fasting period of 24 hours as insufficient and has shown that sheep on a high feeding level may require up to seven days of fasting to reach a minimum heat production. Ritzman and Benedict (1931) subjected four-year-old sheep to a fasting period of 18 - 32 hours and reported a metabolic rate of 4,36 W $kg^{-0,73}$ (*ca.* 58 W m^{-2}). Blaxter (1961), however, corrected this value to represent the true fasting value of 2,86 W $kg^{-0,73}$ (*ca.* 38 W m^{-2}). In the Namaqua-Afrikaner sheep, the lowest recorded metabolic rate was 39 W m^{-2} which corresponds well with the value provided by Blaxter. However, it is highly probable that the metabolic rates reported in this experiment were not only influenced by environmental temperature, but also by the post-absorptive state of the animals.

Finch (1976) found that in Boran cattle reradiation accounted for *ca.* 57% of the total heat loss, while the present study suggests a figure of

Table 14 Mean fasting metabolic rates (M) of Namaqua-Afrikaner sheep

	WINTER	SUMMER		
	Fleeced	Fleeced	Shorn	Fleeced **& Shorn**
$M \pm s\ (Wm^{-2})$	60,1 ± 6,0	49,2 ± 4,7	52,6 ± 12,2	50,7 ± 8,6
Range	53,0 - 72,0	42,0 - 54,0	39,0 - 67,0	39,0 - 67,0
n	8	6	5	11

Winter fleeced vs. Summer fleeced	$p < 0,0025$	H.S.
Summer fleeced vs. Summer shorn	$p > 0,05$	N.S.
Winter fleeced vs. Summer shorn	$p > 0,05$	N.S.
Winter fleeced vs. Summer (F + S)	$p < 0,01$	S

ca. 75%. Her studies on the hartebeest and eland (Finch 1972) showed that these animals lost approximately 75% and 67% of Rabs by reradiation, respectively. Comparative values in the present study were 78% for the winter fleeced sheep, 73% for the summer fleeced sheep and 88% for the summer shorn sheep. Therefore, in all the examples, the greater part of Rabs was reradiated back to the environment. The intensity of reradiation depends on the pelage surface temperature which, in turn, is greatly influenced by solar radiation and windspeed. At the lower windspeeds, the fleeced sheep had a higher surface temperature and thus a higher rate of reradiative heat loss than the shorn sheep. This phenomenon is illustrated in the results of day 2 (summer) which was characterised by low windspeeds. However, when the windspeed increased, reradiative heat loss for the fleeced and shorn sheep became more or less equal. The results of day 1 (summer) illustrate this effect.

The percentage of Rabs which was lost by convection, varied between 8% and 10% (mean = 9%) for the winter fleeced sheep, between 18% and 23% (mean = 20%) for the summer fleeced sheep and between 18% and 31% (mean = 24%) for the summer shorn sheep. Convective heat loss is influenced by the difference between pelage surface temperature and air temperature and this gradient was greater during the summer than during the winter experiments. Consequently, convective heat loss was generally higher during the summer than during the winter experiments. Similarly during day 2 and 3 (summer) when windspeed was relatively low, the gradient between surface and air temperature was greater for the fleeced than for the shorn sheep. The fleeced sheep therefore had the higher average convective heat loss during these two days. On day 1 and 4, however, this position was reversed because of the relatively high windspeed.

Evaporative heat loss comprised between 7% and 21% of the total heat loss in the Namaqua-Afrikaner sheep. Brockway *et al.* (1965) and Hofmeyr *et al.* (1969) reported that in adult sheep, evaporation from the respiratory tract represented the major portion of evaporative heat loss under conditions of heat stress. In contrast, Knapp and Robinson (1954) found that sheep lost 25 - 35% of the total evaporative heat loss from the respiratory tract and, similarly, Ames *et al.* (1971) established a loss of 25% from the respiratory tract. It is important to note that the above results were obtained under artificial conditions in climatic chambers.

Most researchers today accept that respiratory evaporation is of greater importance than cutaneous evaporation in sheep. In contrast, I found in the Namaqua-Afrikaner sheep, that cutaneous water loss was generally greater than respiratory water loss. In the winter experiments, respiratory evaporative heat loss represented between 6% and 29% (mean = 15%) of the total evaporative heat loss. In the summer experiments the range was between 38% and 51% (mean = 43%) for the fleeced sheep and between 15% and 54% (mean = 30%) for the shorn sheep. It is quite possible that cutaneous evaporation was overestimated in these experiments, since the sweat capsule was only applied to one skin area and it is known that evaporative water loss is not uniform on all areas of the skin (McLean 1963). Additional sweat capsules, would, however, have involved shaving of additional areas on the skin. This would have disturbed the normal thermoregulatory function of the pelage and resulted in additional errors to the heat balance. Nevertheless, even if the absolute values are not exact, they are still valuable for comparative purposes.

Alexander (1974) reported that a loss of 9 mg of water per breath represents the maximum rate of respiratory evaporation. This value falls to about 4 mg during very high respiration rates. He therefore felt that 60 W m^{-2} can be considered as the maximum respiratory evaporative cooling rate. In the heat balance studies on Namaqua-Afrikaner sheep I recorded respiratory evaporative heat losses which varied between 6 and 30 W m^{-2}. The maximum recorded value of 30 W m^{-2} coincided with a respiration rate of 240 $r.min^{-1}$. However, during a previous experiment, I recorded respiration rates as high as 350 breaths per minute and thus 30 W m^{-2} does not necessarily represent the maximum respiratory cooling rate for the Namaqua-Afrikaner sheep.

Brockway *et al.* (1965) reported minimum cutaneous evaporative water losses (CEWL) of 8 g m^{-2} h^{-1} for sheep while Waites and Voglmayr (1963) found that the scrota in rams can produce sweat at a rate of 200 g m^{-2} h^{-1}. Alexander (1974), however, felt that a value of 50 g m^{-2} h^{-1} (35 W m^{-2}) can be considered as an average maximum for cutaneous evaporation in adult sheep. My results for the Namaqua-Afrikaner sheep show that during the summer experiments, cutaneous evaporation rates varied between 17 and 56 W m^{-2} (25 - 83 g m^{-2} h^{-1}). Nevertheless, during the winter experiments values as high as 100 W m^{-2} (150 g m^{-2} h^{-1}) were obtained from one sheep. However, for the second sheep (day 2 winter) cutaneous evaporative heat loss only varied between 18 and 34 W m^{-2} (26 - 52 g m^{-2} h^{-1}). The environmental conditions during day 1, 2 and 3 were very much the same and the same technique was used to determine cutaneous evaporation. Therefore, the high cutaneous evaporation values obtained for the one sheep during the winter experiments, cannot be disregarded on the basis of experimental error. I am, however, unable to advance any explanation for this unusual result other than individual variation. Consequently, it is impossible to evaluate the effect of seasonal changes on the cutaneous evaporation in these experiments.

The summer results, however, show some clear differences between the evaporative heat losses of the fleeced and shorn sheep. Figure 33 shows that, while a positive correlation between ambient temperature and cutaneous evaporative heat loss was found in the fleeced sheep, this relationship was negative for the shorn sheep. Moreover, the relationship between skin temperature and cutaneous evaporative water loss was also negative for the shorn sheep and positive for the fleeced sheep. Therefore, it is clear that while the fleeced sheep showed increased cutaneous evaporation with increasing environmental heat load, the shorn sheep reacted in the opposite way. In a previous section I have shown that, although studies on both the shorn and fleeced sheep showed a positive relationship between ambient temperature and respiration rate and between skin temperature and respiration rate, in both instances, the fitted regression for the shorn sheep accounted for a greater percentage of the variation in respiration rate. Therefore, a high environmental heat load and a concomittantly high skin temperature

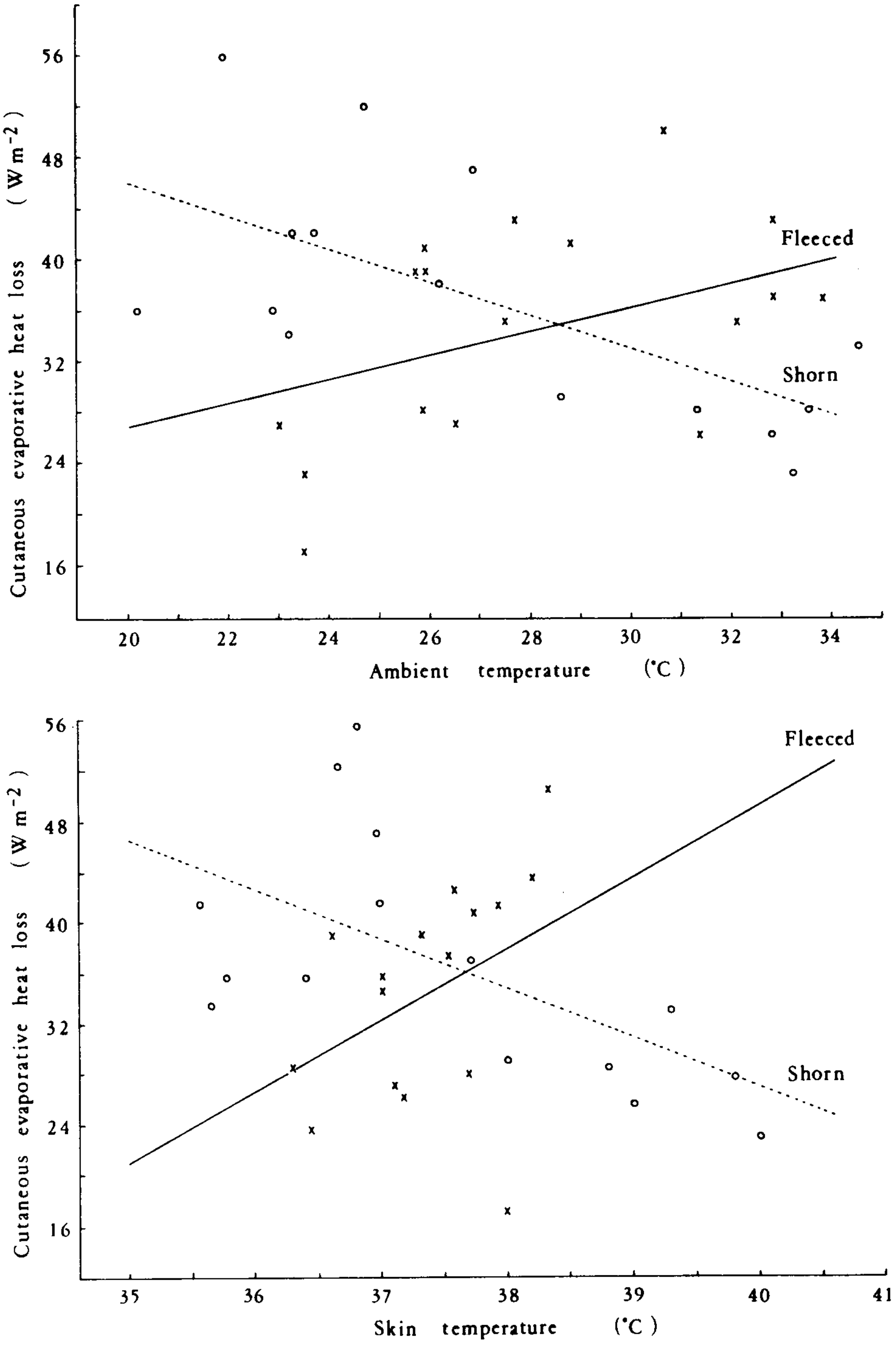


Figure 33 The relationship between cutaneous evaporation (Hcut) and ambient temperature and between Hcut and skin temperature

resulted in a lowered cutaneous evaporation and increased respiratory evaporation for the shorn sheep. However, for the fleeced sheep, both cutaneous and respiratory evaporation were increased at high environmental heat loads. These apparently contradictory results are difficult to explain and were probably influenced by different combinations of peripheral and central stimuli. In the shorn sheep, environmental conditions had a greater effect on skin temperature than in the fleeced sheep and consequently, the skin temperature of the shorn sheep displayed greater variations. High skin temperatures probably caused the high respiration rates and the latter would have had a cooling effect on the hypothalamus (and brain). Under these circumstances cutaneous evaporation was partially inhibited. In the fleeced sheep, skin temperatures remained more stable and the respiration rate did not increase to such high levels as in the shorn sheep. Consequently in these circumstances, cutaneous evaporation was not inhibited.

The results of the heat balance during summer and winter conditions show that for the fleeced sheep total heat gain was always greater than total heat loss. The percentage error was always positive and varied between 2% and 15%. Hutchinson *et al.* (1976) suggested that the heat balance equation should be rearranged to show the sensible heat flow from the environment into the animal (Hs_1).

$$Hs_1 = Rabs - Ls - C$$

This additional heat load at skin level can be stored by the animal or lost by evaporative cooling. Therefore Hs_2 can also give an indication of the size of this additional heat load.

$$Hs_2 = Hcut + Hex + Hst - M$$

In the fleeced sheep Hs_1 represented an additional heat load which varied between 71% and 225% of the metabolic heat. In view of the sheep's good insulative cover, I would suspect that these values represent an overestimation especially during the winter experiments.

The results obtained from the shorn sheep during the summer experiments, show that average daily heat loss was always larger than heat gain. Furthermore, Hs_1 indicates that sensible heat flow was away from the skin towards the environment. In this case, heat load at skin level was probably underestimated. In the calculations, I assumed that all the radiation was absorbed at the pelage surface. However, Hutchinson and Brown (1969) have demonstrated that solar radiation penetrates deeply into light coloured coats. Therefore, the contribution from short-wave radiation towards the total heat gain of the shorn sheep was most probably underestimated.

During the summer experiments, the fleeced and shorn sheep experienced high environmental heat loads without any ill effects. In the fleeced sheep, the thick insulative cover protected the animal against excessive radiative heat gain. In contrast, the thin pelage of the shorn sheep provided little protection against heat gain but on the other hand, this factor would have enhanced heat loss. In addition, shearing resulted in a lighter coloured fleece which had a higher reflectance for short-wave radiation. In the colder environment, during the winter experiments, the thick fleece offered great resistance against heat loss. Moreover, solar radiation increased the pelage surface temperature and thus heat loss through the fleece was further reduced. Therefore, the pelage of the Namaqua-Afrikaner sheep contributes a great deal towards this breed's adaptation to both warm and cold climates and may explain in part its success in semi-arid regions.

CONCLUSIONS

1. The Namaqua-Afrikaner sheep maintained a stable body temperature under widely different environmental conditions despite the fact that they could not use behavioural thermoregulation. In contrast with observations in the laboratory, outdoor results show no clear relationship between ambient and rectal temperature.

2. The fleece provided a very good thermal insulation against heat loss and therefore, surface temperatures were always very close to ambient temperatures when the sheep were not exposed to solar radiation. In the shorn sheep, however, the resistance against heat flow was lower and body heat was lost to the environment. Therefore, while the surface temperature of the fleeced sheep was predominantly determined by external factors, both internal and external heat influenced the surface temperature of the shorn sheep. When the sheep were in the sun, the higher absorptance for short-wave radiation resulted in a higher surface temperature for the fleeced sheep. However, when the windspeed exceeded *ca.* 2 m s^{-1}, pelage colour became of minor importance and the surface temperature of the shorn sheep often exceeded that of the fleeced sheep.

3. Environmental temperature and solar radiation had a greater effect on the skin temperature of the shorn than on the fleeced sheep. At low ambient temperatures, the shorn sheep had a lower skin temperature, while at high ambient temperatures the shorn sheep exhibited a higher skin temperature.

4. Solar radiation had a pronounced effect on the vasomotor response of the peripheral blood vessels. When the sheep were exposed to solar radiation, either the increased heat load, or the direct effect of the sun on the peripheral sensors, caused vasodilation to occur at a much lower ambient temperature than in the absence of solar radiation.

5. Respiration rate was positively correlated to ambient and skin temperature. However, great individual differences between the sheep were observed in this respect. These individual differences masked the effect of shearing to some extent. Nevertheless, the shorn sheep generally had the lower respiration rate at the lower ambient temperatures and a higher respiration rate at the higher ambient temperatures. This phenomenon can be explained by the poor insulation which the shorn fleece afforded against heat loss and heat gain. Furthermore, variations in rectal temperature seemed to have little effect on the respiration rate, except in the case of extremely high rectal temperatures (greater than *ca.* 40,5°C).

   The sheep displayed open-mouth panting when respiration rate exceeded *ca.* 280 - 310 r. min^{-1} and when rectal temperatures exceeded *ca.* 40,5°C. At the very high rate of 350 r. min^{-1}, the tongue was extruded. In contrast to the laboratory studies, no indication of a slow deep panting (SDP) was apparent.

6. Photographic determinations of the profile areas exposed to direct

solar radiation at different simulated elevations of the sun, showed the limitations of the widely used cylindrical models. However, the formula proposed by Monteith (1973) gave a reasonable approximation of $^{Ap}/A$ when the azimuth was equal to 0°.

7. The lower absorptance for short-wave radiation in the shorn sheep, resulted in a lower short-wave radiative heat load than in the fleeced sheep. This heat load on the shorn sheep was, however, probably underestimated, because the effect of penetrance was disregarded. This conclusion is substantiated by the heat balance results.

8. Long-wave radiation represented the greater part of the total effective radiative heat load. Long-wave radiation from the ground was also the largest single component of the total heat load on the sheep. However, long-wave radiation exchange resulted in a net heat loss while the addition of short-wave radiation leads to a net radiative heat gain in all the experiments.

9. The effective radiative heat load was, on average, between 8,2 times (Winter-Fleeced) and 15,3 times (Summer-Fleeced) greater than the metabolic heat. On average between 73% (Summer-Fleeced) and 88% (Summer-Shorn) of the radiation absorbed, was reradiated back to the environment, while 8% - 10% (Winter-Fleeced), 18% - 23% (Summer-Fleeced) and 18% - 31% (Summer-Shorn) was lost by convection. Therefore, the primary compensation to a high heat load was by physical processes which occurred automatically on the external surface of the sheep.

10. Evaporative heat loss represented between 7% and 21% of the total heat loss, with cutaneous evaporation generally greater than respiratory evaporation. Cutaneous evaporation contributed between 38% and 51% of the total evaporation in the fleeced sheep (summer) while its contribution was between 15% and 54% in the shorn sheep (summer). It is possible that cutaneous evaporation was over-estimated since it was only determined on a small skin area which might not be representative.

11. Evaporative cooling varied in relation to changes in skin and ambient temperature and had little relation to changes in rectal temperature. These results substantiate those of Finch (1972a), also obtained in an outdoor environment and contradict the results of Taylor (1969) who found that evaporative cooling was positively correlated with body temperature in laboratory studies. Although both cutaneous and respiratory evaporation in the fleeced sheep were positively related to skin temperature, in the shorn sheep cutaneous evaporation showed a negative relationship with skin temperature. In the shorn sheep high ambient and skin temperatures resulted in a very high respiration rate. This in turn may have lead to cooling of the brain, thereby depressing the rate of cutaneous evaporation via hypothalamic control.

12. The heat balance results show that heat gain was always larger than heat loss in the fleeced sheep and I obtained a positive percentage error of 2-15%. Nevertheless, the fleece functioned as an excellent

insulator and the heat load at skin level was probably over-estimated. In contrast, the measurements on the shorn sheep showed a negative percentage error of 7% and 15%. Although the thin pelage definitely enhanced heat loss, the heat load at skin level was probably underestimated because the penetrance of short-wave radiation into the fleece was ignored.

13. The pelage of sheep plays an important role in the adaptation of this species to both hot and cold environments. The thick fleece provides excellent insulation against heat gain and loss. Nevertheless, the thin fleece of a shorn sheep probably enhances heat loss under summer conditions and, furthermore, the lighter colour decreases short-wave radiative heat load. Therefore, the physical heat exchange at the external surface reduces the demands for physiological thermoregulation and assists the sheep in maintaining a stable body temperature.

CHAPTER 3

THERMOREGULATION AND RENAL FUNCTION IN THE SPRINGBOK, *ANTIDORCAS MARSUPIALIS*

INTRODUCTION

Ungulates are very widely distributed and, in consequence, display a variety of thermoregulatory patterns. Due to their large size, they cannot escape from climatic stress efficiently and have in many instances developed considerable tolerance to thermal stress. Previously, thermoregulatory studies on ungulates were mainly concerned with domestic species. However, more recently the importance of studies on wild ungulates has been appreciated but the total number of studies still remains small (Schmidt-Nielsen 1959; Taylor 1970 and 1972; and Maloiy and Hopcraft 1971). Most of these studies have been conducted in climatic chambers and as yet, very little work has been done on wild ungulates in their natural environment. Bligh and Harthoorn (1965) and Harthoorn *et al.* (1970) measured the deep body temperature of a number of wild ungulates in an outdoor environment. They reported wide nychthemeral variations in body temperature with comparable variations in respiration and heart rates.

Finch (1972) studied the energy exchange between the eland and hartebeest and their environment. She concluded that the colour and structure of these animals' coats play an important role in their thermal adaptation to their environment.

In the first chapter, I examined the importance of the pelage *per se* in thermoregulation. The role of the pelage can, however, be evaluated far better when the live animal is studied in an outdoor environment. Under natural conditions the full repertoire of thermoregulatory adjustments, including shade-seeking, orientation of the long axis of the body and exploitation of the convective effect of wind, can be examined. Also by measuring the micro-climate the relative importance of the above adjustments in relation to solar radiation, wind and other physical factors can be evaluated. For these reasons the present study was conducted in a natural environment and wherever possible, use was made of radio-telemetry to minimise the stressful effects of restraint.

In the previous chapter, I described the energy exchange between Namaqua-Afrikaner sheep and the environment in depth. The sheep is a domestic ungulate and possesses a very thick pelage. I decided to study another ungulate species in an outdoor environment to compare with the sheep. In this instance, I wanted a wild ungulate species with interesting pelage characteristics. The springbok (*Antidorcas marsupialis*) was my choice because this species has a relatively thin pelage with interesting colour patterns. Also, the springbok occupies semi-desert to desert habitats in southern Africa and many authors (Shortridge 1934; Greenwald

1967; Child *et al.* 1971; and Bigalke 1972) have reported that this species can survive in hot, arid areas with little or no drinking water. Moreover, nothing has been published as yet about the thermoregulatory abilities of the springbok. I therefore decided to study physiological thermoregulation in restrained and unrestrained springbok in a natural environment. I was also interested in examining behavioural thermoregulation and the importance of the physical pelage properties in the thermal balance of this species. In view of the springbok's ability to survive without drinking water, an attempt has also been made to study the renal physiology of this species as an integral part of the thermal balance.

PROCEDURE

Study on restrained springbok

This experiment was conducted on the farm Vrolijkheid (19° 53'E, 33° 55'S), situated in the semi-desert, Little-Karroo region of South Africa. Data were collected on ten different days during the months February, March and April. The animal was confined outdoors in a crate constructed of thin steel piping. The crate restricted the animal to one position (facing North) and provided a minimum amount of shade. Water and food were provided *ad lib.* My original intention was to use eight experimental animals, but circumstances beyond my control caused the accidental death of all the animals, apart from one tame male. This sole survivor was used in the experiment, after it had been subjected to a training period of several months. Springbok are very restless, nervous animals and even tame animals resist handling. In the beginning of the training period this animal often attempted to break out of the crate and tried to remove the thermisters with its hooves and horns. At the end of the training period, however, the springbok became calm and even allowed me to make alterations to the probes without the need to restrain him forcibly. In my opinion, the animal was calm during the experimental procedures but I cannot claim that it suffered no psychological stress.

The following environmental and physiological measurements were monitored hourly: Ambient temperature was measured with a shaded S.A.B.S. approved mercury thermometer. I standardized all the thermister probes against this thermometer and connected them to a YSI telethermometer. Sun temperature was measured at the crate with an air temperature thermister probe (No. 405). I used surface probes (No. 409) to measure ear and horn temperatures. The probe on the ear was fixed with surgical tape to the inside of the ear, 8 cm from the tip. Similarly, the probe on the horn was fixed on a smooth area, 5 cm from the proximal end. Rectal temperature was measured with a general purpose probe (No. 401) and was inserted to a depth of 10 cm. A Barnes infrared thermometer was used to measure dorsal surface temperature. Four measurements were taken, namely on the neck, shoulders, back and rump, and the mean surface temperature was calculated. Respiration rate was determined visually by counting movements of the thoracic cage with the help of a stop-watch. I checked the accuracy of this method with a pneumograph belt, connected to a Washington oscillograph. I used a wet and dry bulb swinging hygrometer and conversion tables to determine relative humidity of the ambient air. The windspeed was measured with a three-cup anemometer. During each reading, notes were made on the general sun or shade conditions and the proportion of the sky covered by clouds (fractions of eight).

For comparative purposes, a Namaqua-Afrikaner sheep was studied simultaneously with the springbok on three different days. The measurements on the sheep included respiration rate, rectal and surface temperature, which were recorded in the same manner as described in the previous chapter.

Telemetry studies

The first experiment was conducted during January, 1978 on the farm Benfontein (24°49'E, 28°49'S) 10 km from Kimberley. Three experimental animals were caught in nets, weighed and anaesthetised with Nembutal. Thereafter, a small incision was made on the lateral surface of the abdomen, immediately posterior to the last rib. The sterile temperature transmitter was then inserted into the peritoneal cavity and the wound was sutured. Finally, Penicillin (compropen) was administered and Necrospray (gentian violet) was applied to the surgical incision. Each operation lasted for *ca.* one hour and the animals were released into the study-paddock after they began to show signs of recovery. Each transmitter was calibrated against a S.A.B.S. approved mercury thermometer before it was implanted into the animal. The accuracy of the transmitter was ± 0,2°C.

The study-paddock was *ca.* 40 000 m^2 in size and contained grasses, low shrubs and a water trough. One side of the fence was covered with hessian to provide a blind and thus the animals could be observed without being alarmed. The meteorological equipment was installed in this area and the following measurements were recorded:- Total incident short-wave radiation was measured with a Kipp's solarimeter. A small black shield was used to obscure the direct rays and diffuse radiation from the sky was also measured. The solarimeter was then rotated by 180° to measure short-wave radiation reflected from the ground. I used a three-cup anemometer, which was installed one metre above the ground, to measure the windspeed. The meterage was recorded over a one-hour period to obtain an average windspeed. Ambient temperature was measured in the shade with the S.A.B.S. approved mercury thermometer, which was used to calibrate the transmitters. The ground-cover in the study-paddock was mapped and I selected four cover-types as being representative. The mean ground temperature was then calculated from four measurements made on each cover-type during each observation. I used a Barnes infrared thermometer to measure the ground and cloud-base temperatures. A wet and dry bulb swinging hygrometer and conversion tables were used to determine relative humidity of the air. Finally, the fraction of the sky covered with clouds as well as the type of clouds present were recorded during each observation.

The observations were made hourly over a period of seven days. During each observation, I recorded the meteorological data and the animals' deep body temperatures. I also recorded certain behavioural responses of each animal:

a) whether the animal was in the sun or in shade;

b) whether the animal was standing, walking or lying; and

c) if the animal orientated its long body axis parallel to the sun or not.

My original intention was to study the three springbok for seven days while water was freely available and then to remove the water supply. However, on the eighth day of study, the springbok were disturbed by an unauthorized intruder, took fright and escaped by clearing the 2,2 m high enclosure. This incident necessitated a second experiment, which was conducted several months later.

This second study was conducted during January 1979 in the Tygerberg Zoopark (18° 50'E, 33° 48'S) *ca.* 50 km from Cape Town. Two springbok were darted with a mixture of M99, Sernylan and Siquil. The same temperature transmitters were used, and the surgical procedure was the same as described in the previous experiment. The animals were released in an enclosure (*ca.* 40 000 m²), which contained grasses and low shrubs. They were left for two days to recover from the operation and the water supply was removed on the third day. The enclosure contained a small tree which the animals sometimes used for shading.

I recorded the same meteorological data and used the same methods as described in the previous experiment.

Profile area measurements

Individual springbok were photographed from the front, back and side. A piece of cardboard with fixed dimensions was placed next to the springbok to serve as a reference area. Subsequently, the photographs were enlarged and the profile areas were measured on a planimeter. The true profile areas were calculated in the same way as described in the previous chapter for sheep. The total skin surface areas of the springbok were calculated from Mitchell's (1927) formula, where $A = 0{,}09\ W^{2/3}$ (W is in kg). Furthermore, I used the photographs and the planimeter to determine the proportion of the different colours in a front, back and lateral profile.

Behavioural thermoregulation

This study was conducted on the farm Benfontein directly after the telemetry experiment had been concluded. I observed the animals in a large camp (*ca.* 50 ha) in which hunting had been prohibited for several years and consequently, the springbok were quite tame and never appeared to be disturbed by my presence. Observations were recorded every ten minutes by scanning a random group of 30 animals in a herd of 150. During each observation the number of springbok in each of the following positions was counted:

a) Standing with their faces orientated towards the sun;
b) Standing with their rumps orientated towards the sun;
c) Lying down;
d) Shading;
e) Random orientation.

I also recorded:

a) The presence or absence of direct solar radiation;
b) The cloud cover as fractions of eight;
c) The windspeed;
d) Ambient temperature and relative humidity at hourly intervals.

The observations were recorded on five consecutive days.

Renal function

Plasma and urine samples were collected on three different occasions from springbok which were killed by headshots. The blood was aspirated directly from the ventricle, centrifuged in the field, and both plasma and urine were immediately frozen for later analysis. The analyses included the following determinations. Osmolalities were determined by freezing-point depression, using an automatic osmometer (Advanced Instruments, model 6731 RAS). The concentration of urea was determined enzymatically by the method of Fawcett and Scott (1960) and a Beckmann (Model 25) spectrophotometer. Sodium and potassium concentrations were determined, using standard flame photometric techniques (Instrumentation Laboratory, IL 243). The concentration of chloride was determined by the method of Schales and Schales (1941).

Kidneys from 62 springbok were collected on the farm Benfontein and used to determine gross morphology. The kidneys were weighed and the width (W), length (L) and depth (D) were measured with vernier calipers. Thereafter, the kidneys were bisected medially and the widths of the cortex and medulla were measured at 10 intervals along the periphery. The cortico-medullary ratio was calculated from the means and I used Sperber's (1944) method to determine kidney size and relative medullary thickness (RMT).

$$\text{Kidney size} = \sqrt[3]{L \times W \times D}$$

$$\text{RMT} = \text{Medullary thickness} \times 10 \, / \, \text{kidney size}$$

RESULTS AND DISCUSSION

PHYSIOLOGICAL THERMOREGULATION

Surface temperature

In Fig. 34 I have illustrated surface and rectal temperatures recorded on the restrained springbok during an exceptionally hot day. When the animal was exposed to solar radiation dorsal surface temperature was much higher than ambient temperature. In chapter 1 I reported that the fawn-coloured part of the springbok pelt had a mean absorptance of 0,60. Thus, despite the fact that *ca.* 40% of the solar radiation was reflected, surface temperature reached values as high as 60°C. However, in this particular example, windspeed varied between 0 - 2 m s^{-1} during the hottest part of the day. Therefore, convective cooling would have been minimal and thus high surface temperatures would be expected. Between 14h00 and 16h00 a further increase in ambient temperature occurred, while windspeed remained very low. Nevertheless, dorsal surface temperature decreased considerably because of the decreasing solar elevation. In the early afternoon, pelage surface temperature was higher than rectal temperature. Therefore, the animal should have gained heat from the environment. The fact that rectal temperature rose above 40°C illustrates that some heat was stored during the hottest part of the day. In the late afternoon, however, pelage surface temperature decreased below rectal temperature. At this stage, heat flow was reversed towards the environment and as expected rectal temperature decreased below 40°C. Finally, Fig. 34 illustrates that while in the shade,

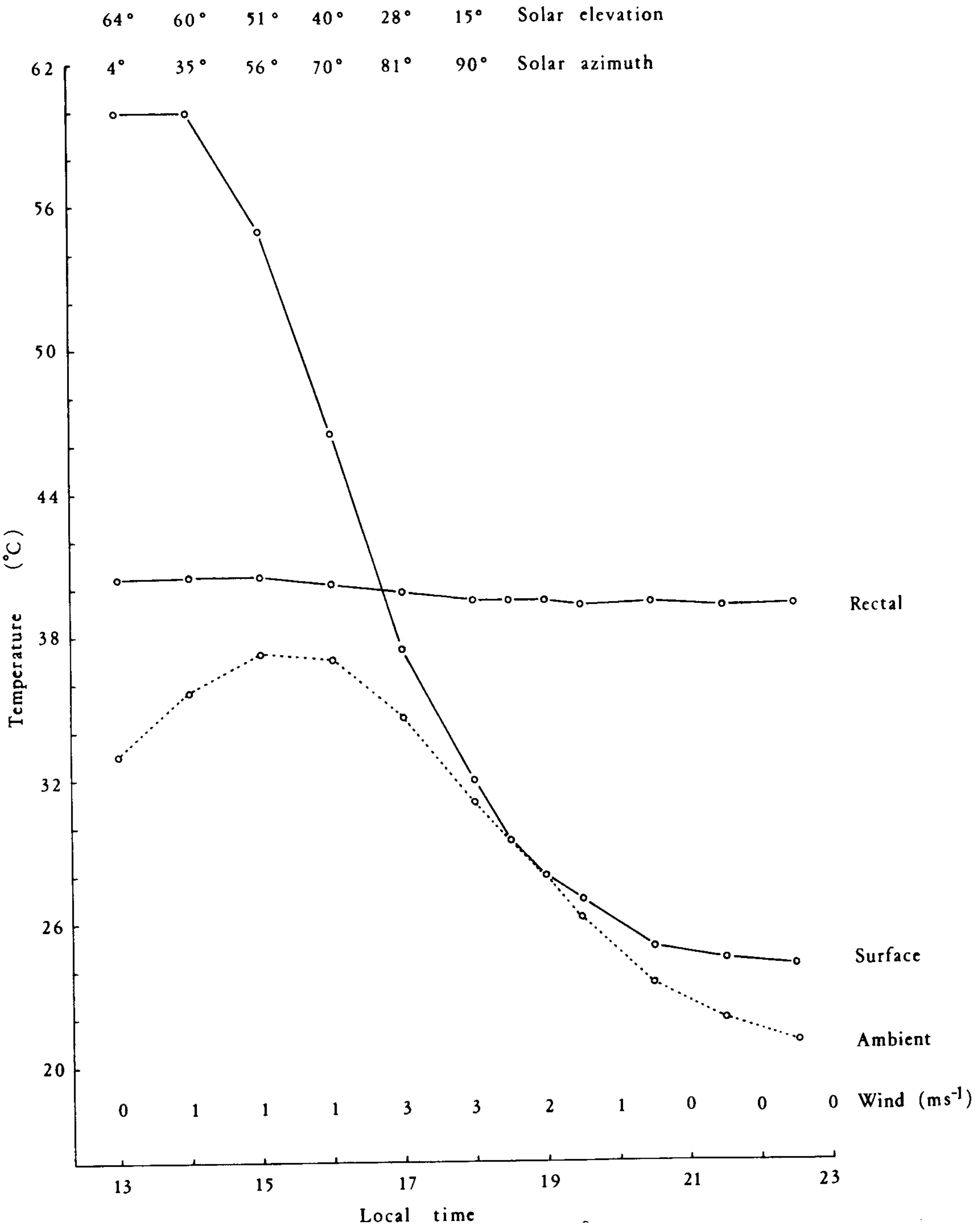


Figure 34 Surface and rectal temperatures of a restrained springbok during an exceptionally hot day

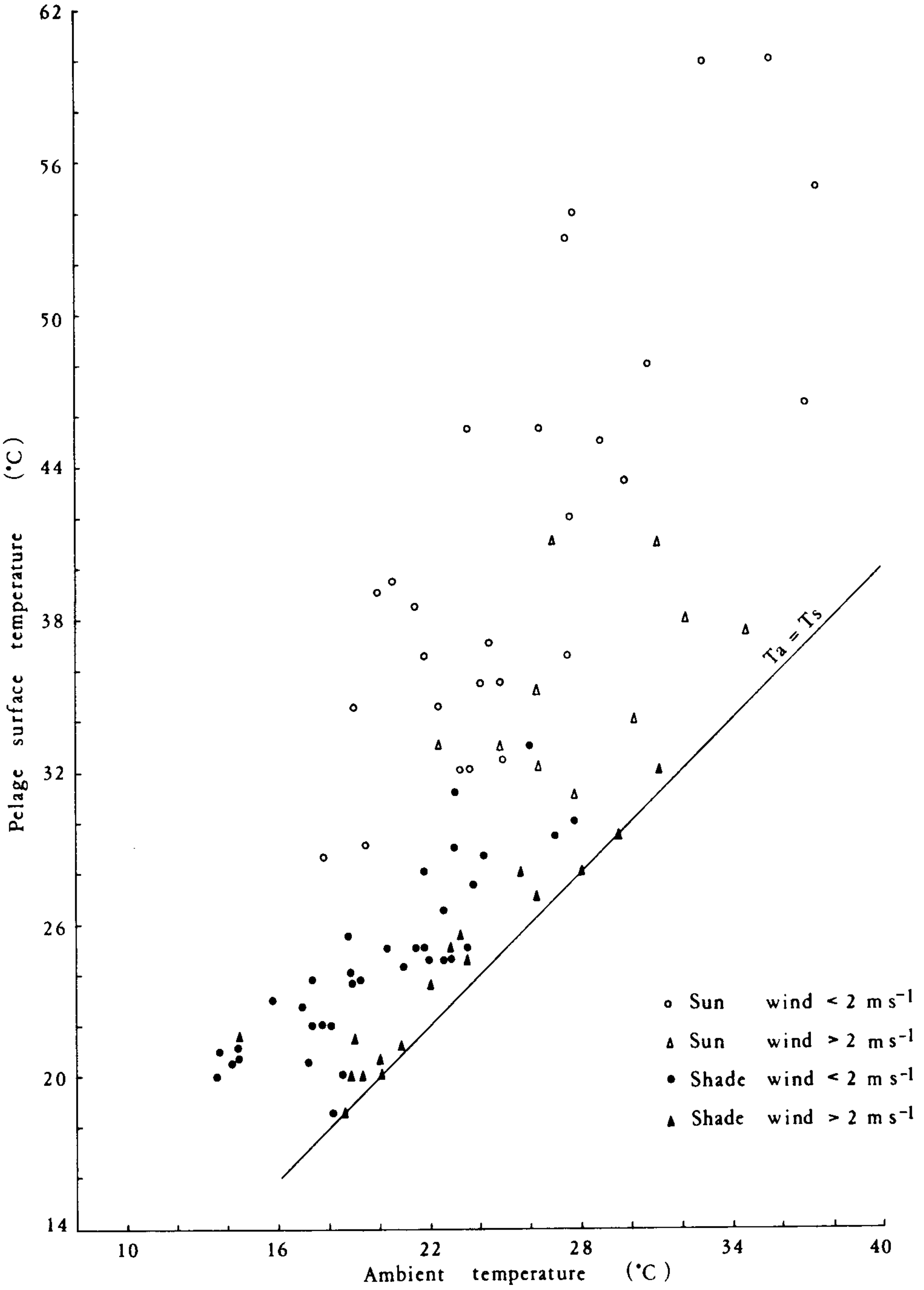


Figure 35 The influence of the sun, wind and ambient temperature on the pelage surface temperature of springbok

pelage surface temperature was still higher than ambient temperature. This suggests that the pelage provided imperfect insulation and that body heat was responsible for raising the pelage surface temperature above ambient temperature.

Surface temperature was not only influenced by ambient temperature, but also by solar radiation, windspeed and the insulative properties of the pelage. Certain of these aspects are illustrated in Fig. 35. This figure shows that an increase in ambient temperature caused an increase in surface temperature. While in the shade, the difference between ambient and surface temperature fluctuated between 0 and 8°C. However, when the animal was exposed to solar radiation, the difference fluctuated between *ca.* 3 and 27°C. Figure 35 also illustrates the cooling effect of wind. At all ambient temperatures, the smaller gradients generally coincided with the higher windspeeds. Thus higher windspeeds would, as expected, be highly beneficial for the animal in a hot environment, if $Ta < Tb$, and would reduce the environmental heat load on the animal. However, in a cold environment, high windspeeds would result in an elevated 'lower critical temperature' and thus increase the demands on metabolic heat production.

Rectal temperature

Effect of surface temperature

In any homeotherm the animal can only maintain a stable body temperature

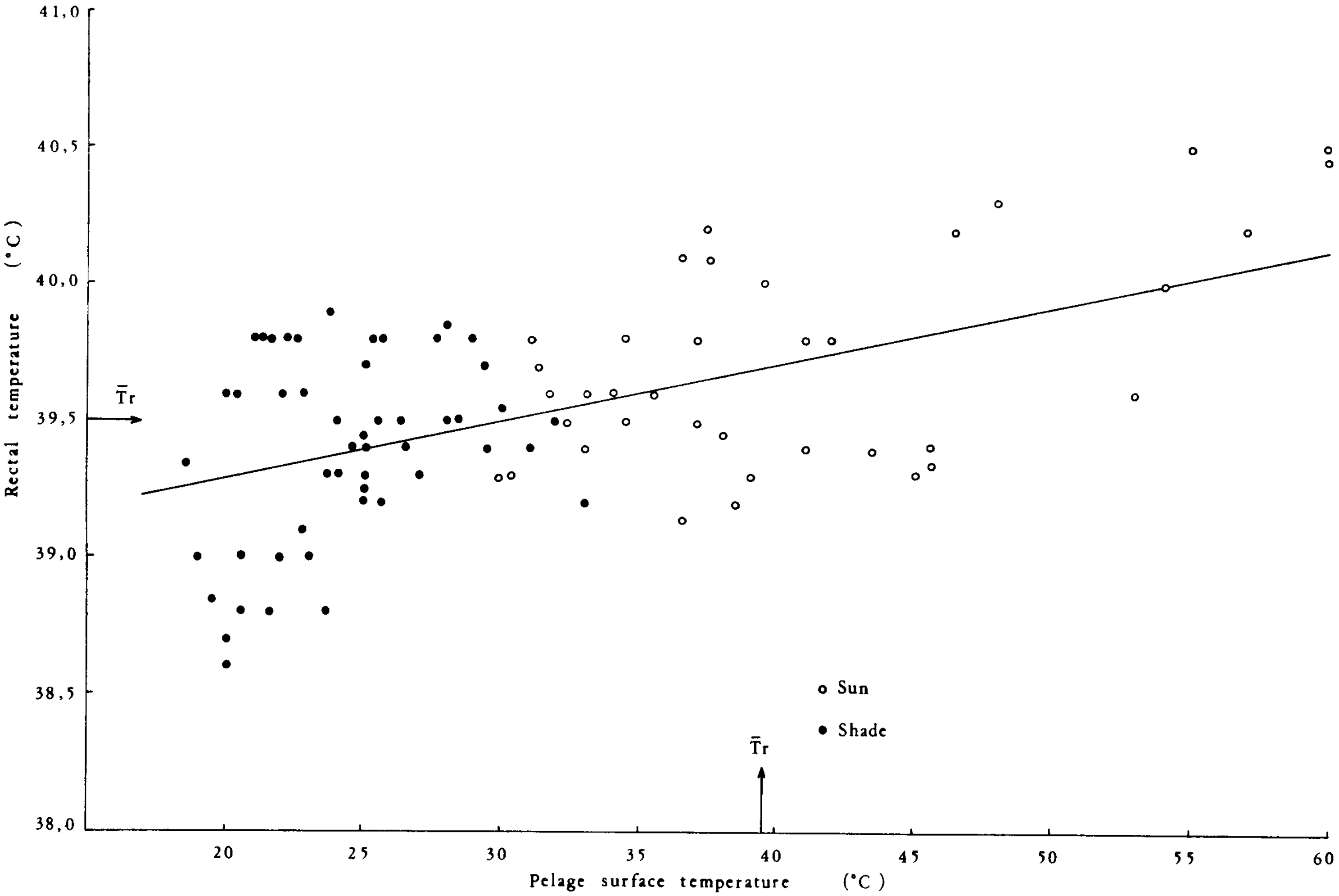


Figure 36 The influence of the pelage surface temperature on the rectal temperature of springbok

if heat gain equals heat loss. In the absence of solar radiation, ambient temperature gives a reasonably good indication of the heat load on the animal. However, in an outdoor environment, surface temperature gives a better indication. The relationship between pelage surface and rectal temperature is illustrated in Fig. 36. The mean rectal temperature was 39,52 ± 0,39°C while surface temperatures frequently exceeded mean rectal temperature. The highest surface temperature recorded in the sun was 60°C, while 33°C was the highest surface temperature recorded in the shade. Thus in the shade, heat flow was always away from the animal, while it was often directed towards the animal in the sun. As expected, rectal temperature showed a slight increase with increasing surface temperature and the relationship between these variables can be expressed by the regression equation: $y = 0{,}02\ X + 38{,}87$ ($r^2 = 0{,}27$). The increase was, however, very small and the predicted increase in rectal temperature from the regression equation, when surface temperature increases from 20 to 60°C, is only 0,84°C. Figure 36 also shows that greater variations in rectal temperature than the above ~~was~~ were measured at a particular surface temperature. Therefore, it would appear that only a small percentage (27%) of the variation in rectal temperature can be explained by the variation in surface temperature. The springbok thus maintained a comparatively stable body temperature under widely different environmental heat loads.

Degree of thermolability

Yousef (1976) stated that certain species of wild ungulates maintain a rather stable rectal temperature (ΔTr = 1 - 2°C) while others allow their rectal temperature to fluctuate by as much as 7°C. Taylor (1969a), for example, reported fluctuations between 33,9 and 41,2°C for hydrated eland and between 35,7 and 42,1°C for hydrated oryx. His results, however, were recorded under simulated desert conditions in climatic chambers. In contrast, Bligh and Harthoorn (1965) studied the deep body temperature of eight different ungulate species in their natural environment by means of telemetry. They reported nychthemeral variations between 1 and 3°C. Similarly, Harthoorn *et al.* (1970) studied the eland, hartebeest and Boran cattle and perusal of their data shows individual fluctuations between *ca.* 2 and 4°C. Considerable interspecific differences in thermolability appear, therefore to exist.

In my studies on both the restrained and unrestrained hydrated springbok, I obtained measurements of body temperatures when ambient temperatures varied between 13 and 39°C. The minimum and maximum body temperatures recorded for all animals were 37,5 and 41,0°C, respectively (Table 15). However, the maximum fluctuations recorded for individual springbok varied between 0,5 and 3,2°C with a mean of 1,57°C. Consequently, the results obtained for hydrated springbok in this study fall within the ranges reported by other authors for hydrated ungulates under natural conditions and they show only moderate thermolability. Several studies have been conducted on the physiological responses to dehydration in various ungulate species. Schmidt-Nielsen *et al.* (1957) reported that the body temperatures of dehydrated camels fluctuated between 34°C in the morning and 41°C in the late afternoon in contrast to fluctuations of only *ca.* 2°C under hydrated conditions. The results of Harthoorn *et al.* (1970) show that dehydration (15% of original body weight) had very little effect on the body temperatures of eland and Boran cattle. They did, however, find that fluctuations in the body temperature of the hartebeest increased from *ca.* 2°C to *ca.* 3,5°C after dehydration. It would seem, therefore, that dehydration has different effects on the various ungulate species. Table 15 shows that the fluctuations in body temperature of the two dehydrated springbok were significantly greater than the fluctuations measured when they were hydrated. However, these springbok were studied in the hydrated condition for only a short period and thus under limited environmental conditions.

When the dehydrated individuals are compared with all the hydrated individuals, a different picture emerges. The body temperature fluctuations for the dehydrated springbok (ΔTb = 2,0 and 2,5°C) fall well within the range which I reported for hydrated springbok (ΔTb = 0,5 - 3,2°C). Consequently, the results show that individual springbok with a very stable body temperature in the hydrated condition, relax their limits when dehydrated, but that the fluctuations still fall within the range recorded for other hydrated springbok. It is not possible at this stage to predict if the individuals with larger ranges in the hydrated condition would extend their limits even further, when dehydrated, or whether they would stay within the boundaries established when water is freely available.

The previous discussion makes it clear that individual differences between the animals should always be considered. The individual springbok did

Table 15 The mean body temperatures and ranges recorded from hydrated (hyd) and dehydrated (dehyd.) springbok

Animal			n	$\bar{T}a \pm s$	Ta range	$\bar{T}b \pm s$	Tb range	ΔTb
Crate	A	hyd.	93	23,0 ± 5,3	13,6 - 37,3	39,5 ± 0,4	38,6 - 40,5	1,9
Benfontein	B	hyd.	37	26,9 ± 5,2	16,3 - 34,0	39,8 ± 0,7	37,5 - 40,7	3,2
	C	hyd.	78	28,4 ± 5,5	16,3 - 38,5	39,3 ± 0,4	38,4 - 40,4	2,0
	D	hyd.	47	28,2 ± 4,6	17,0 - 34,0	40,5 ± 0,3	39,7 - 41,0	1,3
Tygergerg	E	hyd.	16	25,5 ± 2,6	21,5 - 32,0	39,2 ± 0,2	39,0 - 39,5	0,5
	F	hyd.	16	25,5 ± 2,6	21,5 - 32,0	38,4 ± 0,2	38,0 - 38,5	0,5
	E'	dehyd.	43	27,7 ± 5,0	17,5 - 37,5	39,0 ± 0,5	37,0 - 39,5	2,5
	F'	dehyd.	43	27,7 ± 5,0	17,5 - 37,5	38,7 ± 0,5	38,0 - 40,0	2,0
	F"	dehyd.	71	27,8 ± 5,4	17,0 - 38,5	38,8 ± 0,6	38,0 - 40,0	2,0

D vs. B - H.S. $(p < 0{,}001)$
B vs. A - S. $(p < 0{,}05)$
A vs. C - H.S. $(p < 0{,}001)$
C vs. E - N.S. $(p > 0{,}05)$
E vs. F - H.S. $(p < 0{,}001)$
A vs. E - H.S. $(p < 0{,}0005)$
E vs. E' - S. $(p < 0{,}05)$ ✱ $\frac{S_1^2}{S_2^2}$ $(p < 0{,}01)$
F' vs. F" - N.S. $(p > 0{,}05)$

F" vs. F - H.S. $(p < 0{,}0005$ ✱ $\frac{S_1^2}{S_2^2}$ $(p < 0{,}001)$
F' vs. F - H.S. $(p < 0{,}0005)$ ✱ $\frac{S_1^2}{S_2^2}$ $(p < 0{,}001)$
E' vs. F' - S. $(p < 0{,}02)$
E' vs. F" - N.S. $(p > 0{,}05)$
C vs. E' - H.S. $(p < 0{,}002)$
E vs. F" - H.S. $(p < 0{,}0005)$
E' vs. F - H.S. $(p < 0{,}0005)$

not only differ in their degree of thermolability, but also in the mean body temperature which they maintained. Table 15 shows that mean body temperatures of all the springbok, except in two cases, differed significantly from one another. Springbok C and E showed no significant difference and furthermore, the two dehydrated springbok did not differ significantly despite the fact that they showed a significant difference in the hydrated condition. The individual differences are emphasised further by the effect of dehydration upon the two springbok. In the case of springbok E, mean body temperature decreased significantly upon dehydration while, in contrast, it increased significantly in the case of springbok F.

Taylor (1970) found that under simulated desert conditions, the dehydrated oryx and Grant's gazelle allowed their body temperatures to rise above 45°C when ambient temperature was *ca.* 45 - 50°C. In the present study on the dehydrated springbok such high body temperatures were never recorded, even though the study was conducted under conditions of intense solar radiation, with ambient temperatures between 17 and 38,5°C. The body temperature of one dehydrated springbok, for example, fluctuated between 37°C at night and 39,5°C in the late afternoon during day 5 and 6 of dehydration. During the hottest part of the day this animal was subjected to intense solar radiation (1100 W m^{-2}) with ambient temperature at *ca.* 38°C, ground temperature at *ca.* 57°C and a windspeed less than 2 m s^{-1}. It thus seems that both hydrated and dehydrated springbok maintain a reasonably stable body temperature and that adaptive hyperthermia does not play an important role in their adaptation to hot, arid environments.

Effect of ambient temperature

Maloiy and Hopcraft (1971), Yousef and Luick (1975), Taylor (1969a, 1970 and 1972) and others have studied the effect of environmental temperature on the rectal temperature of various ungulate species. In this respect, Yousef (1976) concluded that the degree of change in rectal temperature (Tre) over a wide range of environmental temperatures (Ta) is not related to ecological distribution or to phylogeny and, secondly, that at ambient temperatures above Tre, i.e. 45 - 50°C, all wild ungulates studied to date are able to effectively thermoregulate by maintaining a stable Tre that is well below Ta. In Figs 37, 38 and 39 I have illustrated the relationship between body and ambient temperature for the six different springbok. The coefficients of determination varied between 0,04 and 0,44. Therefore, the maximum percentage of the total variation in body temperature that was explained by the fitted regression was 44%. It would appear then that variations in ambient temperature did not have a pronounced effect on the body temperature of the springbok. Nevertheless, it is also clear that individual springbok differed in their response to ambient temperature. The results become more meaningful if one compares mean body temperatures at different ambient temperature ranges. I have calculated the mean body temperature for each springbok when ambient temperature varied between 10 - 19,99°C, 20 - 29,99°C and 30 - 39,99°C (Table 16). Springbok A was the only animal which showed a significant increase in body temperature at every ambient temperature range. This animal was, however, restrained in a crate and one would expect a greater dependence upon ambient temperature in this case because the potential for behavioural thermoregulation had been excluded.

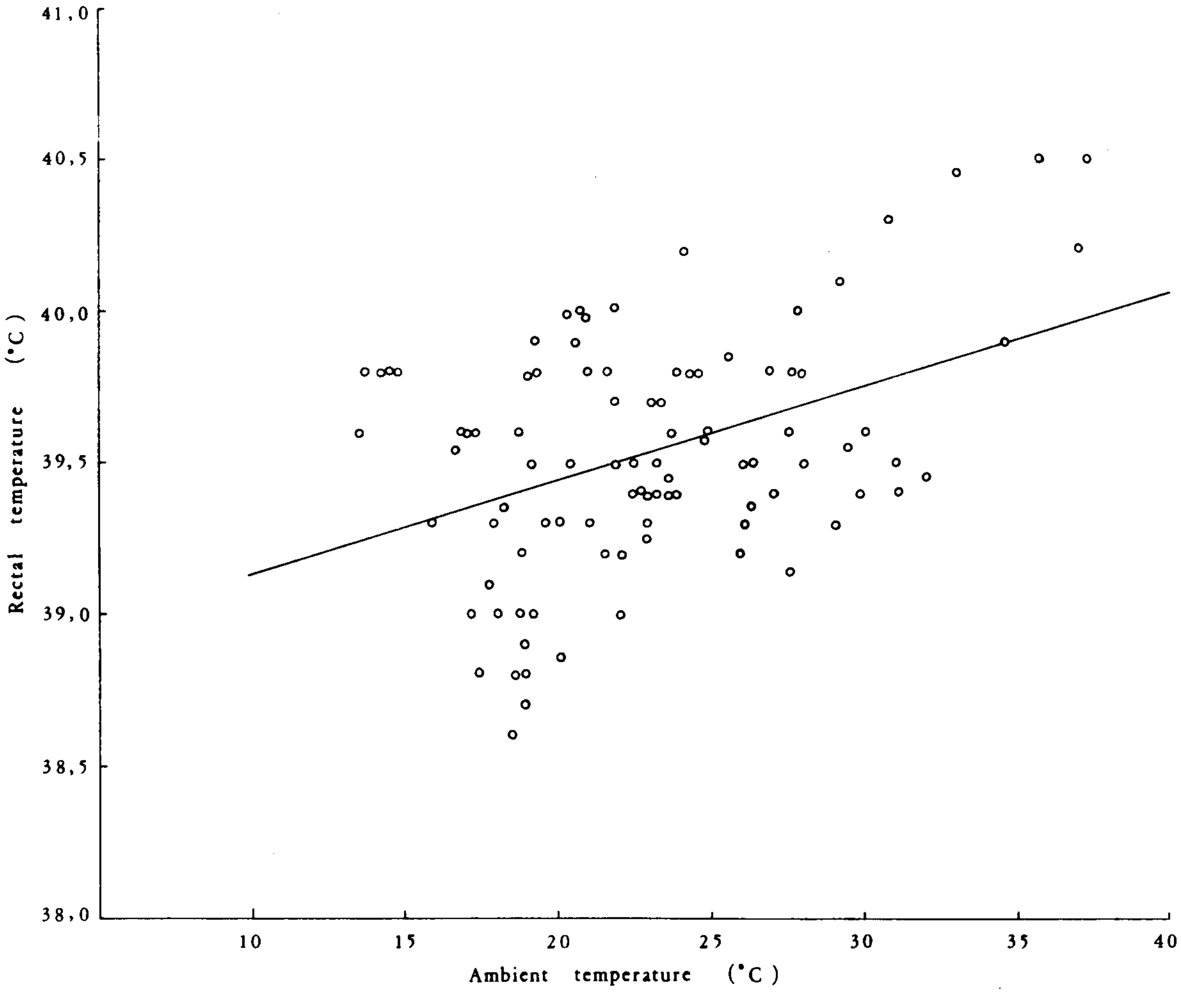


Figure 37 The relationship between rectal and ambient temperature in a restrained springbok

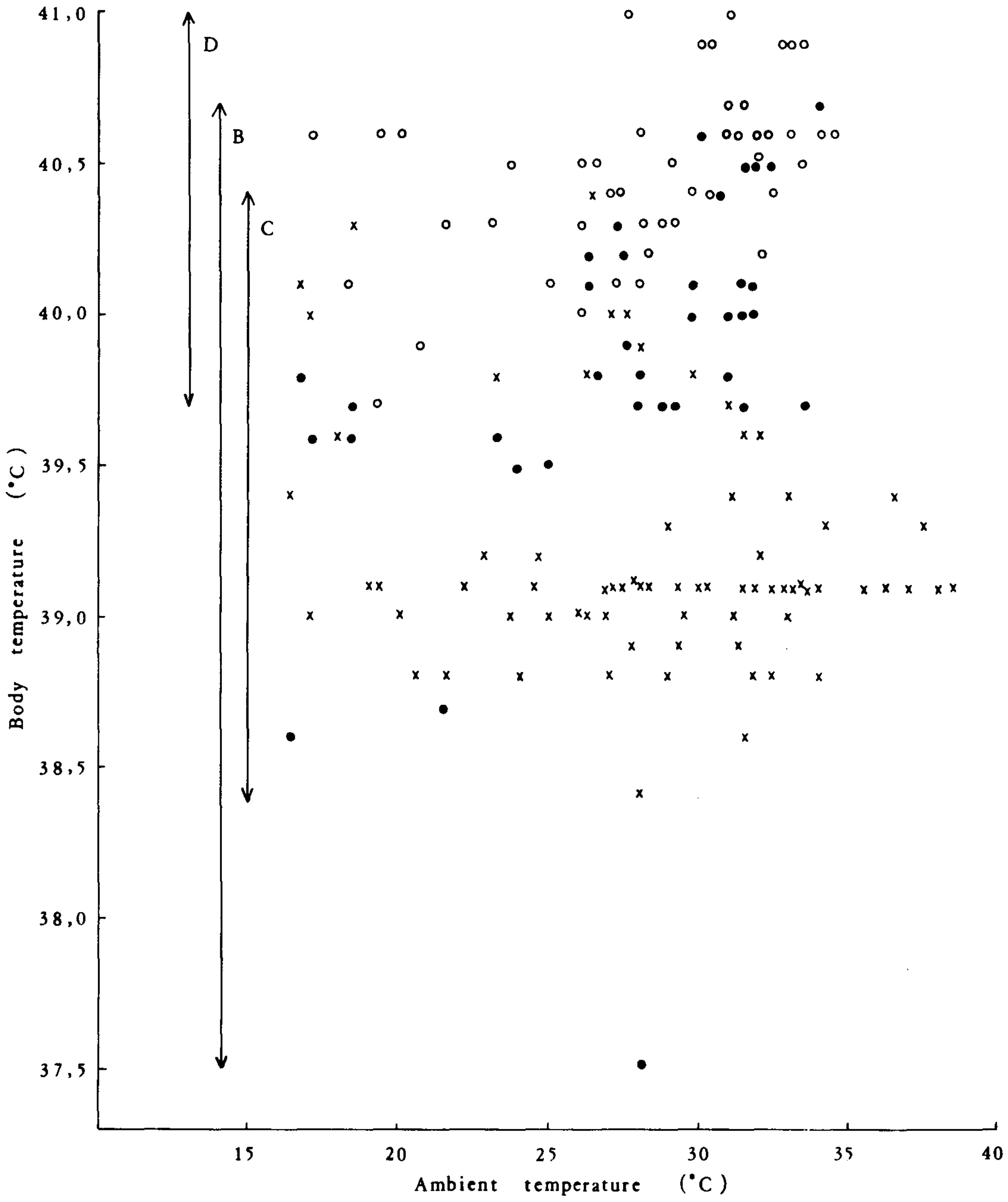


Figure 38 The relationship between body and ambient temperature in unrestrained springbok

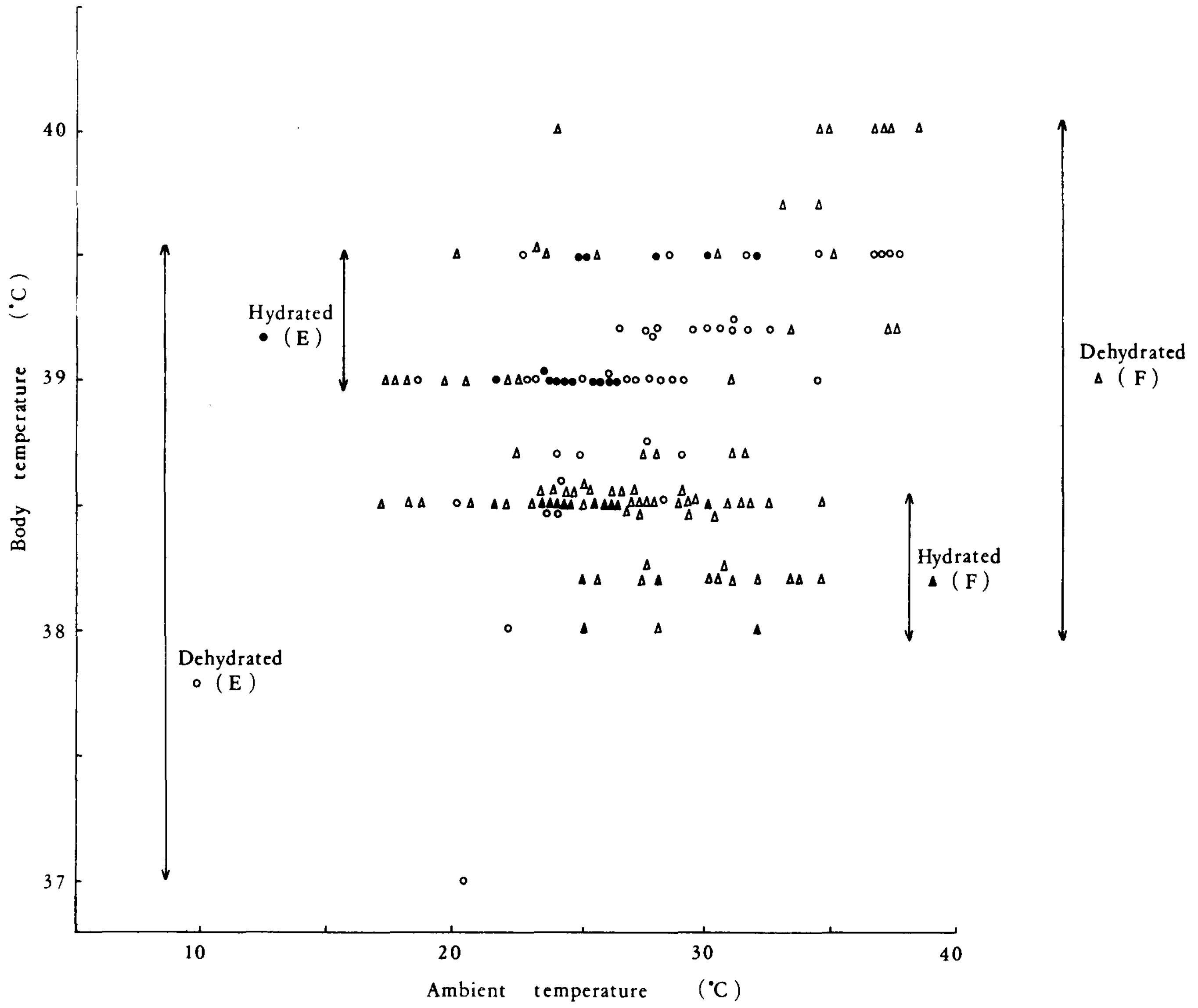


Figure 39 The relationship between body and ambient temperature in unrestrained hydrated and dehydrated springbok (Tygerberg Experiment)

Table 16 The mean body temperatures of hydrated and dehydrated springbok in various ambient temperature ranges

Animal		Condition	1 Ta = 10 - 19,99°C $\bar{T}b$ ± s (n)	2 Ta = 20 - 29,99°C $\bar{T}b$ ± s (n)	3 Ta = 30 - 39,99°C $\bar{T}b$ ± s (n)
Crate	A	Hydrated	39,33 ± 0,39 (30)	$\overset{**}{39{,}57}$ ± 0,27 (53)	$\overset{*}{39{,}98}$ ± 0,46 (10)
Benfontein	B	Hydrated	39,62 ± 0,58 (6)	39,57 ± 0,77 (18)	$\overset{***}{40{,}19}$ ± 0,35 (13)
	C	Hydrated	39,58 ± 0,51 (8)	$\overset{*}{39{,}23}$ ± 0,45 (36)	39,24 ± 0,40 (34)
	D	Hydrated	40,25 ± 0,44 (4)	40,37 ± 0,27 (22)	$\overset{***}{40{,}65}$ ± 0,24 (21)
Tygerberg	E	Hydrated		39,11 ± 0,21 (14)	$\overset{***}{39{,}50}$ ± 0,00 (2)
	F	Hydrated		38,42 ± 0,16 (14)	38,25 ± 0,35 (2)
	E'	Dehydrated	39,00 ± 0,00 (2)	$\overset{*}{38{,}83}$ ± 0,49 (28)	$\overset{***}{39{,}32}$ ± 0,18 (13)
	F'	Dehydrated	38,75 ± 0,35 (2)	38,62 ± 0,39 (28)	$\overset{*}{38{,}96}$ ± 0,59 (13)
	F"	Dehydrated	38,75 ± 0,27 (6)	38,66 ± 0,42 (38)	$\overset{**}{39{,}05}$ ± 0,69 (27)

B_1 vs. B_3 H.S. (p <0,01)
C_1 vs. C_3 S (p <0,025)
D_1 vs. D_3 H.S. (p <0,01)
E_1' vs. E_3' H.S. (p <0,0005)
F_1' vs. F_3' N.S. (p >0,05)
F_1" vs. F_3" S. (p <0,05)

E_2 vs. E_2' H.S. (p <0,01)
E_3 vs. E_3' H.S. (p <0,0025)
F_2 vs. F_2' S. (p <0,025)
F_3 vs. F_3' N.S. (p >0,05)
F_2 vs. F_2" H.S. (p <0,0025)
F_3 vs. F_3" N.S. (p >0,05)

The significance of 3 vs. 2 and 2 vs. 1 are shown by the following symbols
$*$ $p < 0{,}05$
$**$ $p < 0{,}01$
$***$ $p < 0{,}001$

The body temperatures of three remaining hydrated springbok, as well as those of the two dehydrated springbok, increased significantly when ambient temperatures exceeded 30°C. This suggests that, although physiological and behavioural mechanisms were effective, high heat loads resulted in increased body temperatures. The fact that two of the animals showed no significant increase in body temperature, again illustrates the individual differences between the animals.

Effect of exercise

In a previous experiment (Gericke *et al.* 1978) we found that the rectal temperatures of springbok can exceed 42°C after forced exercise. In the present study one of the springbok took fright and escaped from the study-paddock. Its body temperature was measured by means of telemetry immediately before the escape and after it had sprinted a distance of *ca.* 200 - 300 m. The body temperature increased from 39,6°C to 41,4°C (ΔT = 1,8°C) in this short period (Fig. 40). Prior to the sprinting episode, this particular springbok had maintained a very stable body temperature under widely different environmental conditions (38,4 - 40,4°C). It is clear therefore, that exercise can have a much greater effect on body temperature than wide variations in the environmental heat load. Taylor & Lyman (1972) found that in Thomson's gazelle exercise caused a marked increase in heat production and that heat storage accounted for 80 - 98% of the heat produced during running. They also demonstrated that the brain temperatures of exercising antelope rose more slowly than body temperatures did. They ascribed this difference to countercurrent heat

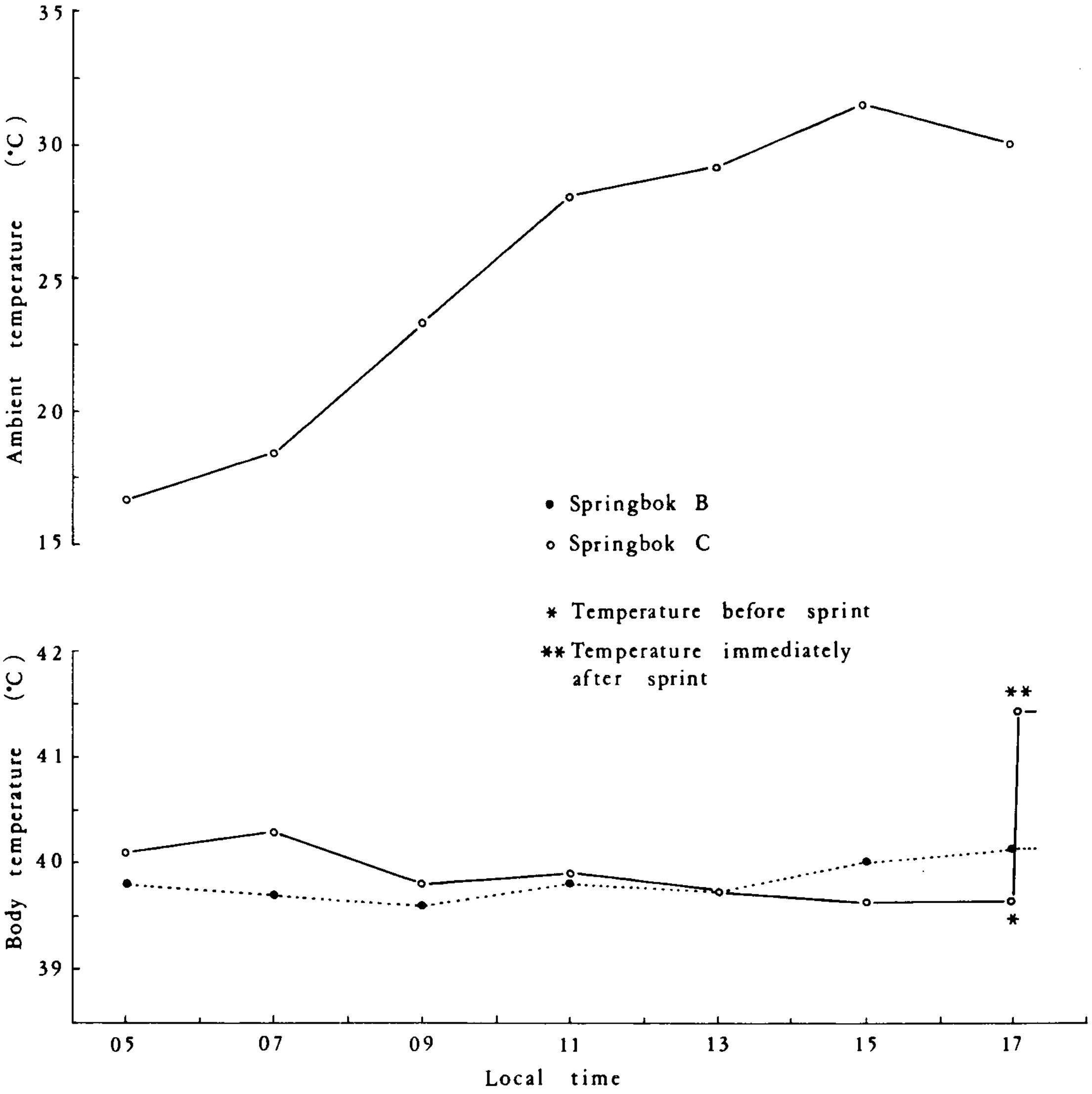


Figure 40 The effect of sprinting on the body temperature of a springbok

exchange in the carotid rete system and recorded a maximum cooling capacity of 2,7°C for this system. Springbok most likely also maintain a difference between body and brain temperature as they possess a well-developed carotid rete. It seems, however, as if the greater value of the carotid rete lies in its cooling effect during exercise rather than during normal thermoregulation at rest. The unusual short and sleek pelage of the springbok would also facilitate heat loss by convection, when sprinting short distances while escaping from predators.

Diurnal fluctuations

A number of authors have reported that fluctuations in body temperature of ungulates follow a diurnal pattern. Bligh and Harthoorn (1965) and Harthoorn *et al.* (1970) reported that the rectal temperature of unrestrained wild ungulates started to rise shortly after sunrise and reached a maximum in the late afternoon. Thereafter, the temperature decreased again to reach a minimum value just before daybreak. Bligh and Harthoorn (1965) also reported differences between species in the amplitude of their diurnal body temperature fluctuations. In Figs 41 and 42 I have indicated the diurnal variations in body temperature for four hydrated and two dehydrated springbok. The highest body temperatures were generally attained during the day while night-time temperatures were lower. However, in a few instances I found that body temperature showed an increase in the early morning, followed by a decrease and then again by a slow increase during the rest of the day. Brown (1971) reported that on a few occasions he recorded higher body

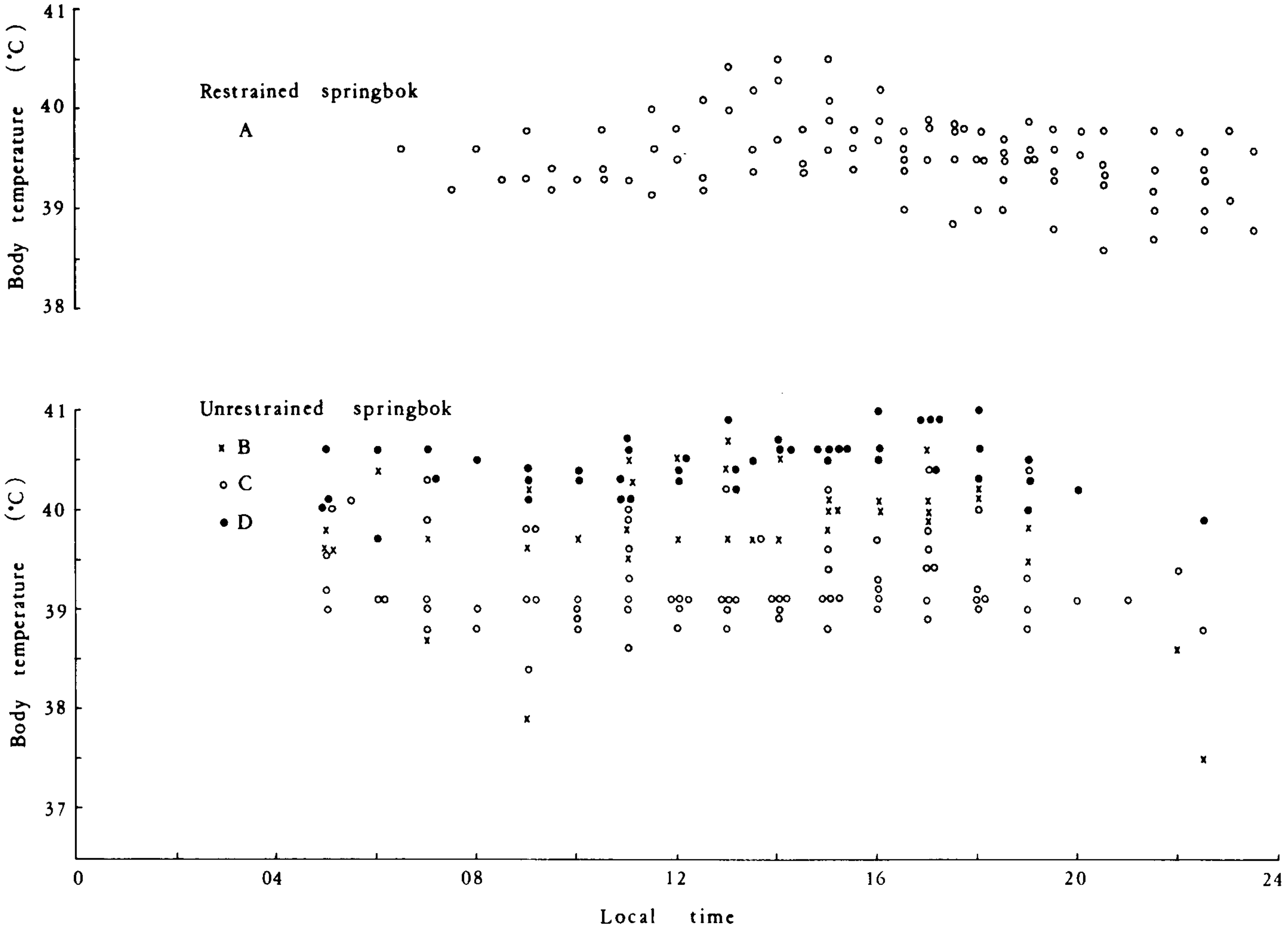


Figure 41 Diurnal fluctuations in the body temperature of hydrated springbok

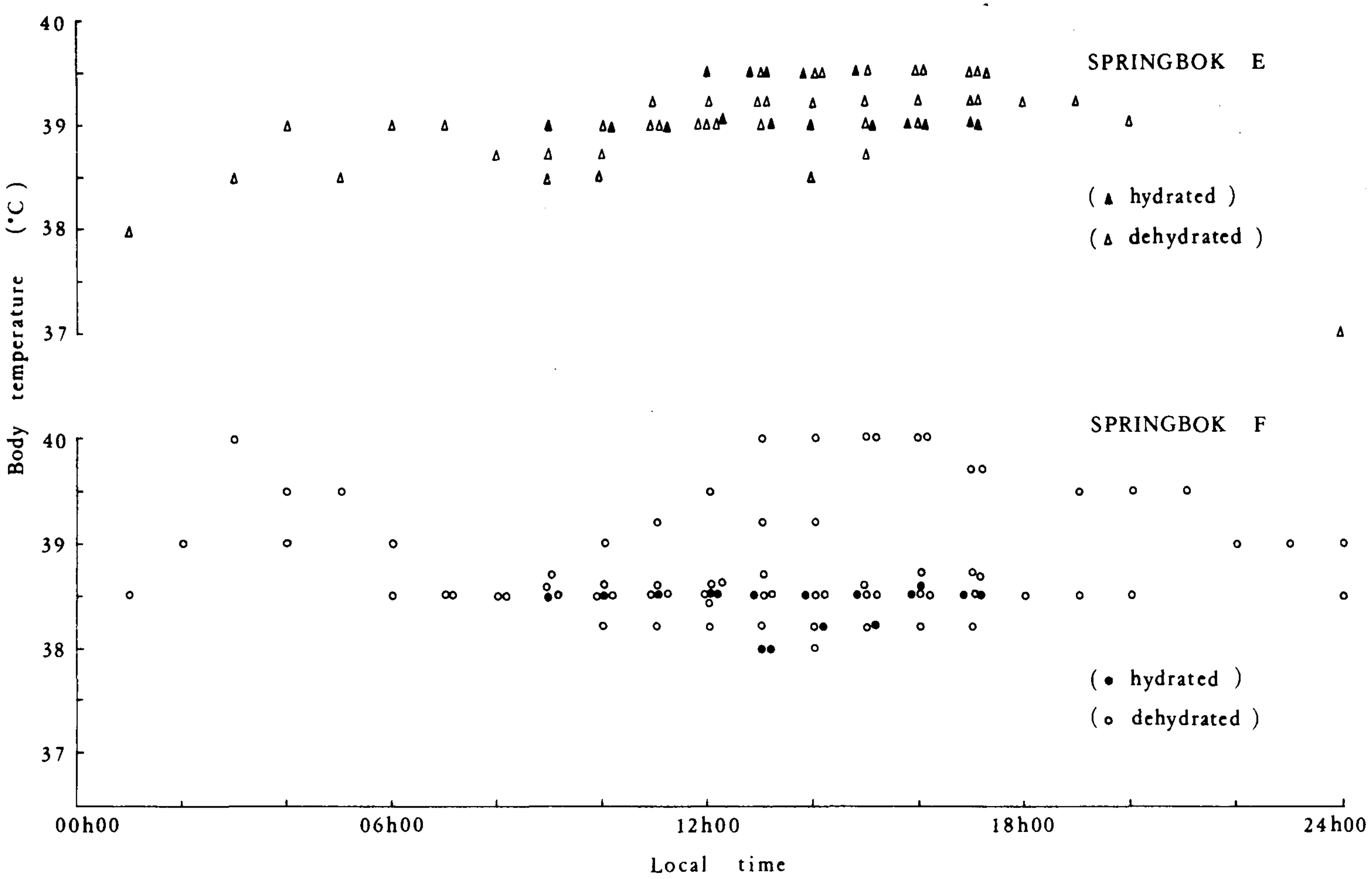


Figure 42 Diurnal fluctuations in the body temperature of hydrated and dehydrated springbok

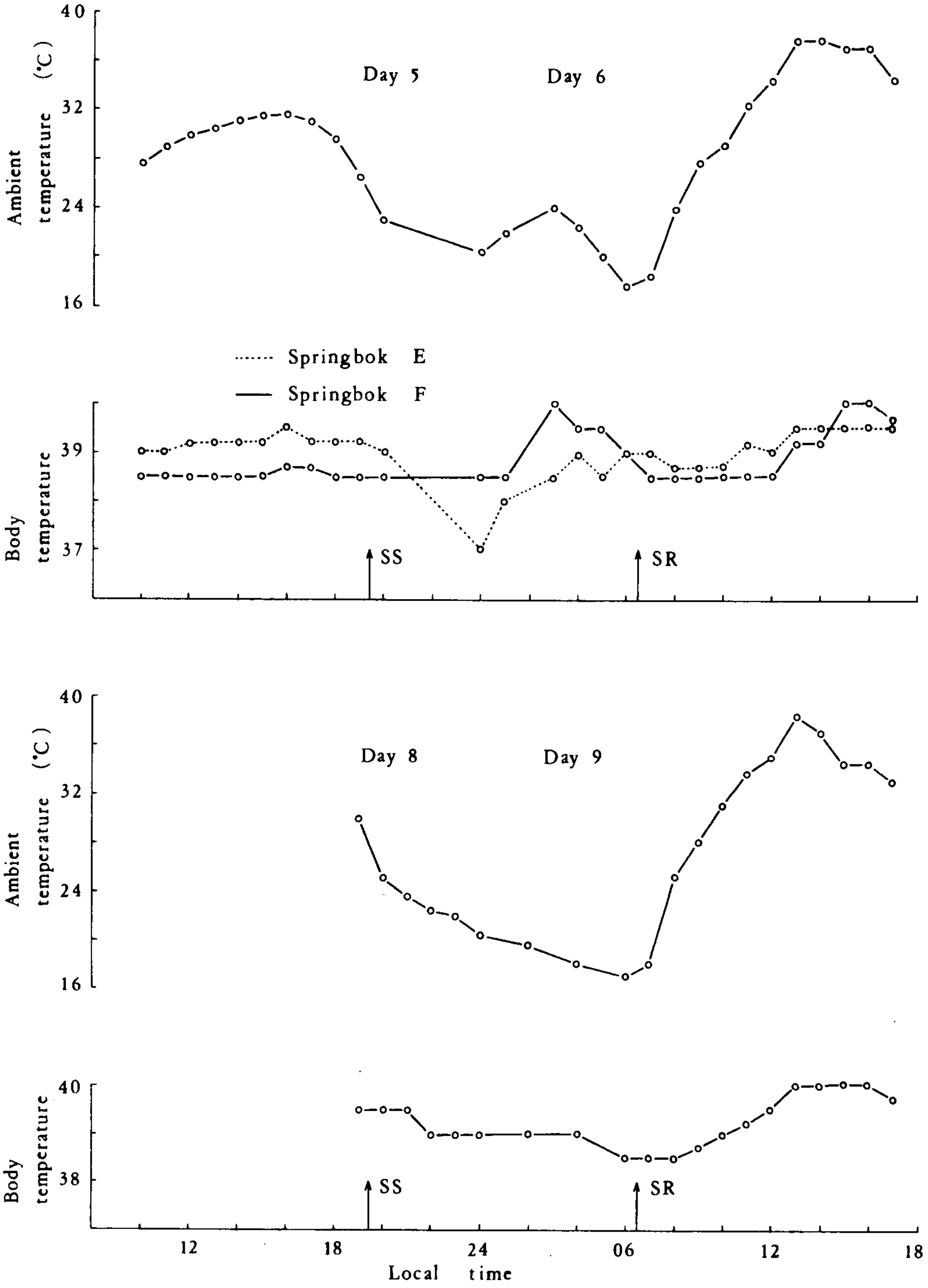


Figure 43 Diurnal fluctuations in the body temperature of dehydrated springbok

temperatures during the night than during the day in unrestrained sheep. He felt that the elevated body temperature at night could be the result of the heat increment of feeding or perhaps reflect a resetting of the set-point temperature, due to peripheral stimuli. In Fig. 43 I have illustrated this pre-dawn rise in body temperature, recorded from the two dehydrated springbok on day 6. In this specific example, ambient temperature showed a simultaneous but slight increase. It seems unlikely that such a small increase in ambient temperature could have caused the increased body temperature. In this case the heat increment of feeding was most likely responsible for the increased pre-dawn body temperature. In Fig. 43 I have illustrated another diurnal record of body temperature for one of the dehydrated animals, but in this case there was no increase in ambient temperature and also no increase in body temperature during the early morning hours.

At this stage I felt it best to analyse the diurnal variations in body temperature statistically to get a generalised picture of the possible patterns. Each day was divided into six four-hour periods and the mean body temperature during each period was calculated (Table 17). The rectal temperature of springbok A remained stable between 04h00 and 12h00 and then increased significantly. At 16h00 the rectal temperature decreased again and reached a minimum after 20h00. In springbok B, C and D, the body temperatures increased steadily during the day, but no significant difference was measured between adjacent four-hour periods. However, in both springbok B and D, the body temperatures between 12h00 and 20h00 were significantly higher than the temperatures

Table 17 Diurnal fluctuations in the body temperature of hydrated and dehydrated springbok

	1	2	3	4	5	6
Animal	00h00 - 03h59	04h00 - 07h59	08h00 - 11h59	12h00 - 15h59	16h00 - 19h59	20h00 - 23h59
A		39,4 ± 0,3	39,5 ± 0,3	39,8 ± 0,4	39,5 ± 0,3	39,3 ± 0,4
hyd.		n = 2	n = 13	n = 22	n = 34	n = 22
B		39,6 ± 0,6	39,7 ± 0,8	40,1 ± 0,4	40,0 ± 0,3	38,6 ± 0
hyd.		n = 6	n = 8	n = 12	n = 10	n = 1
	B2 vs. B4 p < 0,05 B6 vs. B2 p < 0,005					
C		39,4 ± 0,5	39,2 ± 0,5	39,2 ± 0,4	39,4 ± 0,5	38,9 ± 0,3
hyd.		n = 12	n = 18	n = 24	n = 20	n = 4
	C6 vs. C2 p < 0,05					
D		40,3 ± 0,4	40,5 ± 0,4	40,5 ± 0,2	40,6 ± 0,3	40,1 ± 0,2
hyd.		n = 6	n = 10	n = 15	n = 13	n = 2
	D2 vs. D4 p < 0,05					
E	38,5 ± 0,5	38,8 ± 0,3	38,9 ± 0,2	39,2 ± 0,3	39,3 ± 0,2	37,0 ± 0
dehyd.	n = 3	n = 4	n = 12	n = 16	n = 7	n = 1
	E1 vs. E3 p < 0,05 E6 vs. E1 p < 0,05					
F	39,2 ± 0,6	38,7 ± 0,4	38,6 ± 0,3	38,9 ± 0.7	38,9 ± 0,6	39,0 ± 0,4
dehyd.	n = 5	n = 7	n = 19	n = 24	n = 11	n = 5
	F1 vs. F3 p < 0,005 F6 vs F1 p < 0,05					

Underlined values are significantly different from one another (p < 0,05) between 04h00 and 08h00. Springbok B, C and D also showed a significant decrease after 20h00. As far as the dehydrated springbok were concerned, body temperature increased steadily during the day. In the case of springbok E, maximum body temperature was reached between 16h00 and 20h00 and then the temperature decreased again. Springbok F, however, showed a steady increase throughout the day and night and body temperature dropped to a minimum between 04h00 and 12h00. Basically there was no obvious difference between the hydrated and dehydrated springbok, and in general my results show that springbok also display a diurnal fluctuation in body temperature.

Respiration rate

Peripheral vs. central stimulus

The studies on the restrained springbok showed a positive relationship between surface temperature and respiration rate (Fig. 44). The coefficient of determination indicated that 79% of the variation in respiration rate can be explained by the fitted regression for these two variables. An increasing surface temperature obviously results in an increasing heat load and, normally, skin temperatures would also be affected. The question now arises whether the increasing skin temperature controlled the increase in respiration rate or whether a change in deep body temperature *per se* was the major controlling factor.

Figure 45 illustrates the relationship between rectal temperature and

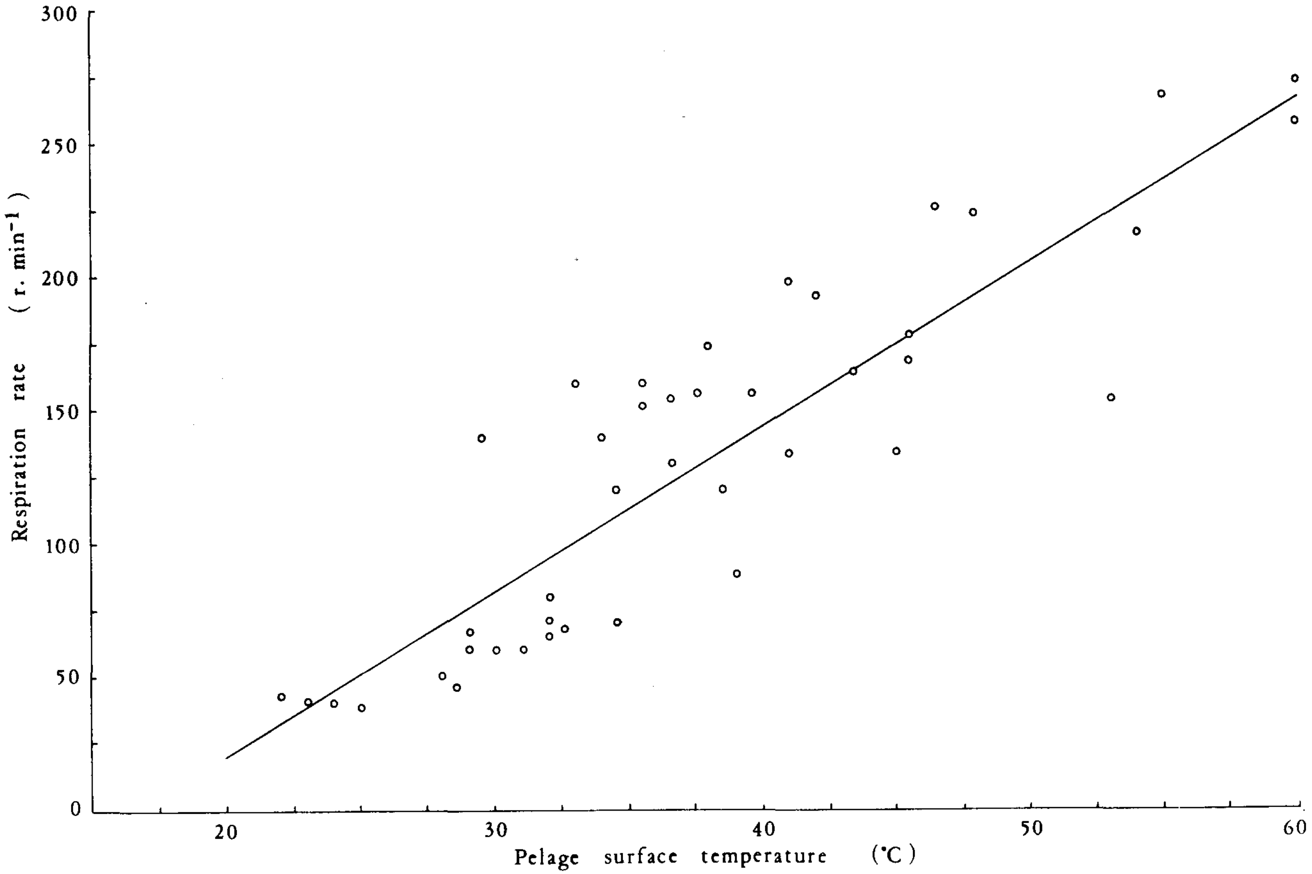


Figure 44 The relationship between respiration rate and pelage surface temperature in the restrained springbok

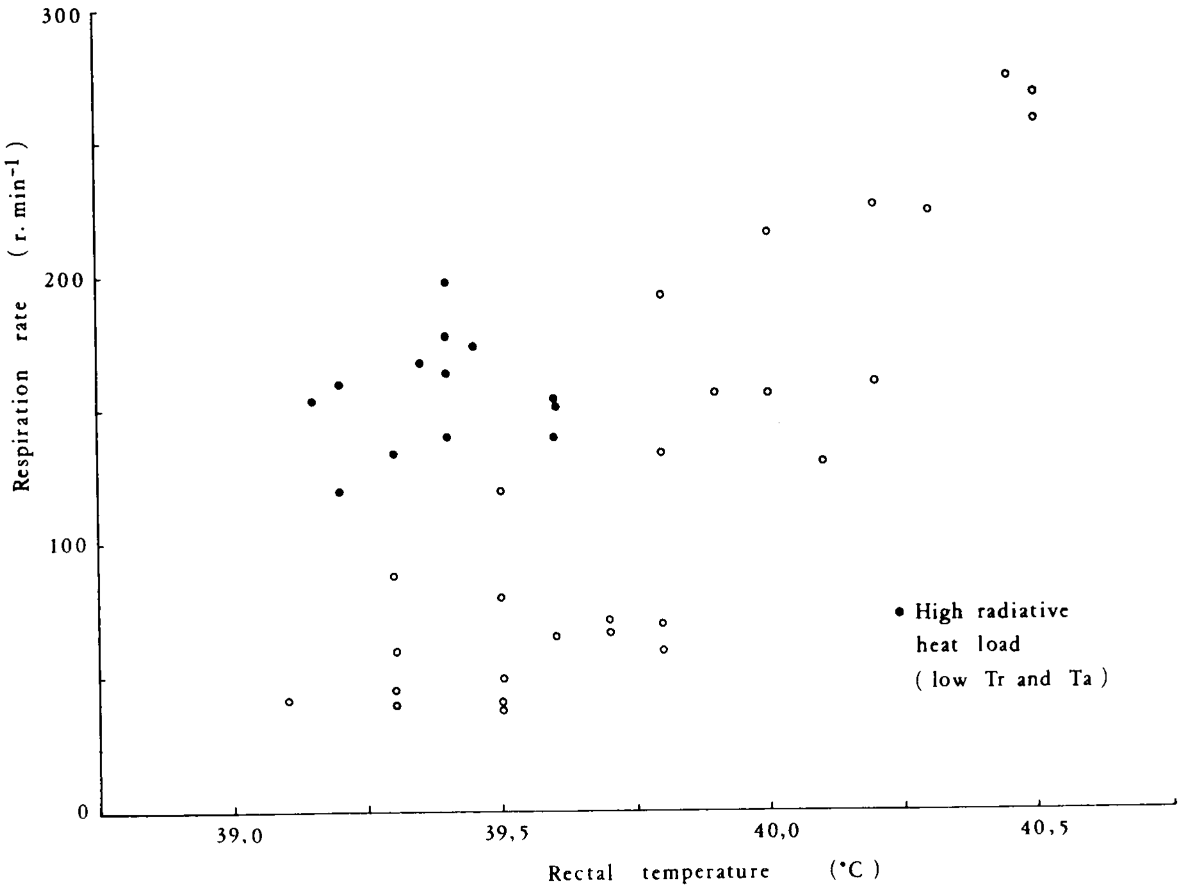


Figure 45 The relationship between respiration rate and rectal temperature in the restrained springbok

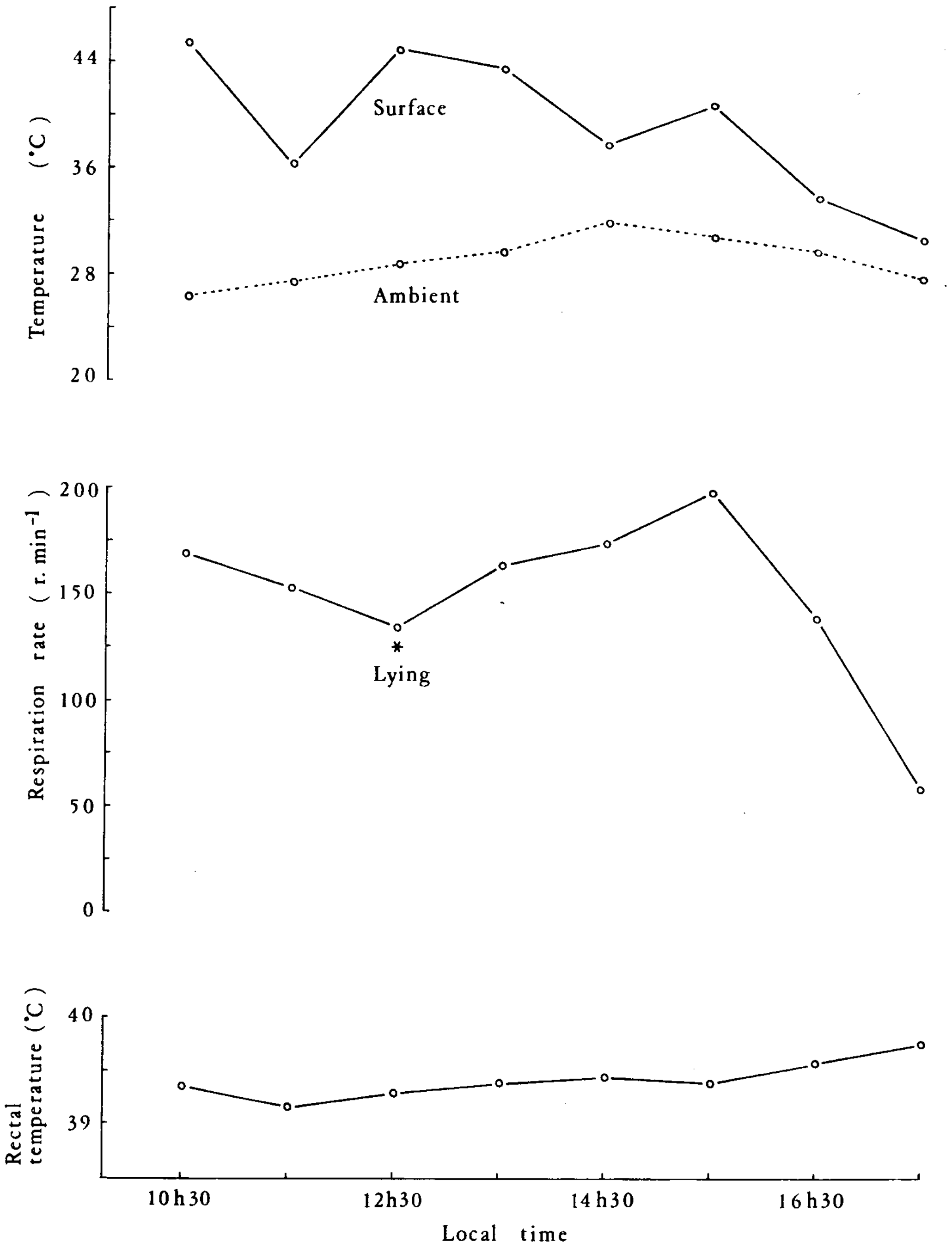


Figure 46 Respiration rate, rectal, surface and ambient temperatures recorded during a single day

respiration rate. In contrast to the previous relationship, this regression line explains only 37% of the variation in respiration rate. Moreover, Fig. 46 shows how respiration rate dropped in the afternoon while rectal temperature was still increasing. It therefore seems that a change in surface temperature had a more important influence on respiration rate than a change in rectal temperature. In Fig. 45 I have also indicated that the higher respiration rates (> 100 r. min^{-1}) which occurred at the lower rectal temperatures (< *ca.* 39,8°C) were always associated with high radiative heat loads. These measurements were recorded in the mornings (or early afternoons) when ambient and rectal temperatures were still increasing and had not yet reached their maximum values.

Harthoorn *et al.* (1970) have reported that the respiration rate of large herbivores shows little relationship with deep body temperature. They also found a relationship between respiration rate and solar radiation. Finch (1972a) demonstrated that changes in the skin temperature of the eland and hartebeest were strongly influenced by the intensity of solar radiation and that skin temperatures were closely associated with the rates of evaporative cooling. These results agree with mine and the phenomenon was also demonstrated for the Namaqua-Afrikaner sheep in the previous chapter. However, Ingram and Mount (1975) are of the opinion that the control of panting in mammals appears to depend on the integration of signals from both peripheral and deep-body sensors. Furthermore, according to Hales (1976) "heating of the hypothalamus, midbrain, spinal cord, abdominal viscera or skin will stimulate panting, and the magnitude of the response to a temperature change induced at one site depends largely upon the temperature of the other sites". In the light of the above, I decided to analyse the relationship between rectal temperature and respiration rate in a different way. Figure 45 shows that respiration rate varied between 40 and 200 r. min^{-1} at rectal temperatures less than *ca.* 39,8°C. Consequently, rectal temperature *per se* could not have determined the rate of breathing. In fact the coefficient of determination showed that only 0,6% of the variation in respiration rate was explained by rectal temperature, when the latter was less than 39,8°C. However, for rectal temperatures higher than 39,8°C, this figure increased to 65%. Therefore, it would appear that deep body temperature *per se* was significantly correlated with respiration rate only when body temperature was elevated (> 39,8°C). It seems then that at the lower rectal temperatures, the initial increase in respiration rate was triggered by peripheral sensors in order to prevent a rise in body temperature. However, when body temperature did increase above a certain level, the central sensors together with the peripheral sensors elicited a still greater response in an attempt to decrease the elevated body temperature.

Effect of environmental temperature

In Fig. 47 I have illustrated the relationship between respiration rate and shade and sun temperature, respectively. Respiration rate increased gradually with increasing shade and sun temperatures and the coefficient of determination was 58% and 66% respectively. Consequently, sun

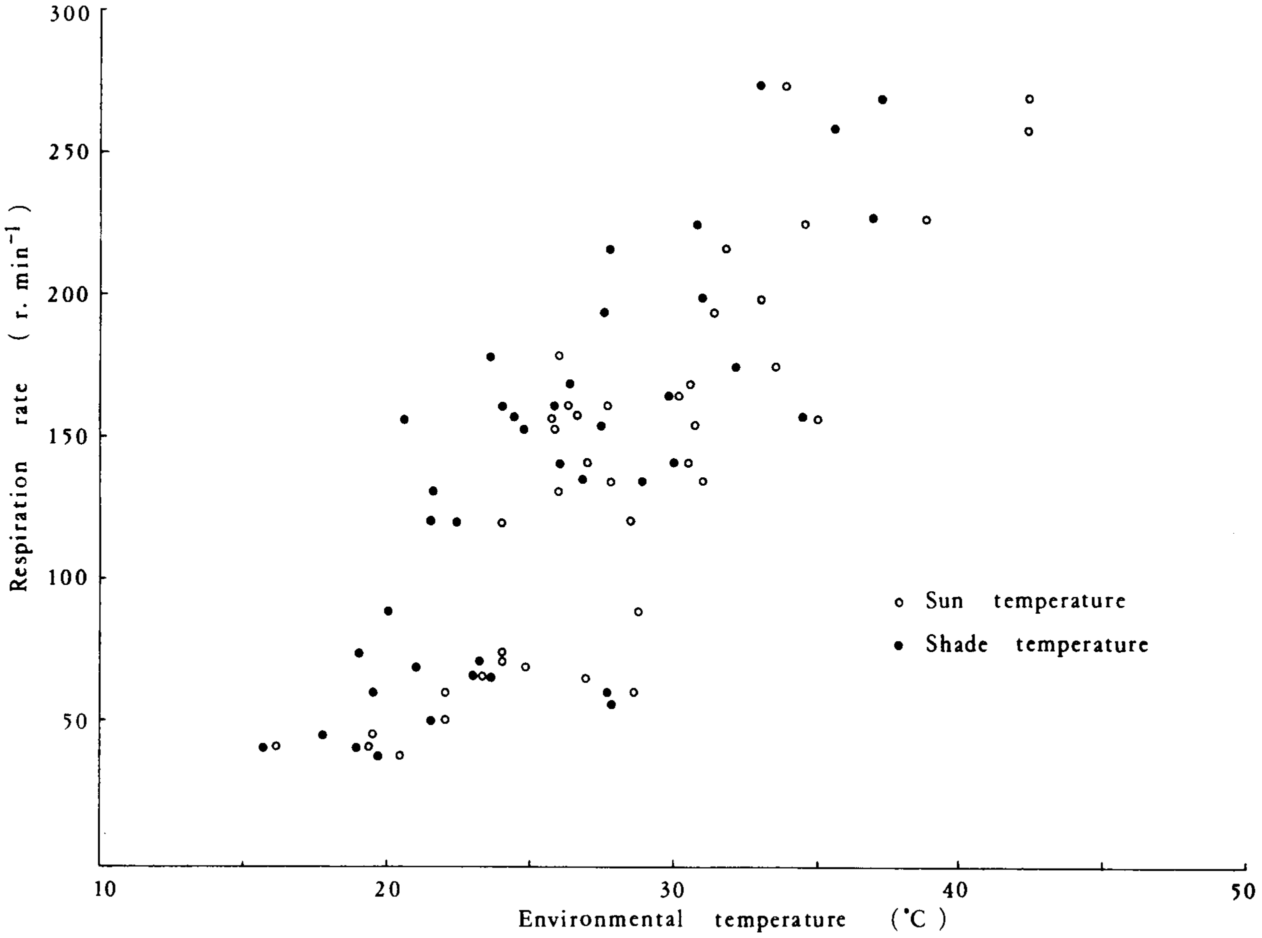


Figure 47 The relationship between respiration rate and sun and shade temperature respectively

temperature which takes account of solar radiation, explains the variation in respiration rate better than shade temperature. Also the relationship between sun temperature and respiration rate shows an initial slow increase in respiration rate followed by a rapid increase and eventually a plateau value, when peak respiration rate was reached. The minimum and maximum respiration rates recorded during this experiment were 38 and 274 r. min^{-1} respectively. However, in this experiment I had difficulty in detecting the thoracic movements at very low respiration rates. In a previous study on tranquilised springbok (Gericke *et al.* 1978) I recorded respiration rates as low as 12 r. min^{-1}.

Many studies on the effect of environmental temperature upon respiration rate in mammals have been described. These studies were, however, for the most part conducted in climatic chambers and under these conditions, environmental temperature reflects the total heat load on the animals. Taylor (1970), for example, reported that the respiration rates of hydrated Grant's and Thomson's gazelles varied between 20 - 295 and 20 - 250 r. min^{-1}, respectively. However, at an environmental temperature of *ca.* 35°C, these animals exhibited respiration rates of only *ca.* 60 r. min^{-1}. These results contrast sharply with my own results on springbok in an outdoor environment. In the latter study a respiration rate between *ca.* 160 and 274 r. min^{-1}, when ambient temperature was *ca.* 35°C, was recorded. The above differences can be explained by the different environmental conditions and once again illustrate the importance of solar radiation in the animal's natural environment.

Robertshaw and Taylor (1969) investigated the relative importance of respiratory and cutaneous evaporative cooling in eight species of East African bovids. They found that the smaller ruminants make greater use of respiratory evaporation while cutaneous evaporation dominates in the larger ruminants. For example, animals like the duiker (*ca.* 7 kg), Thomson's gazelle (*ca.* 14 kg) and Grant's gazelle (*ca.* 25 kg) are predominantly panters. Springbok (*ca.* 34 kg) fall within the weight-class of the smaller ungulates and with a respiration rate which can exceed 250 r. min^{-1}, one can assume that they are also predominantly panters. However, the contribution from cutaneous evaporation cannot be disregarded. The cutaneous water loss of the restrained springbok was measured on a few occasions and a water loss of 79 g m^{-2} h^{-1} (*ca.* 53 W m^{-2}) was recorded while ambient temperature was below 30°C. Cutaneous evaporation might, therefore, be quite important in this species' heat balance, especially in situations where high windspeeds prevail.

Open-mouth panting

The springbok normally panted with a closed mouth. I also noticed that the animals' nasal apertures became dilated when they encountered severe heat stress and respiration rates were very high. I recorded open-mouthed panting in the springbok only once during the entire study. On this particular day the animal was subjected to a very high heat load with intense solar radiation, no wind, and ambient temperatures which exceeded 35°C (Fig. 48). According to Whittow (1971) and Hales (1973),

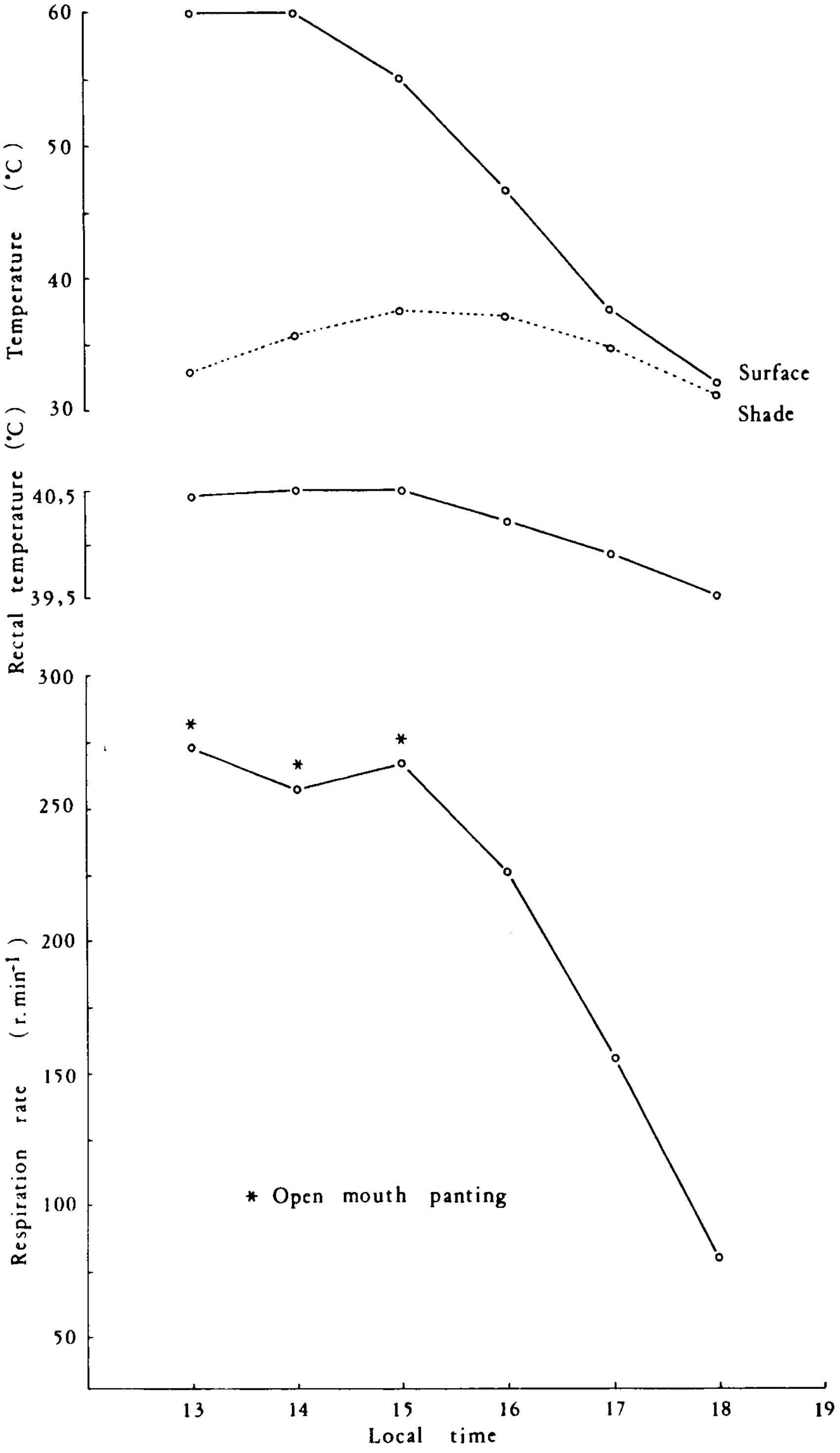


Figure 48 Measurements of respiration rate and rectal temperature from restrained springbok on a very hot day

open-mouthed panting begins at the peak respiratory rate. Thereafter, the animal changes to a slower, deeper panting (SDP) while tidal volume increases. Figure 48 illustrates that while the springbok panted with an open mouth, respiration rate decreased by only 6% at 14h00 and then increased again. It is doubtful if this small decrease was indicative of SDP, especially since windspeed increased from 0 to 2 m s^{-1} during this period.

As the above animal was confined in a crate, it was unable to employ behavioural thermoregulation and because this type of panting was never observed in the free-ranging animals, it is probably only used as an emergency measure. In fact, tame animals in the immediate vicinity of the restrained springbok and kept under identical climatic conditions, but allowed to range freely, did not exhibit open-mouthed panting. They were able to employ various behavioural adjustments and showed far less heat stress throughout the day.

Ear and horn temperature

In Figs 49 A, B, C and D ear and horn temperatures, measured on four different days are presented. Figure 49A shows a sudden increase in both ear and horn temperature which coincided with the appearance of the sun. The temperature of the ear and horn increased by 15,0 and 13,8°C respectively. This sudden increase in temperature appears to be the result of swift vasodilation in response to the effect of solar radiation upon peripheral sensors.

Figure 49B illustrates that ear and horn temperature and thus their vasomotor control operated independently. At 09h30 the horn temperature was 7,4°C lower than the ear temperature and this difference decreased to 2,1°C at 10h30. In contrast with the previous example (49A), ear temperature at 09h30 indicates a vasodilated condition while the animal was still in full shade. However, in this example (09h30) shade temperature was 4,2°C higher than in the previous example (07h30). Figure 49C shows that ear and horn temperature increased above 41°C under conditions of intense solar radiation. This was the only instance where I recorded ear and horn temperatures which were higher than the rectal temperature (40,5°C). Figure 49C also illustrates that horn temperature followed shade temperature much closer than did ear temperature. Ear temperature showed a slower cooling rate and it appears as if vasoconstriction in the afternoons occurred more gradually than did vasodilation in the mornings. Figure 49D shows the normal vasoconstriction and concomittant decrease in temperature in the afternoon. However, after sunset at 20h30 horn temperature started to increase and at 22h30 ear temperature also began to rise. Between 19h30 and 22h30 ambient temperature remained fairly constant and the windspeed remained low. At this time rectal temperature gradually decreased but the surface temperature of the animal increased. I also noticed that there was a tendency for the anterior part of the body to become warmer than the posterior part and in Fig. 50 I have illustrated the surface temperatures recorded between 19h30 and 23h30 on this particular occasion. The increase in surface temperature either indicates local vasodilation or an increase in the local deep body temperature, or both. Most probably, rumen

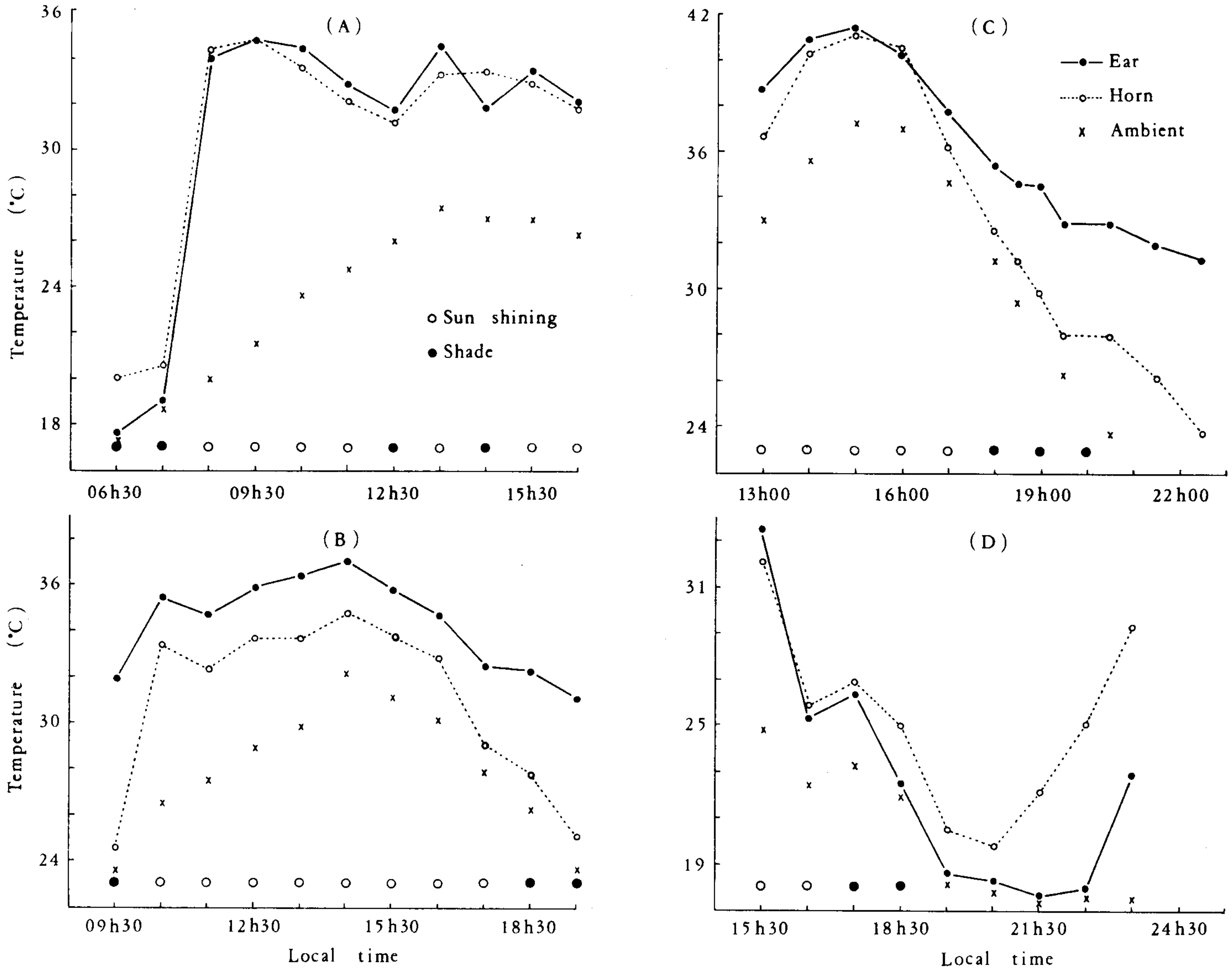
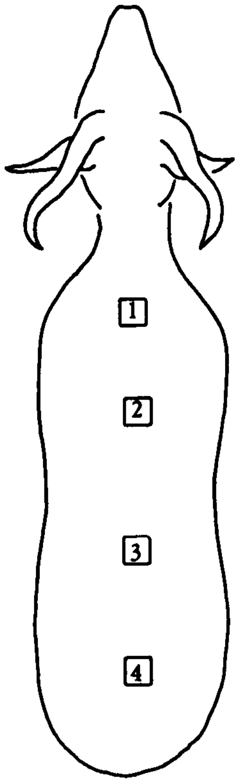


Figure 49 Records of ear and horn temperatures under various environmental and physiological conditions



	19h30		20h30		21h30		22h30		23h30	
	22		20		22		24		25	
		21		19		22		24		24,5
	20		18		22		24		24	
	20		18		20		20		24	
		19		18		19		20		23
	18		18		18		20		22	
Difference between anterior and posterior measurements	2°C		1°C		3°C		4°C		1,5°C	

Figure 50 The observed increase in surface temperature of the anterior part of the body, which coincided with an increased horn temperature.

temperature increased due to fermentation processes and the vasodilation of the ear and horn bloodvessels facilitated heat loss. Ingram and Whittow (1962) reported that feeding affects the skin temperature of the extremities in the ox. They felt that the response was triggered by an increased need to lose heat and, consequently, vasodilation resulted in the increased skin temperature and enhanced heat loss. This response, however, did not occur in a cold environment.

The four different illustrations (Fig. 49) give the impression that environmental temperature, solar radiation and increased heat production can all be involved in the regulation of peripheral blood flow. In Fig. 51 I have illustrated the relationship between ambient and ear temperature. The strong influence of solar radiation made it necessary to distinguish between measurements in the sun and in the shade. When the animal was exposed to solar radiation, vasodilation occurred at ambient temperatures as low as 14°C and a gradient of more than 20°C could then be maintained between the ear surface and the environment. Also, ear temperature remained more or less constant while ambient temperature increased from 14°C to *ca.* 28°C. However, any further increase in ambient temperature resulted in an increase in ear temperature. When the animal was in the shade, ear temperature was normally very close to ambient temperature, but in the late afternoon when ambient temperature was decreasing and rectal temperature was still high, ear temperature remained at a high level or decreased gradually. Therefore, in Fig. 51 I have indicated three different levels for ear temperature when ambient temperatures were below 20°C. The highest level coincided with the

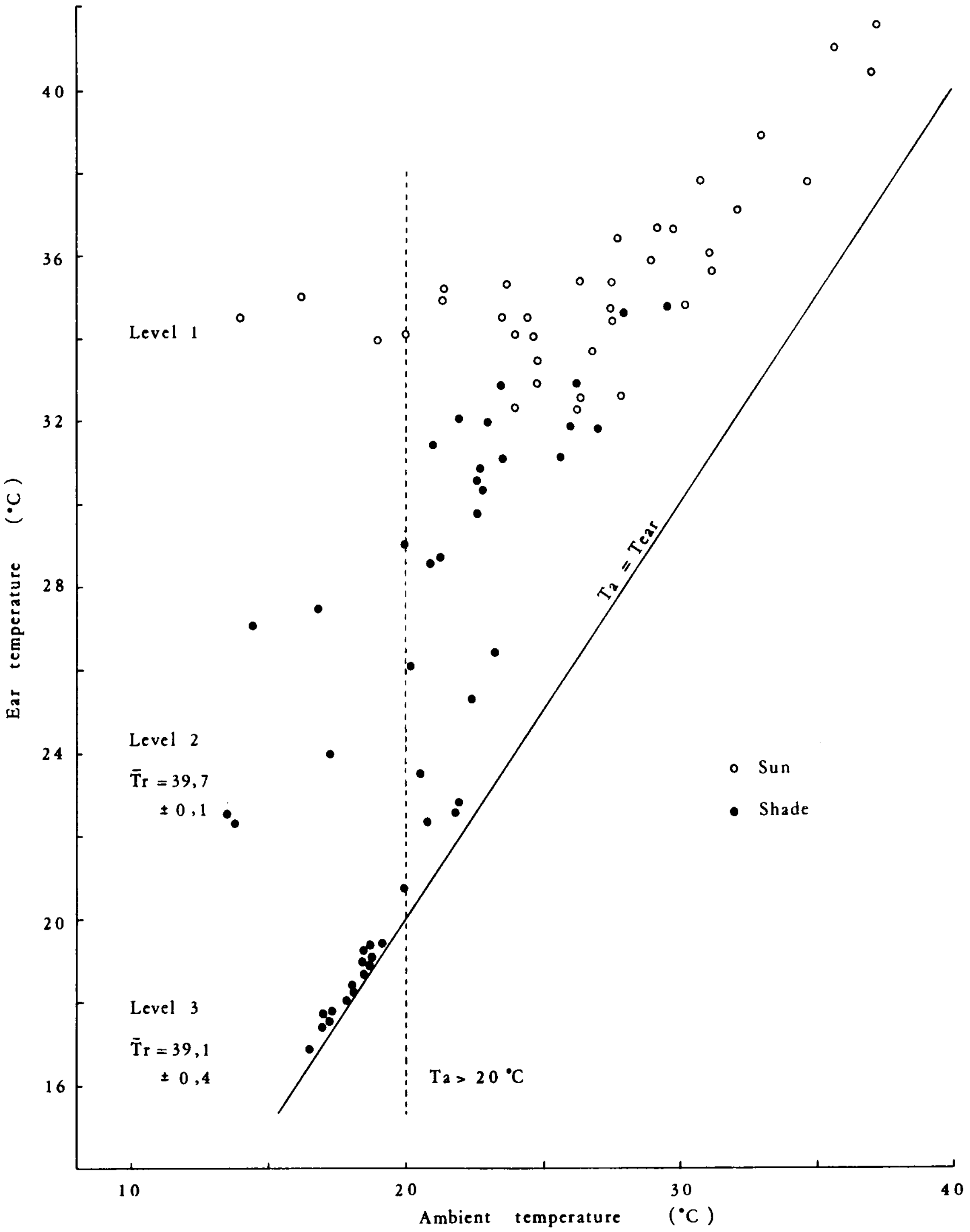


Figure 51 The influence of solar radiation, rectal and ambient temperature on the ear temperature of springbok

presence of solar radiation while the middle and lowest levels were recorded when the animal was in the shade. The lowest level, however, also coincided with a lower rectal temperature and a highly significant difference exists between the mean rectal temperatures at the middle and lowest level. This indicates that the thermal status of the animal, as expected, also had an effect on peripheral vasomotor control. In Fig. 52 I have therefore illustrated the relationship between rectal temperature and ear temperature. At a low rectal temperature (< *ca.* 39,1°C) ear temperatures were always low and indicate a vasoconstricted condition. In contrast, at high rectal temperatures (> *ca.* 40,0°C) ear temperatures were always high and indicate a vasodilated condition. However, when rectal temperature varied between *ca.* 39,1 and 40,0°C, the blood vessels supplying the ear were either in a vasoconstricted or vasodilated condition. These data illustrate that, although deep body temperature had an influence on peripheral blood flow, the effect was not very precise. One rather gains the impression that the peripheral sensors are involved with the finer control of ear temperature. These results are in agreement with the findings of Whittow (1962) and Ingram and Whittow (1962) on the ox. They found that the temperature of the extremities increased before the deep body temperature, when the heat load on the animal was increasing. Thus the warming of the skin *per se* caused the increased blood flow to the extremities. However, Ingram and Whittow (1963) also reported that localized heating and cooling of the anterior hypothalamus resulted in increasing and decreasing temperatures of the extremities respectively.

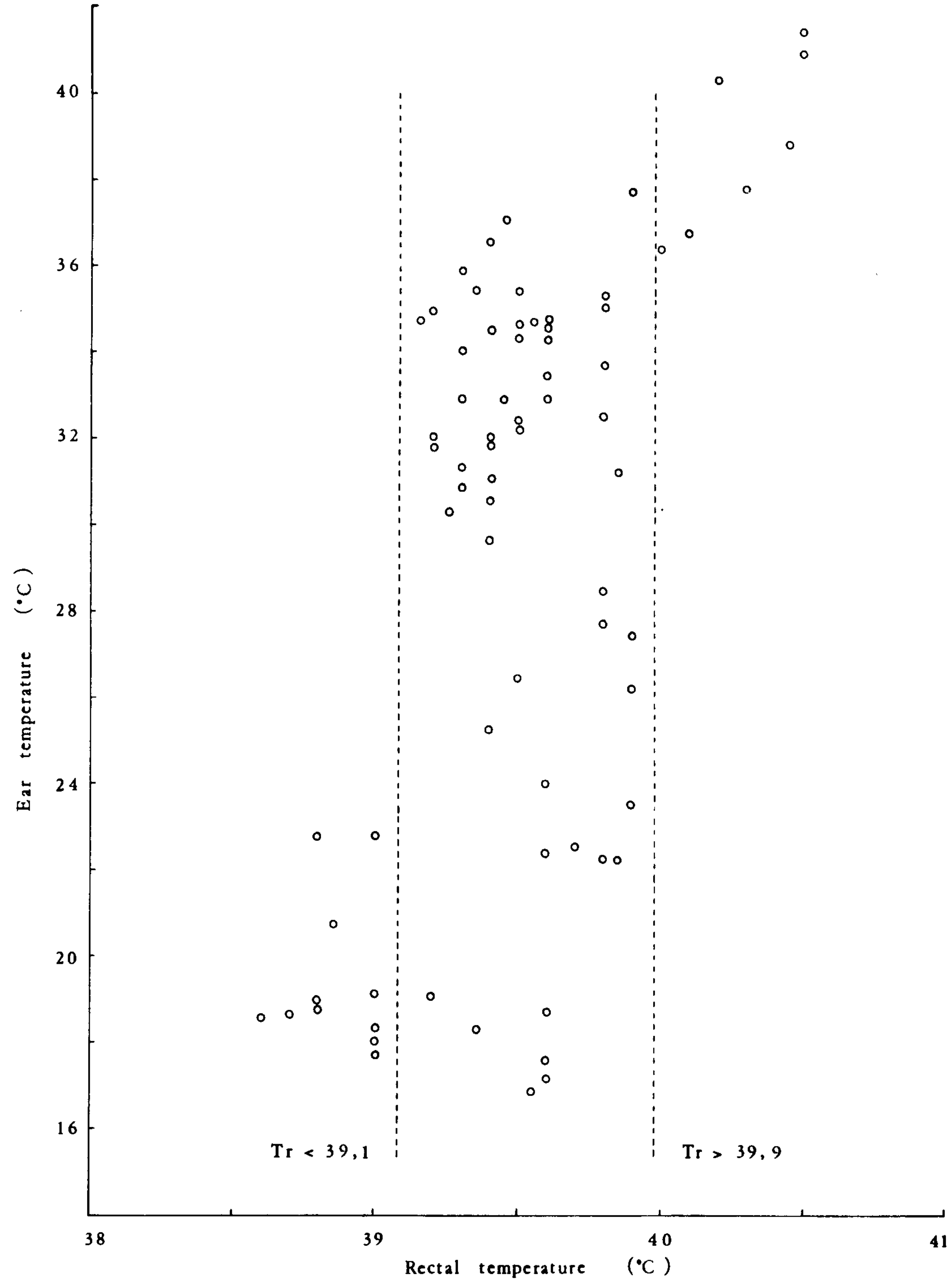


Figure 52 The relationship between ear and rectal temperature in springbok

The surface temperature patterns in the horns of the springbok were generally very similar to those of the ears. Figure 53 shows the relationship between ambient and horn temperature. Horn temperature increased nearly linearly with increasing ambient temperature and the difference between horn and ambient temperature was generally smaller than the difference between ear and ambient temperature. Moreover, the effect of solar radiation on the horn temperature was not as clear cut as it was on the ear temperature. As expected, the temperature variations in the irradiated horn were greater at any specific ambient temperature than was the case in the irradiated ear. The mean horn temperature in the sun was also significantly lower than the mean ear temperature in the sun. These differences are probably due to the thick keratinised layer surrounding the blood vessels in the horn which, unlike the thin tissue in the ear, would dampen the effects of vasodilation and vasoconstriction. Nevertheless, horn temperature was always higher than ambient temperature and thus the horns could have functioned as thermal windows. Taylor (1966) found that Toggenberg goats use their horns in thermoregulation. In a cold environment vasoconstriction occurred and heat loss was reduced. On the other hand, both exercise and high environmental temperatures resulted in vasodilation in the blood vessels supplying the goat's horns with a concurrent increase in heat loss. Taylor also provided evidence to support the view that heat loss from the horns can have a cooling effect on the arterial blood supplying the goat's brain.

The relationship between rectal and horn temperature (Fig. 54) appears to

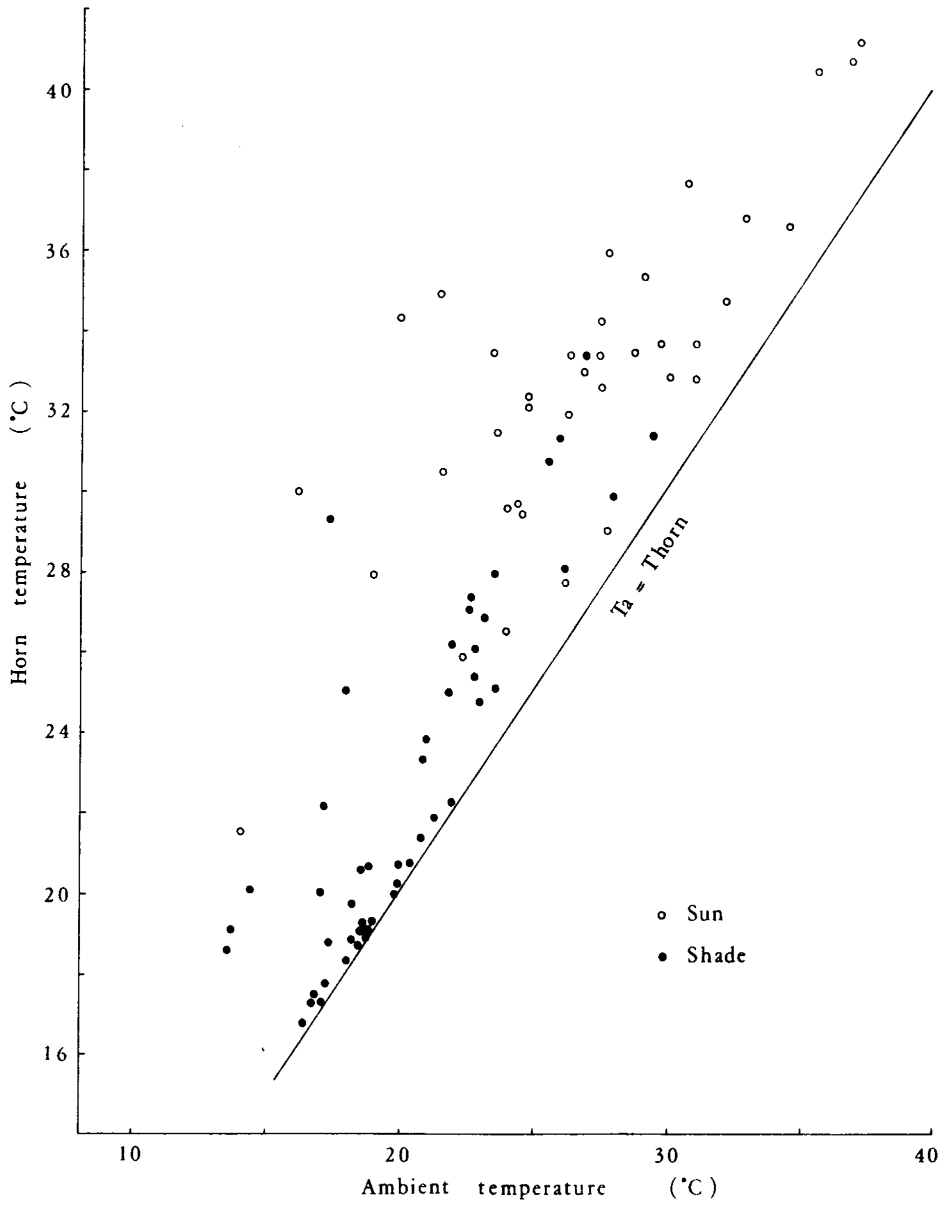


Figure 53 The influence of solar radiation and ambient temperature on the horn temperature of springbok

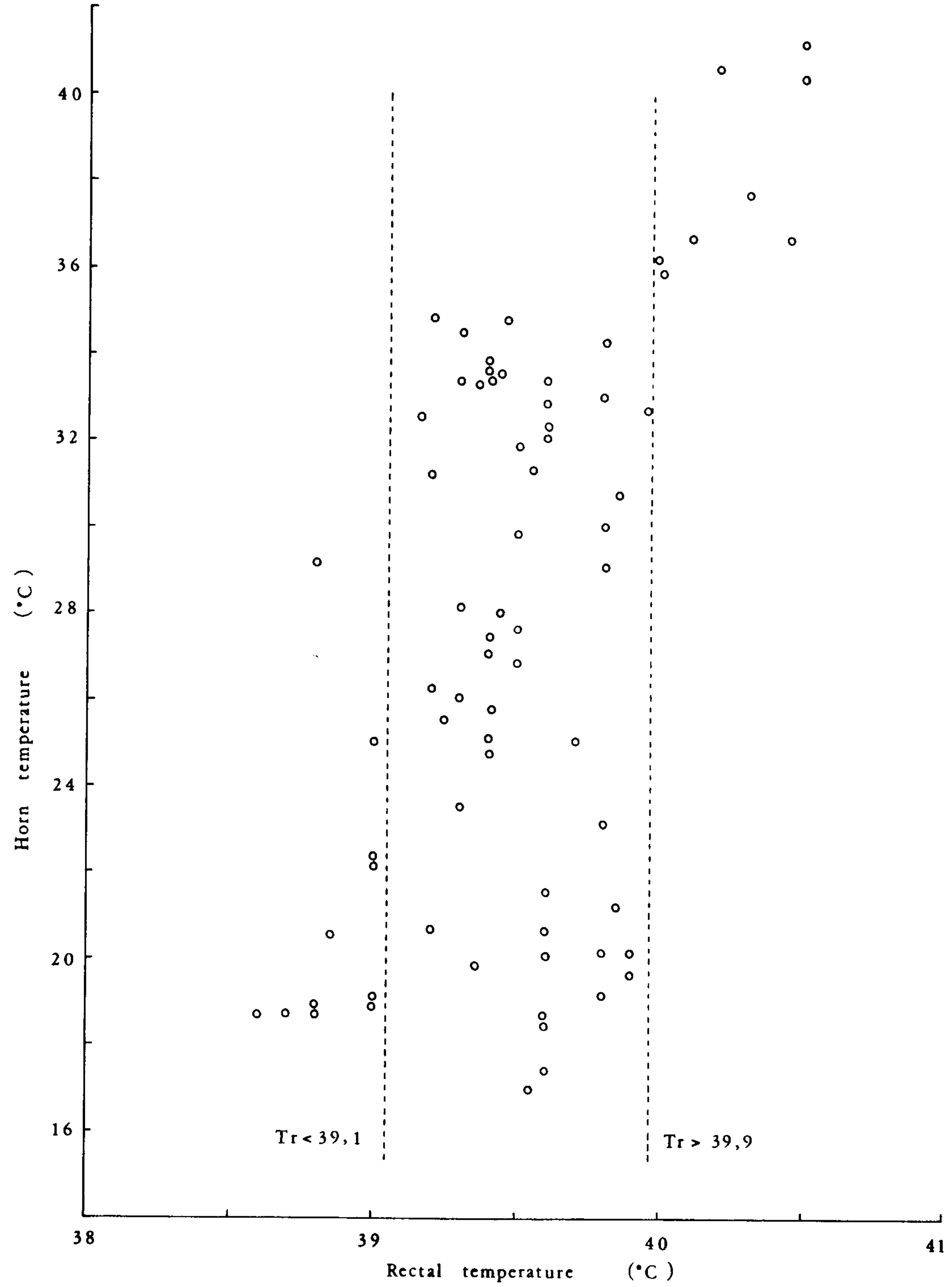


Figure 54 The relationship between horn and rectal temperature in springbok

be very similar to the relationship between rectal and ear temperature. Once again the lowest rectal temperatures coincided with the lower horn temperatures while the highest rectal temperatures coincided with the higher horn temperatures. Also, when rectal temperatures were between *ca.* 39,1 and 40,0°C the blood vessels in the horn could either be in the vasoconstricted or vasodilated condition. It would seem therefore that deep body temperature did not have precise regulatory control on the vasomotor tone of the blood vessels supplying the horns.

Comparison of springbok with Namaqua-Afrikaner sheep

In Chapter 1 I showed that the dorsal, fawn-coloured part of the springbok's pelage has an absorptance of 0,60 for short-wave radiation, while that of the Namaqua-Afrikaner sheep was 0,66. Therefore, the surface temperature of the springbok and sheep should be similar when they are exposed to solar radiation and a low windspeed. This effect is illustrated in the results obtained on day 1 (Fig. 55), when the springbok and sheep were examined simultaneously in an outdoor environment. The sheep, however, had a much thicker pelage than the springbok and therefore, one would expect that the heat load on the skin would be higher in the springbok. As expected then, the springbok exhibited a higher rectal temperature and respiration rate than the sheep.

The results recorded on day 2, show that in the absence of solar radiation, the springbok had a higher pelage surface temperature than the sheep. It would seem therefore that the thin pelage resulted in a higher heat loss in the springbok while the pelage of the sheep provided superior insulation. Under these conditions, the rectal temperature and respiration rate of the two animals were very similar (Fig. 55).

Both springbok and sheep survive well in hot arid environments, despite the large difference in their pelage quality. The pelage of the springbok enhances heat loss while the pelage of the sheep provides protection against heat gain and heat loss. Therefore, the springbok would have to rely to a greater extent on convection and other

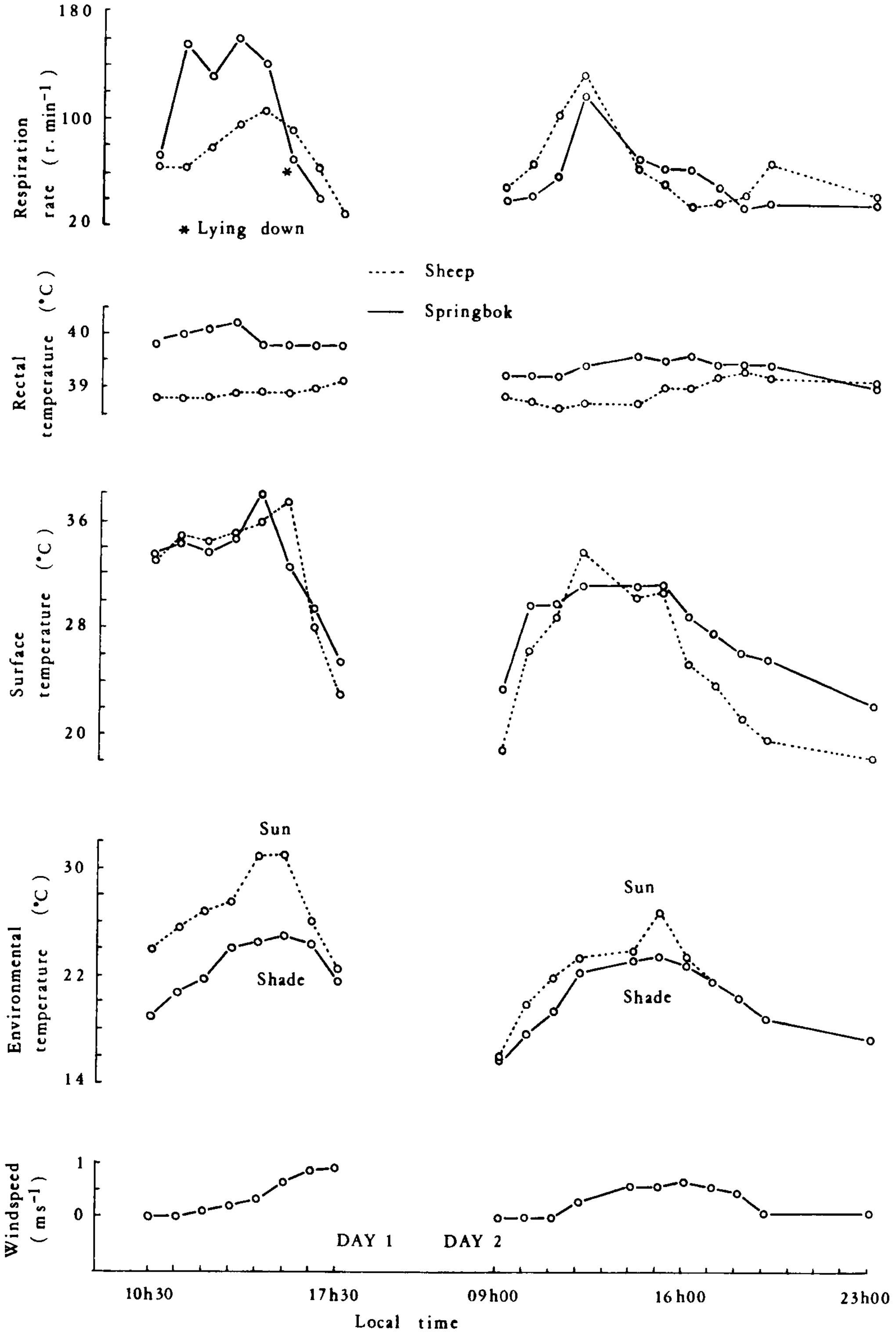


Figure 55 Temperature data obtained simultaneously on springbok and sheep on two different days

mechanisms which reduce heat gain, under conditions of severe heat load.

These very significant differences in pelage quality of two ungulate species, which are of similar size and well-adapted to hot, arid conditions, provide an interesting contrast between natural and artificial selection. In the case of the artificially-selected sheep, although the fleece provides protection against both heat loss and heat gain, these animals are incapable of off-loading metabolic heat accumulated during strenuous exercise. They are, however, seldom required to sprint away from predators because of the protection afforded by man. In contrast, the springbok, among the swiftest of antelope, frequently sprints from predators and their thin pelage facilitates heat loss by convection and radiation in these circumstances. The selection pressure favouring the development of a thin pelage must therefore have been greater than the obvious advantages for saving both energy and water which would have accrued from the evolution of a thick pelage.

BEHAVIOURAL THERMOREGULATION

Profile area

In the previous chapters I discussed the importance of solar radiation in an animal's heat balance and have demonstrated how the profile area of the animal, exposed to direct solar radiation, changed with changes in solar azimuth and elevation. However, when different mammalian species are compared, one should also consider the shape of the animal's body. Two factors can be of importance in this respect, namely the ratio of body length to diameter and also the shape of the cross-section through the long axis of the body. Monteith (1973) regarded the animal as a cylinder when determining profile areas and took the ratio between body length (h) and radius (r), $\left[{}^{h}/r = X\right]$ into account in his formula. I have used his formula to demonstrate this effect in Fig. 56. Springbok have a relatively longer and more slender body than sheep and from measurements, I calculated $X = 5{,}0$ for the springbok and $X = 3{,}53$ for the sheep. Figure 56 shows that when the animals are orientated with their body axes parallel to the sun's rays, the springbok has a smaller profile area than the sheep. In contrast, when the sun's rays are perpendicular to the bodies, the springbok exhibits the larger profile area. I should, however, stress the fact that real measurements of profile area differ greatly from values predicted from formulae. Nevertheless, the calculated differences between the two shapes should still be manifested in actual measurements. As far as the shape of the

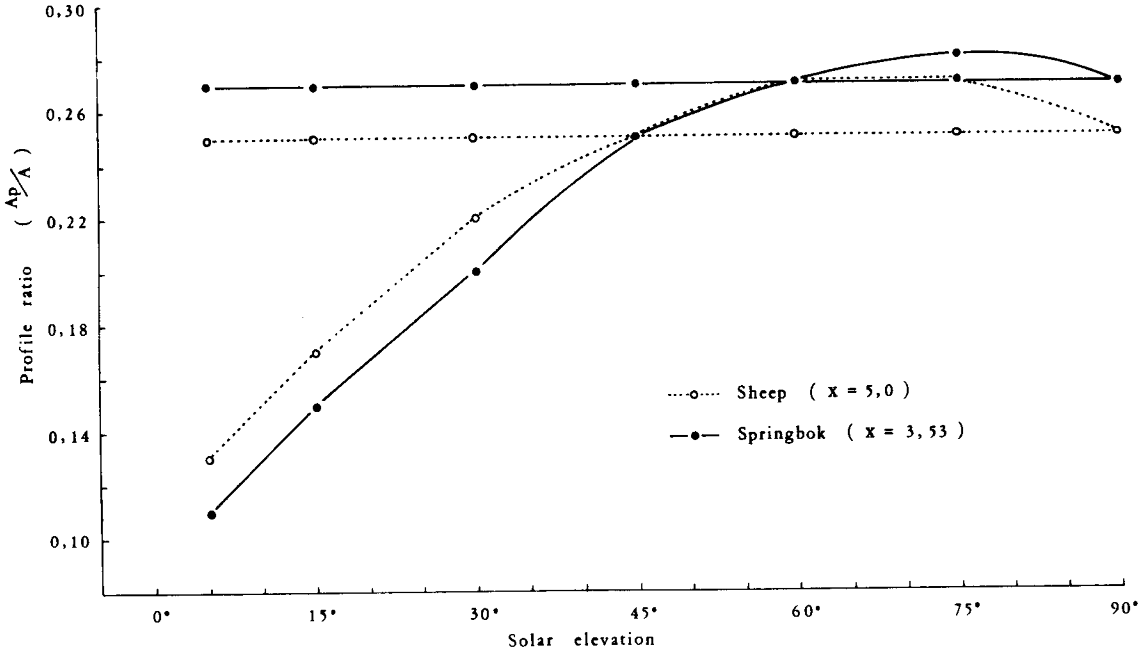


Figure 56 The effect of different body proportions on the profile area exposed to direct solar radiation

$$\frac{Ap}{A} = \sin \beta \left[\frac{\operatorname{cosec} \beta \left({}^{2}/_{\pi}\, \chi\, (1 - \cos^2 \beta \cos^2 \theta)^{\frac{1}{2}} + \cos \beta \cos \theta \right)}{2\ (\chi + 1)} \right]$$

where β is solar elevation; θ is azimuth; $\chi = {}^{h}/_{r}$ with h as the length of the cylinder and r as the radius of the cylinder cross-section through the long axis of the body is concerned, Fig. 57 shows the two basic shapes of a cylindrical body. With the sun's rays parallel to the long axes of the two cylinders, the profile areas would be approximately the same at the lower elevations. When solar elevation increases, the profile area of the oval shape would, however, become smaller than the profile area of the circular shape. Furthermore, with

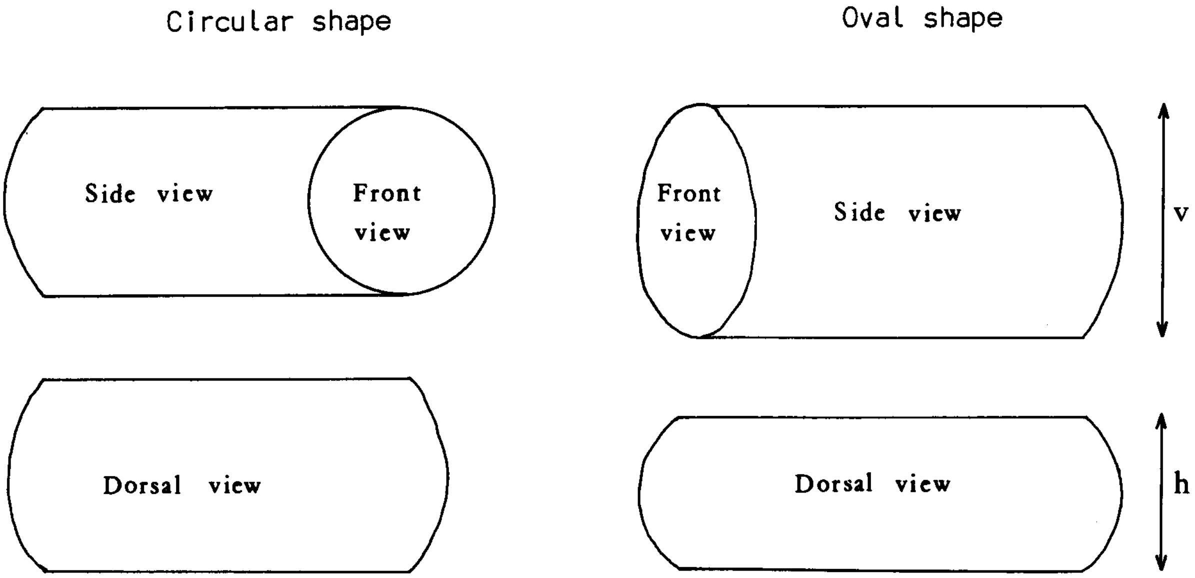


Figure 57. The two basic cylindrical shapes of a mammal's body.

the cylinders orientated perpendicular to the sun's rays, the oval shape would provide the larger profile areas at the lower solar elevations. Nevertheless, with increasing solar elevation, the profile area of the oval shape would decrease, while that of the circular shape would remain constant. Thus the proportional quantity $X = \frac{h}{v}$ (where h is the

Figure 58 Lateral view of a springbok, *Antidorcas marsupialis*, depicting the characteristic colour pattern and body shape

horizontal diameter and v is the vertical diameter) would illustrate this difference in body shape. I found this value to be 0,81 in the springbok and thus the cylindrical body of the springbok had an oval cross-section with $v > h$ (Fig. 58).

I was only able to measure the profile area of the springbok from two different positions namely, with azimuth = 0° and solar elevation *ca.* 5° and, secondly, with azimuth = 90° and solar elevation *ca.* 5°. The springbok has a thin pelage and, therefore, I expressed the profile area as a proportion of the total skin area ($^{Ap}/A$). Riemerschmid (1943) and Clapperton *et al.* (1965) measured the profile areas of a Sussex bull and three breeds of sheep respectively. Clapperton *et al.* determined the mean profile area for all experimental animals, when fully fleeced and when shorn. I decided to construct a hypothetical profile curve for the springbok, based on the results of Riemerschmid and the shorn sheep of Clapperton *et al.* In Fig. 59 I have illustrated their results as profile area per total skin area (henceforth referred to as profile ratio). At a 0° azimuth angle, the measured profile ratio of the springbok lay between that of the bull and sheep. I then calculated the profile ratio of the springbok between that of the bull and sheep for the remaining solar elevations. At an azimuth of 90°, the measured profile ratio of the springbok was higher than that of the bull or sheep. The profile ratio of both the bull and sheep remained more or less constant between solar elevations of *ca.* 5° and 40°. However, a further increase in solar elevation resulted in a decreasing profile ratio. I used this basic pattern for the hypothetical profile curve of the springbok at a 90° azimuth angle.

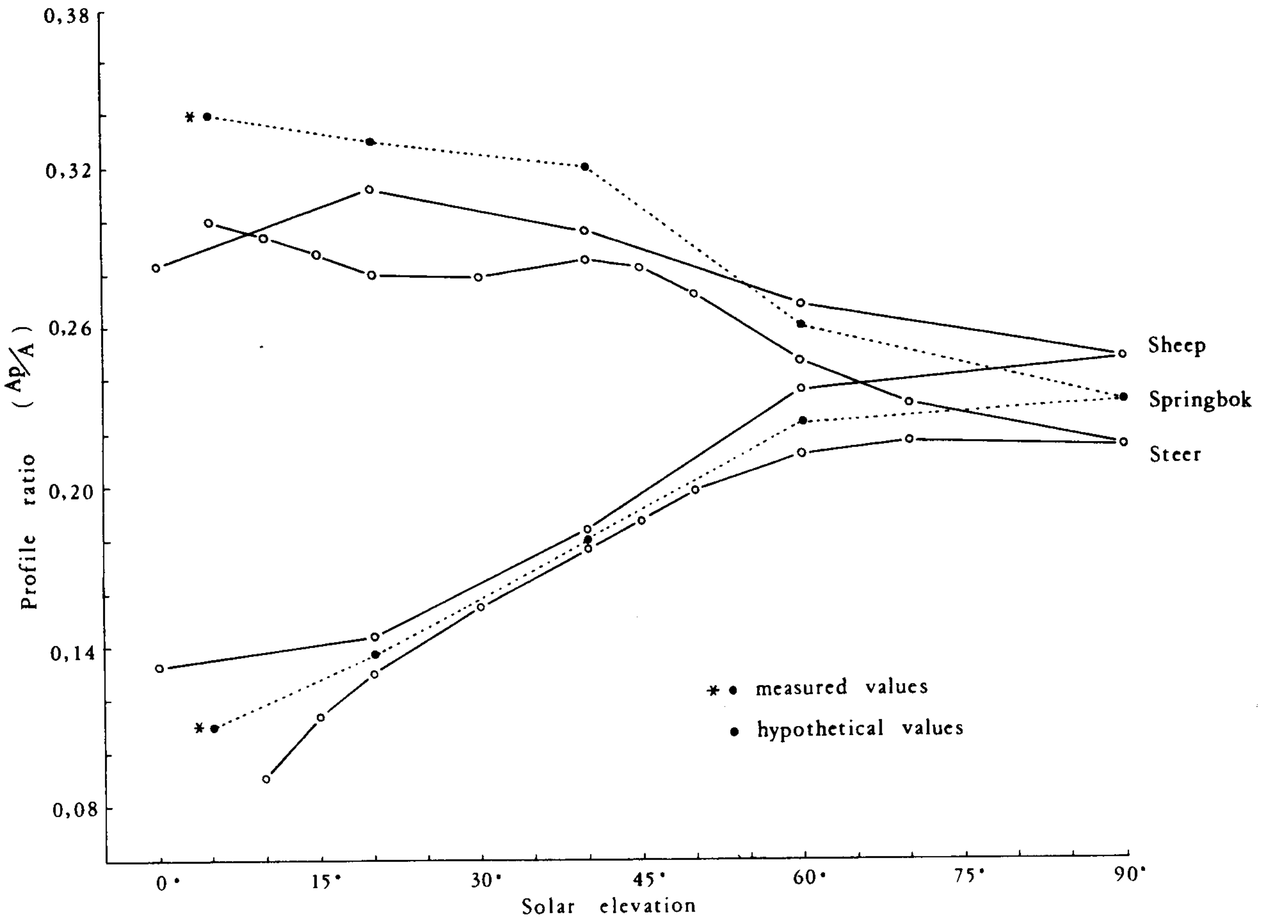


Figure 59 The influence of solar elevation and azimuth on the proportion of total skin area exposed to direct solar radiation. Steer from Riemerschmid (1943) and sheep from Clapperton *et al.* (1965)

Having estimated a hypothetical profile curve of the springbok at different solar elevations, it is now possible to speculate on the theoretical beneficial effect of orientation in this species. In Table 18 I have listed the intensity of direct solar radiation at different solar elevations, measured during the telemetry study at Benfontein. The calculations show that theoretically, a springbok which orientates perpendicularly towards the sun, absorbs on average 62% more direct solar radiation than a springbok which orientates towards the sun. Furthermore, it can be seen that theoretically the amount of radiation absorbed differs throughout the day. However, the differences obtained between 11h00 and 14h00 are rather small.

The question now arises whether there is any difference between a head or tail presentation towards the sun. Clapperton *et al.* (1965) measured the profile areas of both head and tail presentations and found only minor differences between the two. Similarly, I found only very small differences between the two presentations (with solar elevation *ca.* 5°) in the springbok. However, Figs 60 and 61 indicate that the difference between the two presentations increases when the animal lowers its head to graze. Under these conditions the profile area of a head presentation would be the larger one. Thus springbok can theoretically reduce the profile area exposed to direct solar radiation to a minimum if they orientate with either head or tail towards the sun, while a tail presentation is optimal while grazing.

Table 18 Theoretical analysis of direct radiant heat absorbed by a springbok with respectively an end or side presentation towards the sun

(Sh is direct solar radiation intensity on a horizontal surface;
Sp is direct solar radiation intensity on a perpendicular surface;
$^{Ap}/A$ is profile ratio and a is absorptance = 0,60)

Local time	Solar elevation	Sh Wm^{-2}	Sp Wm^{-2}	Azimuth = 0°		Azimuth = 90°		Difference Wm^{-2}	Additional radiation absorbed(%)
				$^{Ap}/A$	$\frac{Ap}{A} \times Sp \times a$	$^{Ap}/A$	$\frac{Ap}{A} \times Sp \times a$		
06h00	3°								
07h00	16°	233	845	0,13	66	0,33	167	101	153%
08h00	29°	430	887	0,16	85	0,325	173	88	104%
09h00	42°	603	901	0,18	97	0,31	168	71	73%
10h00	55°	726	886	0,21	112	0,275	146	34	30%
11h00	68°	915	987	0,225	133	0,25	148	15	11%
12h00	79°	973	991	0,23	137	0,24	143	6	4%
13h00	79°	969	987	0,23	136	0,24	142	6	4%
14h00	68°	917	989	0,225	134	0,25	148	14	10%
15h00	55°	825	1007	0,21	127	0,275	166	39	31%
16h00	42°	614	918	0,18	99	0,31	171	72	73%
17h00	29°	436	899	0,16	86	0,325	175	89	103%
18h00	16°	187	678	0,13	53	0,33	134	81	153%
19h00	4°								

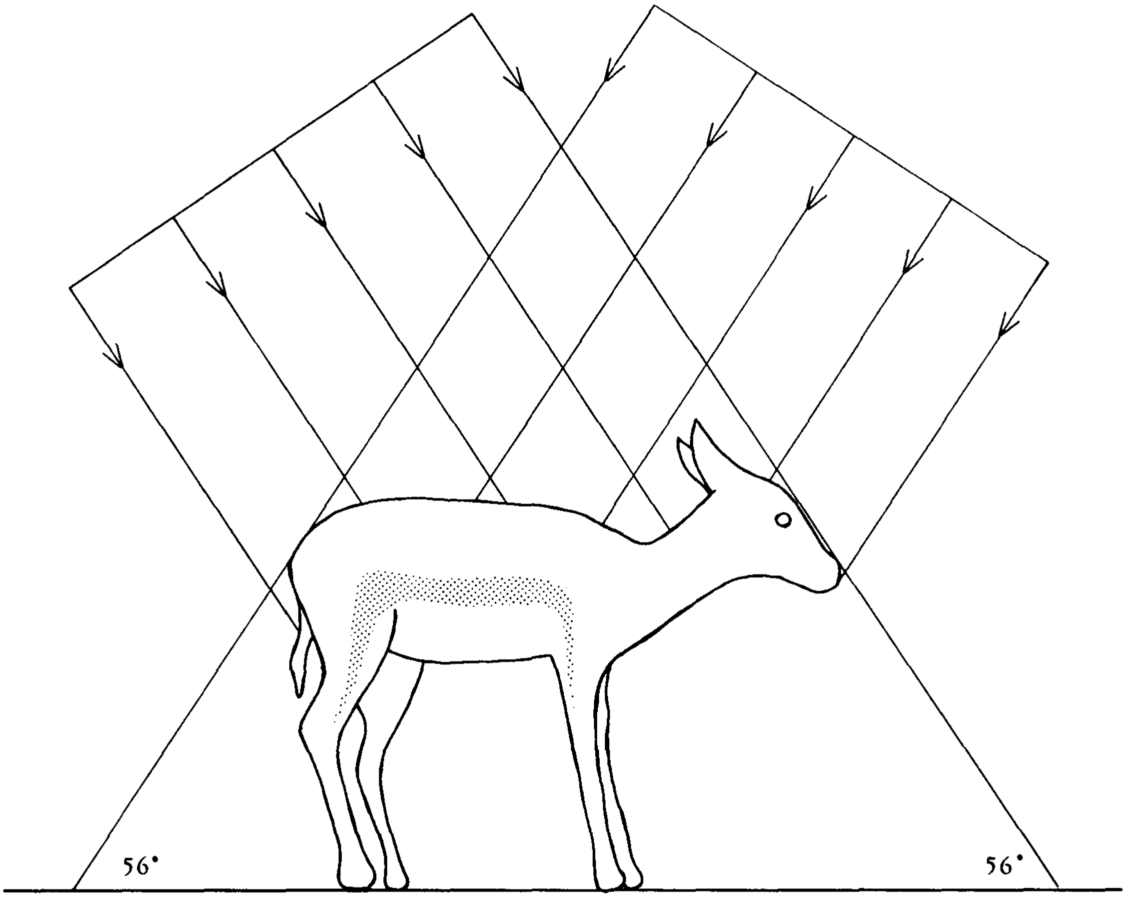


Figure 60 Head and tail profile areas of a springbok in a standing posture

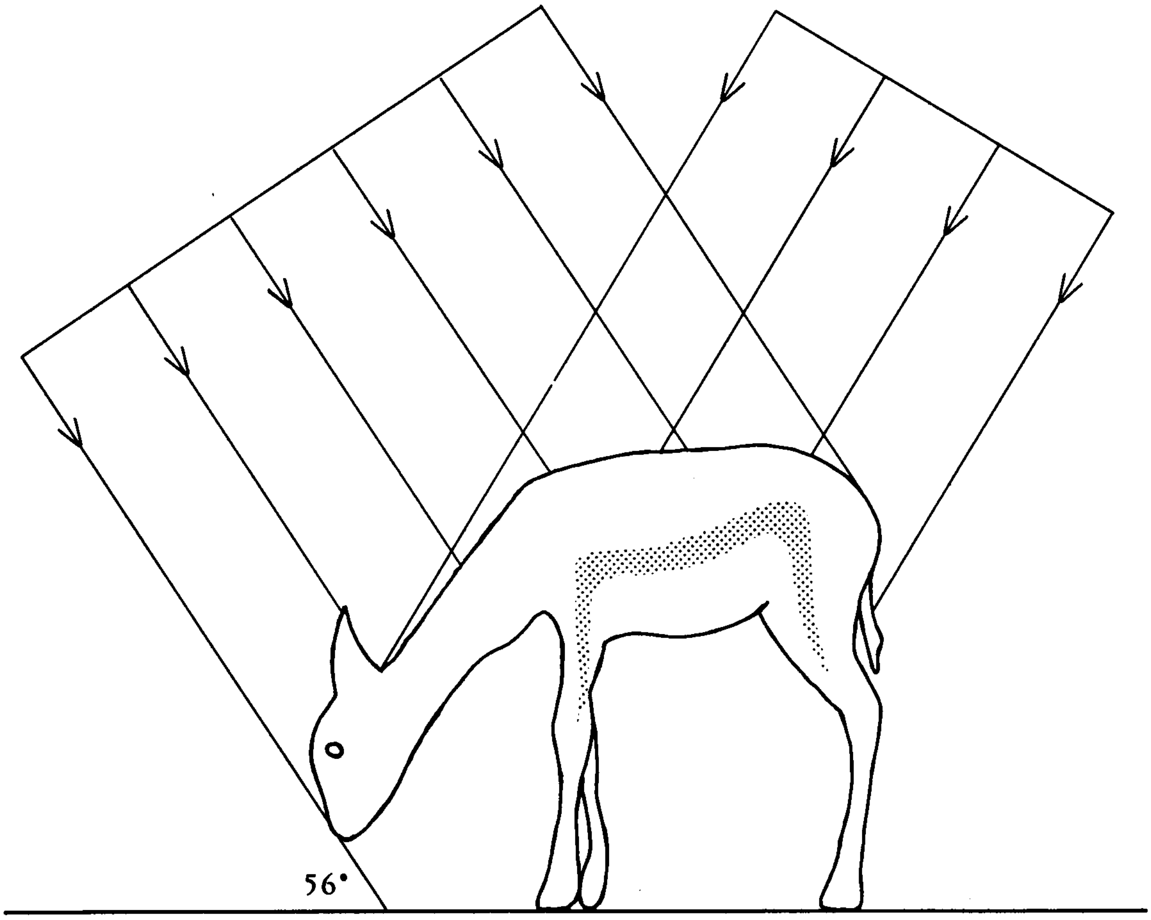


Figure 61 The effect of a grazing posture on the head and tail profile areas of a springbok

The colours of the pelage

The coat of the springbok is mostly fawn in colour with a chocolate-brown lateral band, which separates the flanks from the white ventral surface. The head is white with a dark-brown stripe and the lower rump is also white. In Table 19 I have indicated the proportion of the different colours from a frontal, back and lateral view of the springbok. In addition, I have already shown in Chapter 1 that the absorptance of the white, fawn and chocolate brown areas was 0,28, 0,60 and 0,66 respectively. However, a new weighted mean absorptance must also be calculated for any specific orientation of the animal towards the sun, because of the different pelage colours involved. Based on the above considerations I calculated a weighted mean absorptance for frontal, back and lateral views of the springbok and in all three cases it was 0,55. This absorptance value would also change when the solar elevation increases. I therefore used the method of Riemerschmid to calculate a weighted mean absorptance for a cylinder, with the colour patterns of the springbok, viewed from the side. The colour patterns on the circumference of the cylinder were based on measurements taken from five springbok pelts. Table 20 shows that the absorptance increases with increasing solar elevation. This was expected, since the contribution from the white ventral surface decreases with increasing solar elevation. However, as I have already pointed out, the cross-section through the springbok's body is oval rather than round. The results can therefore not be regarded as absolute but nevertheless illustrate the principle involved.

Table 19 The percentages of the different colours from a frontal, back and lateral view of a springbok

Colour	Front	Back	Side
White	14,4%	14,6%	17,8%
Fawn	85,6%	85,4%	72,5%
Chocolate brown	-	-	9,7%

It is clear therefore that there are good theoretical grounds for assuming that suitable orientation of the long axis of the body could alleviate thermal loads effectively and that the colour pattern of the springbok could further enhance the efficacy of this behaviour.

Table 20 The effect of solar elevation on the weighted mean absorptance of a springbok orientated perpendicularly to the sun's rays. A cylindrical body shape has been assumed

Solar elevation	Weighted mean absorptance
0°	0,49
15°	0,53
30°	0,55
45°	0,58
60°	0,60
75°	0,60
90°	0,60

Behavioural thermoregulation

A brief description of the environmental conditions to which the springbok were exposed is warranted before embarking upon a discussion of behavioural thermoregulation.

Springbok occur naturally in areas where they encounter intense heat loads from the environment during the summer months. In Fig. 62 I have illustrated certain environmental data, recorded on a typical summer's day during the telemetry study on springbok at Benfontein. These graphs show that the total radiative heat loads can be very high during the day when both short-and long-wave radiation are involved. In the absence of clouds, short-wave radiation intensity can exceed total long-wave radiation intensity for a few hours during the day. As far as short-wave radiation is concerned, direct solar radiation has by far the highest intensity. In fact, for a few hours during the day, direct solar radiation is the largest single component of total radiation. For example, on a cloudless day at 14h00, direct solar radiation contributed 43% of the total radiation, thermal radiation from the ground contributed 28% while atmospheric thermal radiation, short-wave radiation reflected from the ground and diffuse sky radiation contributed 18%, 7% and 4% respectively.

Short-wave radiation is naturally only a factor during the day and over a 24 hour period, thermal radiation from the ground is the largest single component of total radiation.

The effect of short-wave radiation can be reduced dramatically by shade-seeking behaviour. Shade is, however, not always available and this type of behaviour would reduce the foraging time during the day. On the other hand, orientation behaviour, by altering the profile area, can reduce the radiative heat load substantially while the animal

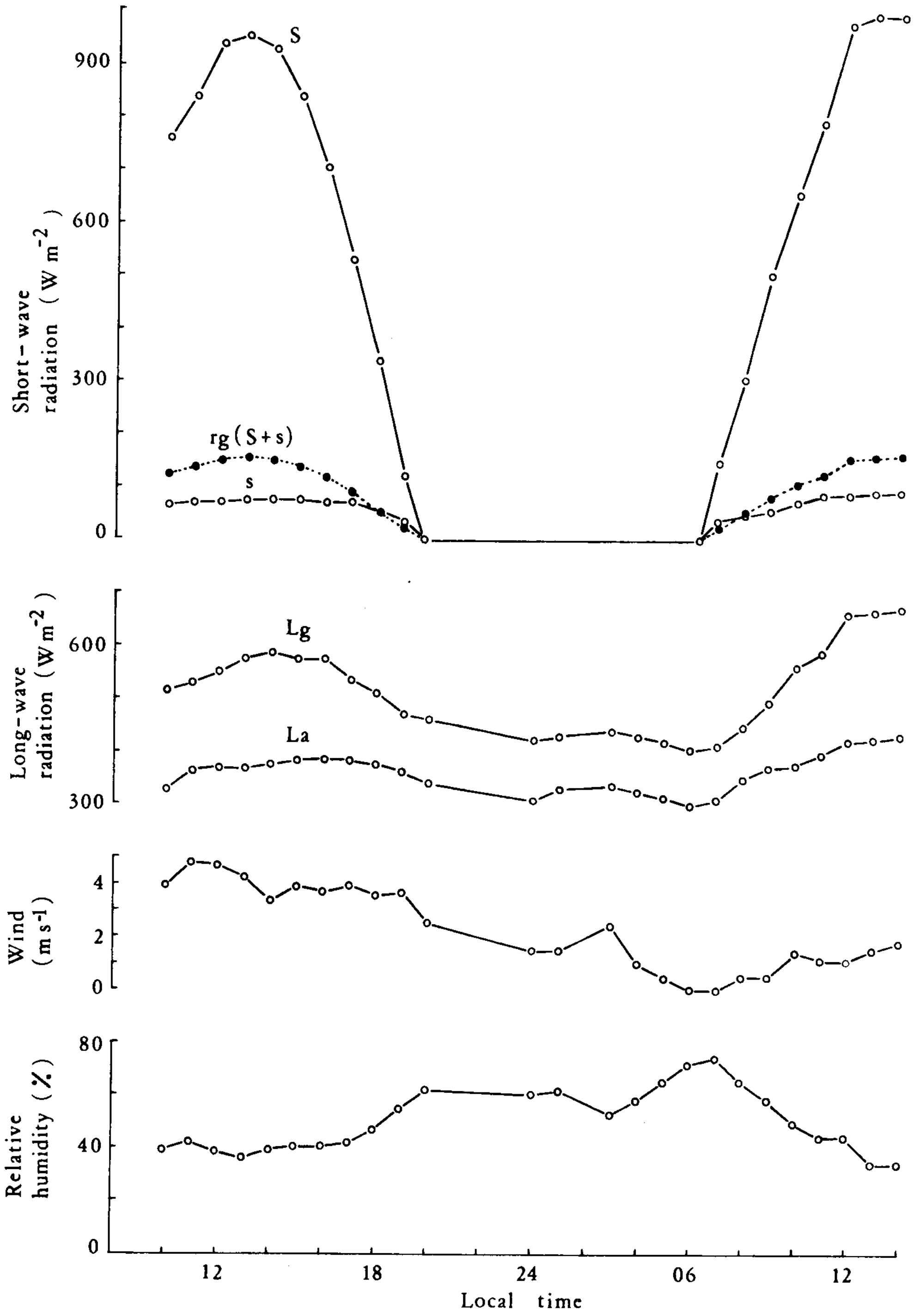


Figure 62 Environmental data, recorded on a typical summer's day during the telemetry study on springbok. (S is direct solar radiation; rg (S + s) is solar radiation reflected from the ground; s is diffuse sky radiation; Lg is long-wave radiation from the ground and La is long-wave radiation from the sky)

continues to feed. Lying down would also alter the thermal environment to which the animal is exposed, and in Table 21 the results of a five-day behavioural study have been summarised. These results show that the majority of the animals orientated with the long axes of their bodies parallel to the sun's rays. The percentage of animals which orientated was always greater than 50%, except on day 5 when it rained and the majority lay down on the ground. The results also show that the springbok made very little use of the available shade. Although the terrain was covered mainly by low shrubs, a few shade trees were present. These results are in contrast with Bigalke's (1972) observations. He reported that springbok rested in the shade (when available) from *ca.* 08h00 till *ca.* 17h00 during hot summer days. The reason for the different observations are not clear to me. It is possible that in Bigalke's study either more shade trees were available, or the radiation intensity was higher.

In Fig. 63 I have illustrated the results obtained during day 1 in greater detail. This figure shows clearly that the majority of the animals under observation orientated towards the sun when the sun was shining. When the sun was obscured by clouds, the majority assumed a random orientation. For statistical analysis, all the observations were divided into two groups, namely when the sun was shining and when the sun was obscured. The proportions of animals in both groups, which were orientated towards the sun, were then calculated. The differences between the two proportions were highly significant ($p < 0,0001$) and show that the springbok did orientate when the sun was not obscured by

Table 21 Environmental and behavioural data, recorded on five different days and expressed as a percentage of the number of animals engaged in a specific behavioural posture during each day (n = number of animals x number of observations)

Observation	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5
Orientating towards sun (%)	53	61	61	60	32
Shading (%)	0	0	0	5	1
Lying down (%)	5	0	16	15	31
Random orientation (%)	42	39	23	20	36
Sun shining (% of day)	47	100	100	100	47
Sun obscured by cloud (% of day)	53	0	0	0	53
Raining (% of day)	0	0	0	0	26
Ta range (°C)	29,0-32,2	28,9-33,5	29,3-36,3	29,1-37,5	21,6-33,8
n	1087	274	898	1560	381

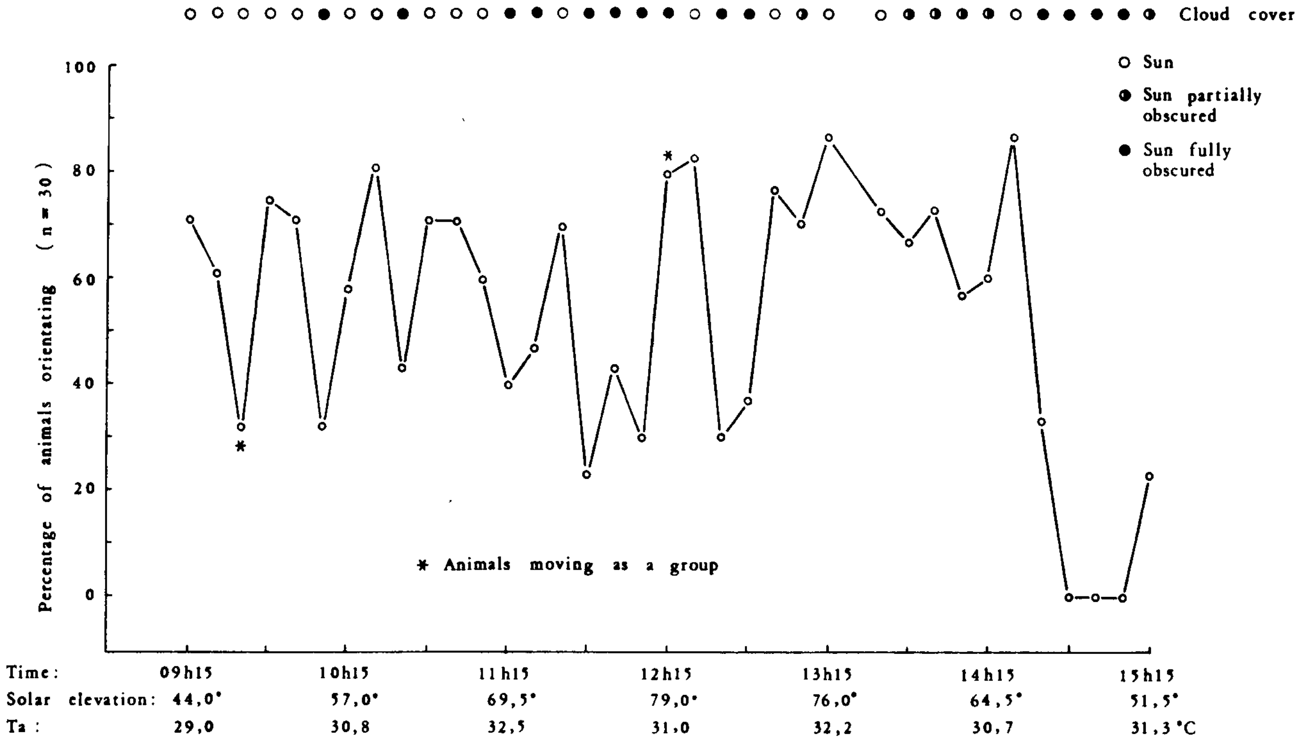


Figure 63 Percentage of springbok orientating long axis of the body towards the sun

clouds. The same test was applied to the data obtained on day 1 and 5 and in both cases, highly significant differences were found.

When the animals orientate with the long axes of their bodies parallel to the sun's rays, they can either turn their face or rump towards the sun. The results show that a greater proportion of the animals turned their rumps towards the sun and the difference was highly significant ($p < 0{,}0001$). I have already demonstrated that the face and rump profiles have more or less the same proportion of white and fawn coloured areas. Therefore, a difference in solar radiation absorptance can not explain the preference of the animals to orientate with their rumps towards the sun. The animals, however, grazed intermittently throughout the day and, as the rump profile is smaller than a face profile when the animals' heads are lowered while grazing, this would explain their preference for rump orientation.

RENAL FUNCTION

The osmolality and chemical Composition ~~compositon~~ of the springbok plasma are shown in Table 22. The results show a typical mammalian pattern.

The table also shows that the kidneys have the ability to produce a fairly concentrated urine. The high concentration can be ascribed mainly to the high concentrations of potassium and urea in the urine although at site 2 a remarkably wide range of sodium concentrations was recorded. This could be due to nutritional influences as the natural vegetation included a wide variety of plants. I recorded a maximum osmolality of 1620 mOsm kg^{-1} in this study, but this figure is by no means an indication of the maximum concentrating ability of the springbok's kidneys. Ingram and Mount (1975) stated that although urine concentrations over 1500 mOsm kg^{-1} are rare in the normal life of Merino sheep, values as high as 3800 mOsm kg^{-1} have been recorded during water deprivation. Maloiy and Hopcraft (1971) have also shown that the urine osmolality of hartebeest increased from 1080 mOsm kg^{-1} when hydrated to 2010 mOsm kg^{-1} when the animals were dehydrated and subjected to heat stress. Similarly, they found that the urine osmolality of the impala increased from 1385 mosm kg^{-1} to 2250 mOsm kg^{-1}. In the present study, the level of hydration in the springbok was unfortunately not known. When the plasma and urine samples were collected from the springbok at site 1, samples of plants, favoured by the springbok, were also collected during midday. The water content of these plants was high and varied

Table 22 Plasma and urine analyses of springbok

	Na^+ mEq l^{-1}	K^+ mEq l^{-1}	Cl^- mEq l^{-1}	Urea mM	Osmolality mOsm kg^{-1}
SITE 1 PLASMA					
Mean ± s		3,2 ± 1,1	112 ± 10	3,8 ± 2,0	229 ± 32
Range		2,0 - 5,0	99 - 130	1,0 - 7,0	193 - 274
n		9	9	9	9
URINE					
Mean ± s	87 ± 57	245 ± 111	141 ± 86	314 ± 98	1114 ± 213
Range	25 - 190	135 - 405	55 - 311	201 - 436	760 - 1350
n	7	7	7	7	7
SITE 2 URINE					
Mean ± s	414 ± 227	185 ± 124	93 ± 29	185 ± 31	1307 ± 193
Range	16 - 724	48 - 468	52 - 155	144 - 243	860 - 1620
n	17	17	17	17	17
SITE 3 PLASMA					
Mean ± s	159 ± 4	6,9 ± 1,5			
Range	155 - 165	4,9 - 8,6			
n	7	7			
URINE					
Mean ± s	210 ± 80	430 ± 50			
Range	145 - 329	368 - 495			
n	5	5			

between 61% and 80%. This collection period also coincided with the rainy season and consequently water was freely available in the field. They appear therefore to have been in a reasonably well hydrated condition and the maximum value of 1350 mOsm kg^{-1} recorded was probably far below their maximum concentrating ability.

Sperber (1944) and Schmidt-Nielsen and O'Dell (1961) have demonstrated a correlation between the ability to concentrate urine maximally and the gross morphology of certain mammalian kidneys. The kidney dimensions of springbok are given in Table 23 and in Table 24 I have compared their theoretical concentrating ability with those of other species, with known dimensions.

Table 23 Kidney dimensions of springbok

Mean weight ± s (g)	Cortex/Medulla	Kidney size (mm)	Relative med. thickness	n
44 ± 6	0,25 ± 0,05	37,8 ± 2,2	5,33 ± 0,61	124

The relative medullory thickness indicates that springbok have the potential to excrete urine with an osmolality higher than that of the hedgehog, in other words, greater than *ca.* 3000 mOsm kg^{-1}. However, the gross morphology of the kidney can only give an indication of the concentrating ability and the efficiency of the springbok kidneys must still be evaluated experimentally. Nevertheless, the following values from the literature show the maximum urine concentrations of ungulates which live in similar environments as the springbok - eland, 2050 mOsm kg^{-1} (Taylor and Lyman 1967); hartebeest, 2010 mOsm kg^{-1} (Maloiy and Hopcraft 1971); oryx, *ca.* 3000 mOsm kg^{-1} and dik-dik antelope, *ca.* 4000 mOsm kg^{-1} (Maloiy 1972).

Table 24 Relative medullary thickness and maximal urinary concentration in various mammals

Animal	Relative medullary thickness	Max. osmolar $^{u}/_{p}$	Max. urinary osmolality (mOsm kg^{-1})
Beaver[1]	1,3	2,7	516
Pig[2]	1,6		1075
Man[2]	3,0	4,2	1398
† Hedgehog[3]	4,8	9,0	3062
Bontebok[4]	4,9	* 5,4	
Springbok[5]	5,3	7,0	* 2700 - 3000
White rat[2]	5,8	8,9	2900
Kangaroo rat[2]	8,5	14,0	5500

Sources: Chew, 1965[1]; Schmidt-Nielsen and O'Dell 1961[2]; Yaakobi and Shkolnik 1974[3]; Van Zyl 1978[4] and present study[5]

† *Ericaneus europaeus*

* Theoretical values obtained by interpolation

CONCLUSIONS

1. Solar radiation frequently increased the surface temperature of springbok to 20°C above body temperature. The heating effect of solar radiation was, however, greatly reduced by forced convection and consequently, convective cooling would be an important factor in the heat balance of springbok in a hot environment. In a cooler environment, considerable heat loss occurred across the pelage and the relatively thin pelage could be a disadvantage under cold conditions.

2. The springbok maintained a reasonably stable body temperature between *ca.* 37 and 41°C under widely different environmental conditions both when water was freely available and during dehydration. The mean body temperature of the individual animals differed significantly and the individual fluctuations in body temperature varied between 0,5 and 3,2°C. The animals differed individually in their degree of thermostability and it seems as if dehydration did not extend the temperature range previously established by the hydrated animals.

3. Ambient temperatures below 30°C had little effect on the body temperature of unrestrained springbok. However, when ambient temperatures exceeded *ca.* 30°C, body temperature increased significantly. In contrast, variations in ambient temperature had a much greater influence on body temperature of the restrained

springbok. This phenomenon illustrates the importance of behavioural thermoregulation.

4. The observed variations in body temperature generally followed a diurnal pattern where body temperature increased to a maximum in the afternoon and thereafter decreased to reach a minimum value during the night or early morning.

5. A short burst of exercise resulted in an immediate rise of 2°C in body temperature. This dramatic rise in temperature far exceeded the effects of intense solar radiation over many hours.

6. Respiratory evaporation is an important avenue of heat loss in the springbok and a maximum respiration rate of 274 r. min^{-1} was recorded. Solar radiation, which influences surface and skin temperature, had a strong influence on respiration rate and 79% of the variation in respiration rate could be accounted for by variations in surface temperature. In contrast, variations in rectal temperature seemed to have little effect on the respiration rate. However, when rectal temperature exceeded *ca.* 39,8°C, its influence became more apparent.

7. The restrained springbok resorted to open-mouth panting under conditions of intense heat stress. Under identical environmental conditions unrestrained springbok generally exhibited a lower respiration rate and never displayed open-mouthed panting. Again the importance of behavioural thermoregulation was apparent in this respect.

8. Peripheral vasomotor tone was influenced by solar radiation, ambient temperature, the thermal status of the animal and possibly also by local fermentation heat in the rumen. In the absence of solar radiation, vasodilation occurred at a higher ambient temperature than in the presence of solar radiation. Also, in the absence of solar radiation, when ambient temperature was below *ca.* 20°C, rectal temperature appeared to have a pronounced influence on ear temperature. The springbok appears to be able to use both the ears and horns as thermal windows, under conditions of both external and internal heat loads.

9. The amount of direct solar radiation absorbed by an animal is greatly influenced by the profile area exposed to the direct beam. The profile area is influenced by the relationship between body length and diameter and also by the relation between the horizontal and vertical diameter of the cylindrical body. In the springbok, theoretical analyses have shown that the animal will absorb on average 62% more direct solar radiation throughout the day, if the long axis of the body is perpendicular to the solar rays. However, at the higher solar elevations (> *ca,* 60°) orientation has very little effect on the amount of direct radiation absorbed. Nevertheless, the behavioural study has shown that under conditions of intense solar radiation springbok will orientate the long axis of the body parallel to the sun's rays, throughout the day. The majority of the animals assumed a random orientation when the sun was obscured by clouds.

10. Head and rump presentations towards the sun resulted in approximately equal profile areas. However, when a springbok lowers its head to graze, the rump presentation is smaller than the head presentation. This fact is exploited by the springbok and the behavioural study has shown that a statistically greater proportion of springbok turned their rumps towards the sun when they orientate.

11. It is possible that the colours of the springbok's pelage have a thermal function in addition to their cryptic function. The dorsal and lateral surfaces have a fawn colour with a relatively low absorptance for short-wave radiation. The presence of white areas on the face, rump and ventral surface reduces the general absorptance of short-wave radiation even more. However, these white areas only reduce total absorptance significantly when diffuse radiation and direct solar radiation at the lower angles of elevation are considered.

12. From morphological studies it would seem as if the kidneys of springbok have the potential to produce highly concentrated urine. This has obvious advantages in a hot, arid environment.

13. In general, springbok do not rely on hyperthermia or thermolability to survive in a hot, dry environment. Their adaptation to such an environment rather resides in their thermal behaviour and specific physical qualities of the pelage. The relatively thin pelage can be a disadvantage because it does not provide

significant protection against environmental heat gain in a hot environment, or heat loss under cold conditions. Nevertheless, the high reflectance of the pelage reduces excessive heat gain to a certain degree and, as the pelage is quite dense, this would also reduce the penetrance of radiation into the pelage. In spite of certain thermal disadvantages, the thin pelage is of great importance to this species when sprinting away from predators by facilitating heat loss by convection and radiation.

GENERAL CONCLUSIONS

Detailed conclusions have been presented at the end of each chapter and the reader is referred to these for additional information. This section will merely highlight certain of the more important conclusions.

In Chapter 1 certain physical characteristics of the pelages of wild African ungulates were studied for the first time. One of the more interesting results to emerge from these studies was that the thickness of the pelage decreases exponentially with increasing body size and disappears completely in the very large ungulates such as the rhinoceros and elephant. This relationship is closely associated with the progressive increase in relative surface area which occurs with decreasing body size and could be interpreted as an effect of natural selection to ensure reduction in heat loss in the smaller ungulates. This phenomenon could, however, also be the result of enhancing heat loss in the larger ungulates, particularly when they are required to sprint away from predators under the hot conditions prevailing in the African savanna. The latter conclusion is supported by the fact that the springbok, among the swiftest of antelope, has a pelage thickness which is significantly less than that predicted by the regression line. These studies also showed that conductance decreased exponentially with increasing pelage depth, despite the fact that conductivity increased with increasing depth. Total insulation was largely determined by air trapped within the pelage and the boundary layer of still air above the pelage. The importance of the boundary layer, however, decreased with increasing pelage thickness. Consequently forced convection, which disturbed the still air, had a more pronounced effect upon the insulation of thin pelages than on thick pelages. Nevertheless, windspeeds greater than *ca.* 2 m s^{-1} could penetrate the thicker pelages and thereby increase their conductance dramatically. Important differences in respect to reflectance of the different colours of the various pelages were established and these have been discussed in terms of their thermal and ecological significance.

In Chapter 2 a complete thermal balance was constructed for the Namaqua-Afrikaner sheep, while restrained in a metabolic cage in an outdoor environment. The results showed that the major avenue of heat gain under hot conditions was from thermal radiation from the ground surface. The major avenues of heat loss under hot conditions were via reradiation and, under windy conditions, convection. Detailed results with respect to the major influences on respiration rate, cutaneous water loss and vasomotor tone have been described and discussed. In general, these results have again emphasised the important role of the pelage in providing protection against both heat loss and heat gain, thereby facilitating the maintenance of a stable body temperature.

In Chapter 3 the first studies on free-ranging and restrained springbok have again highlighted the importance of studying thermoregulation under natural conditions as opposed to studies in artificially controlled climate chambers. The results show that springbok are able to maintain a stable body temperature (37 - 41°C) under a variety of climatic conditions and even when dehydrated. They exhibit all the expected physiological responses to thermal stress such as sweating, thermal panting, shivering and marked changes in vasomotor tone; the latter being reflected in sudden changes in the temperature of the ears and horns which are used as thermal windows. In sharp contrast to the Namaqua-Afrikaner sheep, however, the thin pelage of the springbok offers minimal protection against heat loss and heat gain. Consequently they rely heavily on behavioural thermoregulation to compensate for this disadvantage. Important behavioural adjustments include shade-seeking, seeking cover under cold, windy conditions and by reducing the profile area exposed to direct solar radiation by orientation of the long axis of the body towards the sun. The effect of the latter adjustment is enhanced by the colour pattern of the pelage. Finally, the springbok was found to possess efficient renal function which would naturally compensate to some extent for excessive evaporative water loss under hot, arid conditions.

In general then it can be concluded that, although marked variation exists in the physical quality, colour and thickness of the pelages of African ungulates, the pelage is of critical importance in the thermal physiology of these animals. For example, my heat balance studies have again confirmed that the primary compensation to high environmental heat loads was via physical processes which occurred automatically on the external surface of the animal and did not necessarily involve physiological responses. Equally important, it has also become clear that the quality, colour and thickness of the ungulate pelage represents an interesting evolutionary compromise, imposed upon the animal by natural selection in its specific ecological niche. The latter conclusion is clearly demonstrated by the marked differences found between the artificially-selected Namaqua-Afrikaner sheep and the naturally-selected springbok.

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