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THE ENERGY EXCHANGES OF RUMINANTS

A thesis submitted to the University of Glasgow for
the degree of Doctor of Philosophy in the Faculty of Science

by

JOHN PATRICK JOYCE

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The Hannah Dairy Research Institute,
Ayr

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The Energy Exchanges of Ruminants

SUMMARY

Experiments have been made to determine the effect of the different components of the weather, singly and in combination, on the energy metabolism of sheep. For this purpose it was necessary to devise methods of measuring the heat production of sheep without the need to keep them in a respiration chamber, and two methods were used. The first depended on tracheostomy and the second on the use of a face mask, and with both methods heat production was estimated from O_2 consumption only.

The results obtained for O_2 consumption of the tracheostomized sheep, as measured by a Douglas bag technique, were the same as those obtained in experiments in which the same sheep were confined in a respiration chamber and given the same food. The amount of CH_4 expired in the pulmonary gases was only 17% of the total CH_4 produced by the sheep, whereas of the total CO_2 produced the proportion expired from the lungs depended on the level of feeding. Evidence is presented to show that both O_2 consumption and CO_2 production were increased during the act of eating. Methods of calculating the heat production of sheep from their pulmonary exchange of O_2, CO_2 and CH_4 are discussed and a method has been evolved of calculating the heat production from the level of O_2 consumption of sheep when in environments effectively below their critical temperature.

Experiments were made with four tracheostomized sheep and with two fitted with face masks to determine the effects of artificial rain and changes in air temperature, wind velocity and infrared radiation on their heat production and body temperature. Responses of O_2 consumption to changes in air temperature, wind velocity and infrared radiation were virtually complete within 60 min after the changes were made, but responses to wetting were

not complete even when the wetting process had continued for 2 h 20 min. Changes in the skin temperature of the trunk were always more rapid than changes in O_2 consumption.

Heat production was increased by wind, and the amount of increase depended not only on the wind velocity but also on the ambient temperature and on the length of fleece of the sheep. When the sheep were wetted with artificial rain, heat production increased, and a level of 5762 kcal/m^2/24 h was reached in one sheep when it was subjected to wind and rain together, compared with a typical value of 1350 kcal/m^2/24 h for the same sheep in a thermoneutral zone. Heat production was reduced in a given air velocity when the hind-quarters, rather than the side of the sheep, were presented to the wind, but only when the fleece was long.

Tissue insulation, defined as the rectal temperature-skin temperature gradient divided by the total heat production, once vasoconstriction had been established, was unaffected by environmental changes and there appeared to be differences in tissue insulation between different breeds of sheep. External insulation, defined as the joint insulation of the air interface and coat, increased linearly with increasing fleece length over the range 5 - 50 mm, but fell with increasing wind velocity.

Direct measurements of the total solar heat load on sheep, using models, showed that the total solar heat load on sheep in Scotland can be as high as 300 kcal/m^2/h. Reflectance values of solar radiation of sheep skins varied from 23 to 48% depending on the length of time that had elapsed since shearing.

A correlation of 0.99 was found between the external insulation of sheep in a natural outdoor climate, when the incoming solar radiation was less than 0.1 cal/cm^2/min, and the corresponding insulation values predicted from the artificial climate experiments. Increases in coat insulation due to solar radiation were not as high as would have been expected from solar heat loads measured on models.

Methods of estimating heat production or external insulation from (1) measurement of climatic factors, (2) skin and rectal temperature measurements, and (3) heat losses from artificial homeostatic sheep are discussed in relation to the measurement of the heat production of free-grazing sheep.

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CHAPTER I

INTRODUCTION AND REVIEW OF LITERATURE

Object of study. The experiments described in this thesis were made to determine in quantitative terms the effects of artificial and natural cold environments on the heat losses of sheep. Unequivocal evidence of the severe effect of cold environments on sheep is that death may occur in inclement weather conditions after shearing. Geytenbeck (1963) in South Australia found that most of the deaths attributed to cold weather, even when feed was adequate, occurred in the 5 days following shearing when as many as 30 - 50% of the sheep in the flock might die. In most cold climates, which prevail over a large proportion of the world especially in winter, the effect of cold weather on sheep is not so apparent because of the managerial precautions that are taken. In large areas of Scotland, for example, sheep are sheared by hand in such a way as to leave a longer staple length of fleece than is usual. It is important to know whether non-lethal cold environments do represent a hidden drain on the output from animal production, but is is often impossible in practice to distinguish between the effects of cold weather *per se* on sheep and the effects of poor nutrition caused by lack of fodder associated with retarded pasture and crop growth during cold weather.

Behavioural studies such as those of Powell (1963) can indicate the percentage of a flock that will seek shelter, huddle together or orientate themselves to the prevailing wind, but results of such studies cannot indicate what is the metabolic 'cost' of the environment to the sheep nor whether the shelter is sufficient to nullify the effects of the cold environment. They may only indicate a period when the animal, already reacting metabolically to the cold weather, finds the environmental situation unbearable, rather than the actual onset of metabolic response to cold.

REVIEW OF LITERATURE

In this section are defined the theoretical environmental limits beyond which the animal must adjust its metabolism to maintain a state of homeostasis. The different physical components of the climate are individually discussed together with methods of measuring the extent to which an animal can adjust its metabolism in response to cold.

Maintenance requirements. A number of grazing studies on sheep, using marker techniques and other methods, have been made in an attempt to assess the effect on maintenance requirements of sheep grazing out-of-doors as compared with those hand-fed indoors (Coop & Hill, 1962; Coop & Drew, 1963; Lambourne & Reardon, 1963; Langlands *et al*. 1963 a,b). Although increases in the maintenance requirement ranging up to 275% in some instances have been measured, it is impossible to assess from the results what proportion of the increase, if any, should be allocated to the different climatic factors, cost of plucking and eating the herbage, cost of locomotion and other avenues of energy expenditure such as those of an endocrinological or neurological nature.

Zone of thermoneutrality. An increase in metabolism due to cold will not normally be elicited unless the environmental temperature of the animal is below the zone of thermoneutrality. This is the range of environmental temperature where the animal does not need to employ thermoregulatory devices to maintain a state of homeothermy. It is as Brody (1945) terms it "the equivalent of the air conditioning engineer's comfort zone".

Critical temperature. At the colder end of the thermoneutral zone is the "critical temperature". This is the air temperature at which the animal must increase its heat production to maintain its body temperature. Before this temperature is reached, vasoconstriction and alteration of the blood supply to the extremities, piloerection and change of body posture are sufficient to control body temperature. The critical temperature, defined as air temperature, will be affected by a number of factors such as level of nutrition and type and length of coat carried. It will also vary with factors that affect the coldness of the climate such as air movement, rain and solar radiation. Critical temperatures that have been determined under still air conditions for different animals under different nutritional circumstances have ranged from as low as -40° for the Arctic fox and -12° for the Arctic lemming (Scholander _et al_. 1950) to 20° for the goat (Brody, 1945), 28° for naked man (Burton & Edholm, 1955) and 35° for the newborn pig (Mount, 1963). The critical temperature of the adult steer has been shown to vary from about 6° at maintenance levels of feeding to about 18° when fasting, both sets of measurements being made when the animals were fully coated. For shorn steers Forbes _et al_. (1926) found a critical temperature of 26°, and Alexander (1961 a) calculated a value of approximately 29° for newborn lambs. Several estimates have been published for adult sheep. Brody (1945), for example, gives a value of 13°, and Ritzman & Benedict (1931) showed that whereas the sheep carrying a full fleece could withstand temperatures of 0° without increasing its heat production, the shorn animal probably increased heat production at 18°. Blaxter _et al_. (1959 b) and Graham _et al_. (1959) calculated from their experiments that the critical temperature of sheep increased from a mean of 25.5° to 40° when the level of feeding was decreased from 1800 g to 600 g of dried grass cubes. When the level of feeding was kept constant the critical temperature was -0.3° for a sheep with a 12 cm fleece and 12° for a closely clipped sheep. The longer fleece not only lowered the critical temperature but also minimized the effect of falls of environmental temperature below the critical. The level of feeding, on the other hand, did not affect the rate of heat loss below the critical temperature and the heat loss increased at a constant rate per

m^2 of surface area per ^{o}C. These studies taken together not only illustrate the effect of coat length and level of nutrition on critical temperature but also show that species differ widely in their critical temperatures.

Environmental components. A criticism that may be levelled at all critical temperature determinations made to date is that they are quoted in terms of ambient temperature. It is obvious, however, that environmental factors other than ambient temperature will influence the critical temperature of a sheep. The components of the environment, other than ambient temperature, that may be expected to have an important affect are (1) air velocity, (2) humidity, (3) radiation flux, long wave (infrared) and short wave (solar), and (4) precipitation of water as rain, hail or snow.

In most environments information other than air temperature is necessary to categorize the environment, and the definition of the critical temperature as an air temperature is an over simplification. With man this problem of defining experimental environments has been overcome by the use of expressions such as "operative temperature" (Gagge, 1941; Winslow & Herrington, 1949), and "effective temperature" (Houghton & Yaglou, 1923; Yaglou, 1949) in which some consideration has been given to air movement and radiation.

Heat production. Once the animal is below its critical temperature, heat production will increase in an attempt by the animal to maintain homeothermy. Graham et al. (1959) showed that when environmental temperature was reduced to 8^{o} which was well below the critical temperature, the mean heat production of the two sheep they used increased from the thermoneutral values of 1100 (low feeding level), 1400 (medium level) and 1700 (high level) kcal/m^2/24 h to 2900 kcal/m^2/24 h. The sheep, of course, cannot increase its metabolic rate indefinitely and eventually a summit or peak heat production is attained. This is the highest attainable heat production in response to cold in the absence of voluntary muscular activity. In the presence of voluntary muscular work, however, heat production can increase far beyond the levels of summit metabolism for short periods.

Except beyond the limits of the summit metabolism and providing that the animal is below its critical temperature and environmental conditions are stable, heat loss is on average equal to heat production and this has been written by Blaxter (1962 a) as:

$$H_p \pm H_s = H_L = H_N + H_E \quad \ldots\ldots\ldots\ldots \quad (1)$$

where H_p = heat production per unit time

H_s = heat storage per unit time

H_L = heat loss per unit time

H_N = sensible heat loss

H_E = evaporative heat loss (insensible)

When environmental conditions are stable and if heat storage within the body is zero, the animal will be in a steady state of metabolism, i.e. $H_p = H_L$. If the environment becomes colder, then to maintain homeostasis heat production must be increased to balance the new level of heat loss. While reaching this new steady state of metabolism there will be a period of increased heat loss and increasing heat production before the animal is in a new state of heat balance, i.e. during this time $H_p < H_L$. Conversely, if the environment becomes warmer there will be an equilibration period during which $H_p > H_L$.

As shown in equation (1), the avenues of heat loss are two-fold: sensible and insensible. Heat is lost from the body by convection, conduction, radiation and vaporization of water from the skin and respiratory passages. The losses by convection and radiation (conduction heat losses are usually considered with those of convection) are the sensible heat losses, and once the sheep has fully altered its blood flow pattern and piloerected, heat losses by this route can no longer be controlled, and then the rate of heat loss conforms closely to Newton's law of cooling in that the rate of heat loss is proportional to the temperature difference between the animal's body and the environment. Bianca & Blaxter (1961) refer to the sensible heat loss as the "environmental demand" for heat.

The rate of vaporization of water from the skin and respiratory passages (H_E) can be controlled to some extent by the animal. Under cold conditions it can be curtailed (Blaxter et al. 1959 b) and under hot conditions increased (Lee, 1950; Alexander & Brook, 1960). Below the critical temperature the basal loss of evaporative heat is constant at approximately 300 kcal/m^2/24 h in man (Winslow, Herrington & Gagge, 1937), cattle (Blaxter & Wainman, 1961) and sheep (Blaxter et al. 1959 b).

In cold conditions another avenue of heat loss is the heat involved in warming the food and water from the environmental temperature to body temperature. This heat loss can normally be computed from the amount and temperature of the food and water ingested.

Insulation (resistance to heat flow). The heat flow per unit time through an insulating layer can be calculated by Fourier's law as:

$$\frac{dQ}{dt} = \frac{\lambda A}{\ell} (T_i - T_e) \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \quad (2)$$

where $\frac{dQ}{dt}$ = heat flow per unit time

λ = heat conductivity of the surface layer

A = surface area

ℓ = thermoconductive thickness of the surface layer

T_i = internal or body temperature

T_e = surface or external temperature

This can be rewritten as:

$$\frac{dQ}{dt} = A\,\frac{(T_i - T_e)}{I} \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \quad (3)$$

where $I = \frac{\ell}{\lambda}$ from equation (2) and is the resistance to heat flow and is the reciprocal of thermal conductivity

$$\text{or } I = \frac{T_i - T_e}{\frac{dQ}{dt} / A} = \text{specific insulation of the surface layer} \quad . \quad (4)$$

In the sheep the resistance to heat flow from the body will be determined by the sum of the specific insulations of the body tissues, fleece and air and is the resistance to total heat flow from the body. The specific insulation of the body tissues is termed the tissue insulation (I_T) and will be maximal only when all the various means of physical control of heat loss such as vasoconstriction and piloerection have been brought into operation. It can be defined from equation (4) as:

$$I_T = \frac{T_R - T_S}{(H_p - H_w - H_L)/A} = \frac{T_R - T_S}{H_p/A} \quad . \; . \; . \; . \; . \quad (5)$$

where T_R = rectal temperature

T_S = skin temperature

H_p/A = total heat loss/unit area/unit time

H_w = heat lost in warming food and water from ambient to body temperature

H_L = heat lost from lungs in warming inspired air from ambient to body temperature

H_w in the experiments described in this study was zero and the heat lost from the lungs in warming the inspired air to body temperature can be neglected since the specific heat of air is so low. The total heat loss in this equation (5) includes both sensible and insensible heat losses.

The transfer of sensible heat from the skin to the air can be regarded as a transfer of heat through two insulating layers, that of the fleece and that of the interface of air at the fleece surface where heat is radiated and convected to the surroundings. If the sensible heat flow is known and skin and air temperatures measured, it is necessary to measure only the surface temperature of the fleece to estimate the insulations of the fleece and air separately. Measurements of the fleece surface temperature using thermocouples have been made by Blaxter _et al_. (1959 a) but the nature of the surface of the fleece is such that it is difficult to be precise about the exact site of the air/fleece interface. If a wind is blowing the situation is even more difficult for it may then be assumed that, although the location of the surface that radiates to the surroundings has not changed appreciably from that in still air, the convective interface has probably moved deeper into the fleece. Indeed it is extremely difficult to determine at what point the process of conduction - convection within the fleece ends and that of convection to the air and radiation to the surroundings begins. This same difficulty of siting the coat-surface-to-air interface is present even in still air when wispy coats, such as that of the erected coat of cattle and of fully fleeced Scottish Blackface sheep with their dense inner and sparse outer hair coats are considered.

For these reasons the approach adopted by Blaxter _et al_. (1959 a) in dealing separately with these two terms appears untenable except under still air conditions where the site of the fleece surface/air interface level can be decided at least approximately. The alternative is to use the whole of the insulation of the sheep's skin, where the surface temperature is relatively easily measured, to the environment. This insulation can be termed the external insulation (I_E) and from Fourier's law as set out in equation (4) it can be defined as:

$$I_E = I_A + I_F = \frac{T_S - T_A}{H_N/A} \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \quad (6)$$

where I_E is the sum of the insulations of the air interface (I_A) and the fleece (I_F)

T_A = temperature of the air for a particular air velocity and radiation condition

T_S = mean skin temperature

H_N/A = sensible heat loss/unit area/unit time

If values of I_E are obtained for different fleece lengths at a constant wind speed, then the value for I_E, when fleece length is zero, can be regarded as an estimate of the insulation of the air interface at the skin at that particular wind speed.

A number of estimations of the thermal insulation of the fleece have been made. Blaxter et al. (1959 a) have estimated the thermal insulation of fleeces using the sensible heat flow and temperature gradient through the fleece as indices. The average value was 6.7 - 8.2° x 10^{-3}/kcal/m^2/24 h per cm of fleece depth and the air insulation 7.0 insulation units (insulation unit = °C x 10^{-3}/kcal/m^2/24 h). Scholander et al. (1950) measured the insulation of the fresh skin and fleece of Alaskan wild sheep (Ovis dalli) with a hot plate apparatus and also obtained a value of about 7 - 8 insulation units/cm fleece depth, although as Hammell (1955) points out, moisture evaporation from the fresh skin may have reduced the apparent insulation. Hutchinson et al. (1960) measured the insulation of a Merino fleeces, ½" and 3/16" in length, using a hot plate apparatus mounted on a model sheep in winds ranging from 4.3 - 10.7 m.p.h. The insulations of the fleece lengths on the windward side of the sheep showed decreases from 18.75 and 8.40 for the ½" and 3/16" fleece lengths respectively to 14.85 and

6.7 insulation units (including air interface insulation) when the wind speed was increased from 4.3 to 10.7 m.p.h. The maximal tissue insulation of new-born lambs has been shown by Alexander (1961)a) to be approximately 7.5 insulation units and that of the fleece plus air to be 7.5 - 15.0 insulation units. Alexander (1961)c) showed also that hairy coated Merino lambs were more resistant to cold than were fine-coated lambs.

In an attempt to assess the effects of exposure of sheep to an outdoor climate, Doney (1963) used Hatfield heat flow discs to measure regional losses of heat by Scottish Blackface sheep. Exposure to moderate winds (22 - 33 m.p.h.) increased the heat flow through portions of the fleece three to five times. It was not possible to demonstrate that any variation in the increase in heat flow was due to any attribute of the fleece other than staple length.

Insulation values for fur of different animals have been determined using hot plate techniques by Hammell (1955), Scholander et al. (1950) and Lentz & Hart (1960). Hammell found that the average value of the insulation per unit thickness of the inner fur of fresh pelts was 11 insulation units with a range of ±10%. Air velocity was found to increase the heat flow through the fur of coats from new-born Caribou (Lentz & Hart, 1960) by up to 50% in a 5 m.p.h. wind compared with still air. The increase was to some extent dependent on the inclination of the sample to the air flow. The addition of water, equivalent to 10 - 12% of the volume of the fur, doubled the rate of heat transfer.

Evaporation of moisture. Sheep, as do other homeotherms, use the evaporation of moisture from the skin and respiratory passages to maintain a constant body temperature under heat stress conditions, and an extensive range of literature exists on the effect of heat on respiratory rate and volume. However, few experiments have been made under cold environmental conditions. As reported earlier, the basal loss of evaporative heat from sheep is comparable to that of other species at 300 kcal/m^2/24 h. The only reference on the effect of a wet fleece on heat loss under cold conditions is that of Cresswell (1961). When shorn sheep were saturated with water at ambient air temperature, O_2 consumption increased from an average of 17.4 l. O_2/h to 21.6 l. O_2/h. When wool is wetted heat is liberated and results in a heat gain to the animal. Hedges (1926) found the heat of complete wetting of wool, initially at a relative humidity of 70 - 90%, to be from 1.0 - 2.4 cal/g wool. Nelbach & Herrington (1942) found that a woollen garment weighing 1.86 kg gave out 44 kcal of heat within an hour after a change in relative humidity from 29 - 77% at an ambient temperature of 32°. In a fleece weighing 4 kg this would amount to a heat liberation of 95 kcal in 1 h which is considerable when compared with the fasting metabolism of a sheep. Alexander (1962 a) has shown that in lambs the effect of wind and water on the coats appeared to be additive in effect.

<u>Solar radiation</u>. The effect of solar radiation on a sheep can be considered to be the joint effects of three components, direct radiation, diffuse radiation and radiation reflected back from the terrain. The direct component is the solar beam incident at the outside of the earth's atmosphere at 1.99 cal/cm^2/min. and is depleted by its optical path through the atmosphere. The diffuse component, measured on a horizontal surface, is normally considered as that incoming from a sky hemisphere and results from a scattering of part of the direct solar beam by dust and water vapour in the atmosphere. The amount of radiation reflected from the terrain is determined by the albedo or reflectance of the terrain.

The effect of solar radiation on the sheep has been measured in areas where the climate is hot rather than cold. MacFarlane *et al*. (1956) found that shorn sheep with only 1 - 2 cm wool suffered higher gains of radiant energy than sheep with full fleece. Almost complete insulation was offered by 4 cm of fleece for half an hour when the sheep was radiated at a level of 0.90 cal/cm^2/min. In some field measurements MacFarlane et al. (1956) found that the wool tip temperature of Merino sheep in a hot sun (1.17 cal/cm^2/min. insolation) at an air temperature of 36 - 42.5° rose to 87°. When the tips of the wool were clipped away, the reflectance of solar radiation was doubled. Priestly (1957) has made calculations of the losses of heat from the tips of the fleece in various winds, treating the sheep as a cylinder. The relief of cold stress by solar radiation is difficult to assess due to the complexity of the physics of heat transfer from the heated tips of the wool staple.

In this review the metabolic responses of sheep to low ambient temperatures have been reviewed. Emphasis has been laid on the lack of information on the effect of other climatic factors such as wind, rain and solar radiation. In this study the effects of these climatic factors, together with that of low ambient temperature, on the energy metabolism of sheep is investigated.

CHAPTER II

EXPERIMENTAL

A. General principles of approach

1. Introduction. To measure the effect of different climatic variables on the energy metabolism of sheep involved measuring the effect of each variable on the external insulation. The use of external insulation rather than heat production/unit area alone allowed comparisons to be made between sheep confined in different environmental temperatures, provided the ambient temperatures were below their critical temperature. The estimation of external insulation involved devising methods of determining levels of heat production and skin and body temperature for sheep not in respiration chambers. Since the assumption involved in determining external insulation is that the animal is in a steady state of metabolism, it was necessary to determine the time period required for an animal to adjust its metabolism following a change in a climatic variable. Thereafter each climatic variable was investigated separately and the results compared with those obtained with sheep in natural outdoor environments.

(i) Tests of methods. Energy metabolism was measured over short periods using either a respiration chamber or a Douglas bag technique. Heat production was calculated from either the calorific value of O_2 consumed and CO_2 and CH_4 produced or else from the calorific value of O_2 consumed alone. This last approach involved the assumption that, when a sheep is in cold stress, the incremental O_2 consumption above a thermoneutral value is used for the combustion of body fat and consequently that a calorific value for the incremental oxygen consumption can be estimated. The validity of this approach was borne out in the results of Graham *et al.* (1959) who showed that under cold conditions the increased heat production of sheep was due entirely to an increase in the combustion of fat. In the Douglas bag method, the respiratory exchange was calculated from the difference in the volumes of CO_2 and O_2 between the expired gas and the inspired air. The total heat produced was divided into sensible and insensible heat losses. The insensible heat loss, i.e. the heat lost by water vaporization, was determined in the respiration chamber at temperatures below the critical, and can be considered constant at all temperatures below the critical (Blaxter et al. 1959 b). To overcome any effects due to variation in level of nutrition, only a level of feeding close to the calculated thermoneutral maintenance requirement was used.

Rectal temperature was taken as a measure of deep body temperature. Mean skin temperature was computed from thermocouple measurements on the fleece- and hair-covered skin areas, and ambient temperature measured directly. From these temperatures the temperature gradients between the rectum and skin ($T_R - T_S$) and between skin and air ($T_S - T_A$), and the insulations of the tissues (I_T) and of the fleece and the air interface (I_E) were calculated after weighting the trunk and extremity temperature measurements in the ratio of 9:1, i.e. in the same ratio as fleece to hair covered areas (Blaxter et al. 1959 a).

(ii) Controlled environmental studies. Experiments were planned to measure the changes in heat production and in tissue and external insulations with changes in an indoor environment. These experiments were designed to measure the time necessary, after a change in any one environmental factor, for the animal to equilibrate and acquire new levels of rectal and skin temperatures and of O_2 consumption. Once the time needed to reach a steady state of metabolism after a change in each climatic factor had been determined, experiments were made under steady environmental conditions and the animal's metabolic rate measured and the resistance to heat loss calculated.

(iii) Outdoor confirmation of indoor studies. Once the indoor artificial climate studies had been completed, the animal's metabolism was measured under natural outdoor conditions. The results of heat production and insulation measurements were then compared with those computed from the indoor trial results and any deviations calculated. Measurements of the solar heat load were made with models of sheep, and the results compared with those obtained with live sheep.

2. General methods of determining energy metabolism. Most methods of determining the energy metabolism of large farm animals involve the enclosure of the animal in closed chambers. Such methods are those of direct calorimetry in gradient layer chambers and indirect calorimetry in closed- or open-circuit respiration chambers. For the purposes of this study it was essential that the confinement and restriction of the animal be kept to a minimum to allow full exposure to the varied natural or artificial climatic stresses imposed upon it. Two methods of indirect calorimetry have therefore been used, both involving Douglas bags, (1) a tracheal fistulation technique, and (2) a face mask technique.

The classical studies of the early German workers, Zuntz et al. (1898), Zuntz & Lehmann (1889) and Lehmann et al. (1894), on short term energy expenditure, involved the use of tracheal fistulated animals. Tracheostomized cattle have been used by Klein (1912, 1915), Möllgaard & Anderson (1917) and more recently by Flatt et al. (1958). Methods for measuring the energy expenditure of tracheostomized sheep have been developed by Hagemann (1899), Hagemann & Karpow (1906) and Ustjanzew (1911). Dougherty et al. (1955) used tracheostomized sheep in conjunction with a closed-circuit spirometer system to measure O_2 consumption during investigations on bloat. Energy metabolism studies using similar methods have also been made on sheep by Cresswell (1957), Webster & Cresswell (1957) and Cresswell & Harris (1961). Except for the work of Klein (1915) on one tracheostomized cattle beast, no results have been published on the accuracy of the technique for measuring energy metabolism.

The mask technique has been more extensively used (Douglas, 1911; Washburn, Brody & Ragsdale, 1937; Blaxter, 1948; Kleiber, 1958; McLean, 1963), and has the advantage that the animal is anatomically intact and natural in its respiratory passages. No surgery is required. The main disadvantage of the tracheal fistula technique - that of the absence of heat exchange and conditioning of the inspired air that must occur in the nasal and pharangeal regions of the intact sheep - is overcome but the complication of the dead air space within the mask on air conditioning is introduced.

There are a number of advantages in the tracheostomy technique. Firstly, no region of the head is occluded from the imposed or natural environment, and the head, due to the presence of hair rather than wool, may be an important region of heat loss to the animal. Secondly, short term respiratory exchange determinations involving measurement of CO_2 and CH_4 production are uncomplicated by irregular or periodic oral emission of belched gases containing high levels of CO_2 and CH_4. Gases resulting from fermentation in the gastro-intestinal tract as opposed to those produced by normal respiration may be determined in conjunction with a respiration chamber. This allows measurement of the proportions of combustible gases which are absorbed from the intestinal tract and eliminated through the respiratory tract. Thirdly, it is possible to conduct experiments where the amount of O_2 consumed and the production of CO_2 and CH_4 during the act of eating can be measured. In the experiments discussed in this thesis, both the tracheal fistula and face mask methods have been used.

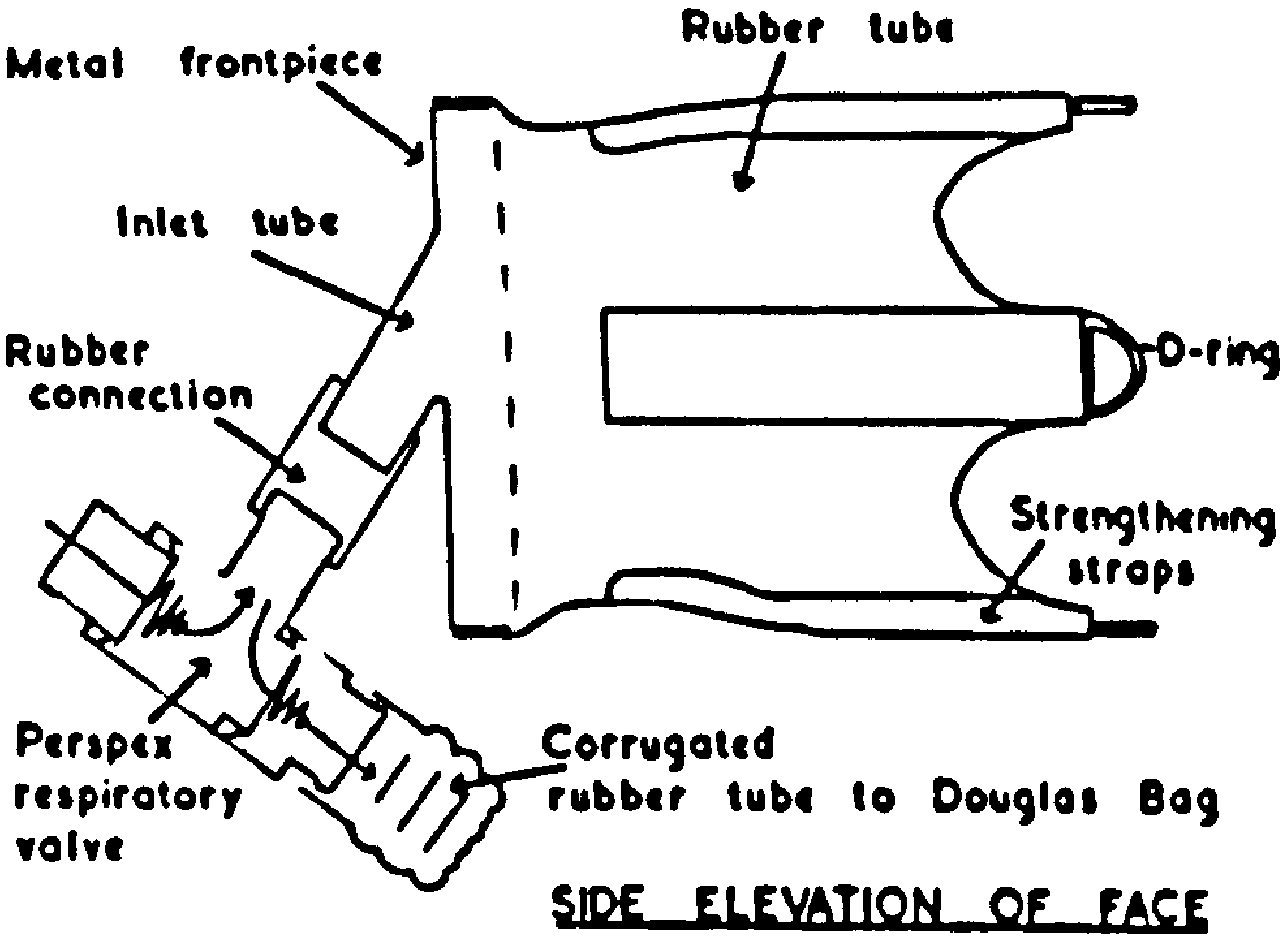
3. <u>Animals</u>. Twelve wether sheep, all over 4 years of age and previously

well trained to calorimetric work were selected as experimental animals. The following breeds were used:-

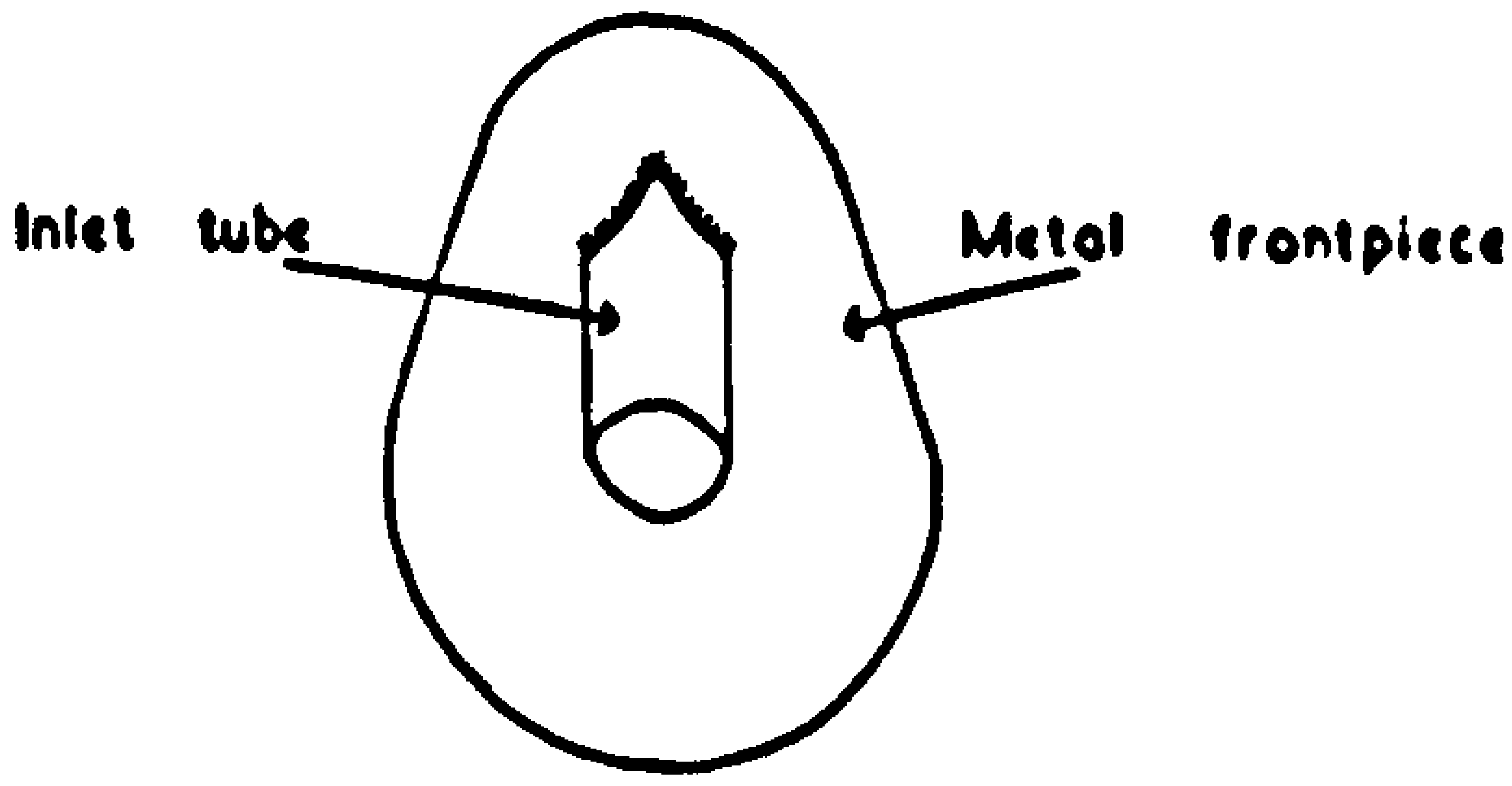
Breed	Sheep
Cheviot	X, Ax, Cs, Se, Jr
Downcross	Yl
Scottish Blackface	Ct, Zk, Dl
Mixed breed	By, Fr, Re

Sheep X, Ax, Cs, Se, Yl, Ct, Zk and Dl were tracheostomized, but sheep Jr, By, Fr and Re were anatomically intact and with them face masks were used. The establishment of the tracheal fistulae in the sheep and their subsequent maintenance and individual histories have been described in a paper by Blaxter & Joyce (1963) which is attached to this thesis as Appendix I. The collection of the expired air, its measurement and analysis are also described in that paper.

4. Pathological findings in the trachea of slaughtered sheep. Microscopic examination by Dr. P. S. Blackburn of sections of trachea taken post mortem from sheep in which tracheal fistulae had been present for long periods showed a tendency for the subepithelial glandular layer to decrease in thickness with the result that the cartilaginous rings were nearer to the lumen of the trachea. The epithelium under the cannula sleeve had changed from a columnar to a stratified squamous type. In two of the tracheas examined a papilliform granuloma had developed near the end of the sleeve in the trachea, one at the cranial end and the other at the caudal end. The epithelium covering the ingrowth was of the columnar type on the side opposite to the edge of the sleeve but of the stratified squamous type on the side next to the end of the sleeve. Where the ingrowth touched the edge of the sleeve, ulceration of the epithelium had developed. The tissue mass was composed of granulation tissue in the centre of which there was the



SIDE ELEVATION OF FACE MASK



FRONT ELEVATION OF FACE MASK

NOT TO SCALE

Fig. 1. Diagram illustrating the construction of the face mask together with the valve assembly attached to it.

remains of a cartilaginous ring. The disappearance of a portion of this ring left a gap in the cartilaginous rings below the palliform granuloma. The ingrowths were dorsal in position and it is possible that the presence of the sleeve in the trachea had allowed the side of the cartilaginous ring, opposite the end of the sleeve, to spring inwards causing the formation of the granuloma.

5. Design of face masks. The design of the face mask is shown in Fig. 1. It consisted essentially of an elliptically shaped light tin front piece, the part of the ellipse with the greater radius corresponding to the jaw of the sheep, while the smaller radius was shaped to fit the nose. Around the outside edge was soldered a $\frac{1}{2}$" width of light copper strap. A light gauge copper tube (outer diameter 1 in.) was inset and soldered into the face of the front plate at an angle. Cemented to the copper edge strap with "Evostick" (Evode Ltd.) was a shaped tube cut from a motor-car inner tube which closely fitted the nose of the sheep. Evenly spaced around the outer surface of the rubber tube and cemented to it were four backward facing rubber straps, each having at its end a D-ring. A collar (1 in. wide) with corresponding D-rings was placed around the sheep's neck. Before placing the mask on the sheep's face, a heavy lanoline cream was smeared around the middle third of the face. The mask was pulled over the nose of the sheep and the D-rings joined to the corresponding D-rings on the collar by string. Care was taken that the mask made a tight fit with the face of the sheep and it was checked visually that a seal of lanoline was present between the mask and the skin at the leading edges of the mask. The sheep's face was not clipped during the experiments since it was found that the hair on the face did not appear to cause any leakage of air.

Table 1. Effect of length of training period on O_2 consumption

Sheep	Days of training sheep using full collection apparatus	O_2 consumption (1./h)
Cs	1	18.96 ± 2.32
	2	16.70 ± 1.79
	3	15.53 ± 1.78
	4	15.51 ± 1.59
Y1	1	17.58 ± 4.40
	2	17.07 ± 1.69
	3	15.88 ± 1.63
	4	15.60 ± 1.49

The method of collecting the expired air using the face mask technique was essentially the same as that used with the tracheostomized sheep. The 2-way mica valve was connected by a very short piece of rubber tubing to the exit copper tube from the mask. The apparatus for collecting the expired air from the 2-way mica valve was exactly the same as that described in Appendix I for the tracheostomized sheep.

6. Training of sheep. Before beginning any experiment each sheep was accustomed to the collection apparatus and restraining apparatus for at least 1 week. Individual sheep varied in their attitude to the attaching of the collection apparatus, but most of them appeared to be accustomed to it after 10 days' constant use. At first oxygen consumption was high and variable, but after 4 days this high consumption and variability decreased rapidly. This is shown by the results given in Table 1 which were obtained in the training of tracheostomized sheep Cs and Ct.

7. Chamber techniques. Respiration chambers, as described by Wainman & Blaxter (1958), were used to obtain reference or standard metabolic data. The respiration chambers are of the closed circuit type and measure O_2 consumption and CH_4 production volumetrically and CO_2 production gravimetrically. The factors used at this laboratory to derive heat production from O_2 consumption, CO_2 and CH_4 production and urinary N excretion are 3.815 kcal/l. O_2, 1.232 kcal/l. CO_2, -1.419 kcal/l. CH_4 and -0.578 kcal/g N in urine. The ambient temperature could be controlled at any desired temperature between -5° and 40°, and air velocity was constant at 0.2 m.p.h.

Four types of experiment were made using the chambers:

(1) 24-h measurements of complete respiratory exchange under thermoneutral conditions.

(2) Hourly determinations of O_2 consumption and CO_2 and CH_4 production under thermoneutral conditions.

(3) Determinations at 3-h intervals of O_2 consumption and CO_2 and CH_4 productions under thermoneutral conditions.

(4) 24-h determinations of respiratory exchange and water vapour loss under cold conditions.

In all the chamber experiments the chamber was opened at 8.45 a.m., the faeces and urine removed and two feeds placed in the feed bins. Each sheep was given the ration for 14 - 21 days before any trial began and it wore the harness described by Wainman & Paterson (1963).

In the first three types of experiment the ambient temperature was regulated so that the sheep was in a thermoneutral environment as estimated from the data of Blaxter et al. (1959 a, b).

The use of 3-h periods of measurement allowed CO_2 production to be determined with reasonable accuracy. Every 3-h the working of the respiration chamber was stopped, and besides the normal measurements of O_2 consumption and CH_4 production, the CO_2 production was determined gravimetrically by weighing the series of absorbers which removed CO_2 from the air circulating in the apparatus. Three consecutive measurements at 3-h intervals could be made between the hours of 9 a.m. and 6 p.m.

Minimal water vapour loss from the sheep was determined at low environmental temperatures. As discussed on p. 6 the data of Blaxter et al. (1959 b) suggest that the basal water loss from sheep varies little from a mean value of 300 $kcal/m^2/24$ h. To provide estimates of this loss from each sheep, the chamber temperature was lowered to $5 - 7^o$, a temperature which was well below the theoretical critical temperature of the sheep when shorn or having short fleeces. All the measurements were made over 24-h periods, and besides determining O_2 consumption and CO_2 and CH_4 production, the total water vapour lost was measured. This water vapour included water evaporated from faeces, drinking water and from food and water reservoirs in the chamber. At each temperature used for the sheep, the chamber was operated empty with a 100 W electric bulb replacing the sheep as the heat source within the chamber. The water bowl and the wet bulb wick reservoir were filled up each day, and half the normal 24-h amount of faeces in a faeces collection bag was hung on a wall of the chamber. The chamber was then operated over the 24-h period, and the total water vapour lost from the chamber then represented the normal water loss from the "non-animal"sources within the chamber. This amount of water vapour was deducted from the total amount measured when the sheep was in the chamber to give the true or corrected water vapour loss from the sheep.

At the beginning and end of each experiment in the chamber the animal was weighed and the fleece depth measured. In most experiments the time which the sheep spent standing and lying in each hour was measured using a micro-switch in series with an electric self-starting clock. The micro-switch was activated by the animal standing up and was switched off when the animal lay down.

8. Skin surface and rectal temperature measurements. Thermocouples were made of 40 s.w.g. copper and constantan wire. The e.m.f. developed was measuring either on a Pye potentiometer or on an 8-channel potentiometer recorder using a set of reference thermocouple junctions maintained at a constant temperature of 45°. The thermocouples were calibrated against an N.P.L. thermometer to ±0.1°. Each thermocouple was cemented with floor sealing compound to a skin surface that had previously been clipped free of wool or hair, and the thermocouple was covered with a small patch of very thin rubber sheeting. In the respiration chambers twelve thermocouples were used but in all the other experiments only eight were available. In the chamber, rectal temperature was measured once daily using a mercury-in-glass clinical thermometer but otherwise in experiments outside

the chamber a thermocouple encased in a sealed polythene (Portex) tube was used to give continuous records of rectal temperature. In all the experiments the normal sites at which thermocouples were attached were the right and left shoulders, the right and left midsides, the right and left hips and the fetlock of one of the hind legs. If other thermocouples were available, additional sites on the trunk, ears and legs were used.

Fleece depth was measured using an engineer's depth gauge calibrated in mm. On the wool covered area 40 - 50 sites were used to calculate the mean fleece depth.

9. Measurement of climatic variables

(i) Ambient temperature and relative humidity. Ambient temperature was measured using a mercury in glass thermometer accurate to ±0.1°. The thermometer was shielded with polished aluminium foil to obviate radiation anomalies. Relative humidity was calculated from wet and dry bulb temperatures.

(ii) Air velocity. High air velocities were measured using precision cup anemometers (Messrs. Casella, London). Wind speeds were normally measured at a height similar to the mid position of the sheep. Silvered katathermometers were used to measure low air velocities, and Bedford & Warner's (1933) formula was employed to convert cooling powers to air velocities.

(iii) Solar radiation. Total solar radiation incident on a horizontal surface was measured with an actinograph (Messrs. Casella, London) using a 24-h chart. This was calibrated against a secondary standard solarimeter maintained at Eskdalemuir Observatory. All other solar radiation measurements, e.g. solar radiation reflected from sheep skins, were made using three solarimeters. These solarimeters were a modified form of that described by Monteith (1959 a). Fifty turns of bare constantan wire (42 s.w.g.) were wound on a cylindrical perspex former which was 8 cm long, 1.3 cm wide and was shaved off along its length on two opposing sides, so that the wire wound on it had two flattened areas 0.8 cm apart. On one flat face only, the windings were coated with Durofix along the centre line. After plating the unit with copper in an electrolytic plating bath there were 32 opposing copper-constantan junctions on the same plane but separated by 1.0 cm. The windings were cemented with Araldite at the thermocouple area on to a Tufnol disc 8.5 cm in diameter, and previously roughened on both sides. On the other side of the disc two hemicircles were painted, one black (Parson's Optical Black) and the other white (matt white paint) and positioned so that one set of thermocouple junctions lay underneath the black hemicircle and the other set under the white hemicircle. The perspex former was then withdrawn from the windings without distorting them. The resulting unit was cemented onto a perspex ring 1 cm in depth and with two 10 B.A. brass screws in the wall as terminals onto which the two thermocouple leads were soldered. The base of the ring was joined to a solid 8.5 cm diameter circle of perspex, and sandwiched in between the two was a thin temperature equilibrating aluminium circle 11 cm in diameter. All were joined together with eight concentrically placed 6 B.A. screws. A few silica gel crystals were included in the unit before it was sealed to prevent water condensation. Over the top of the Tufnol disc was cemented a glass dome 10 cm in diameter and 1 mm wall thickness. The actinograph was used to calibrate the solarimeters using a Pye potentiometer for measuring the thermopile output.

One solarimeter had joined to its top a removable cylindrical guard (8.5 cm diameter and 7.0 cm height). This guard, polished on the outside and painted black inside, acted as a solar radiation shield and allowed the solarimeter to be used as a directional instrument when determining the

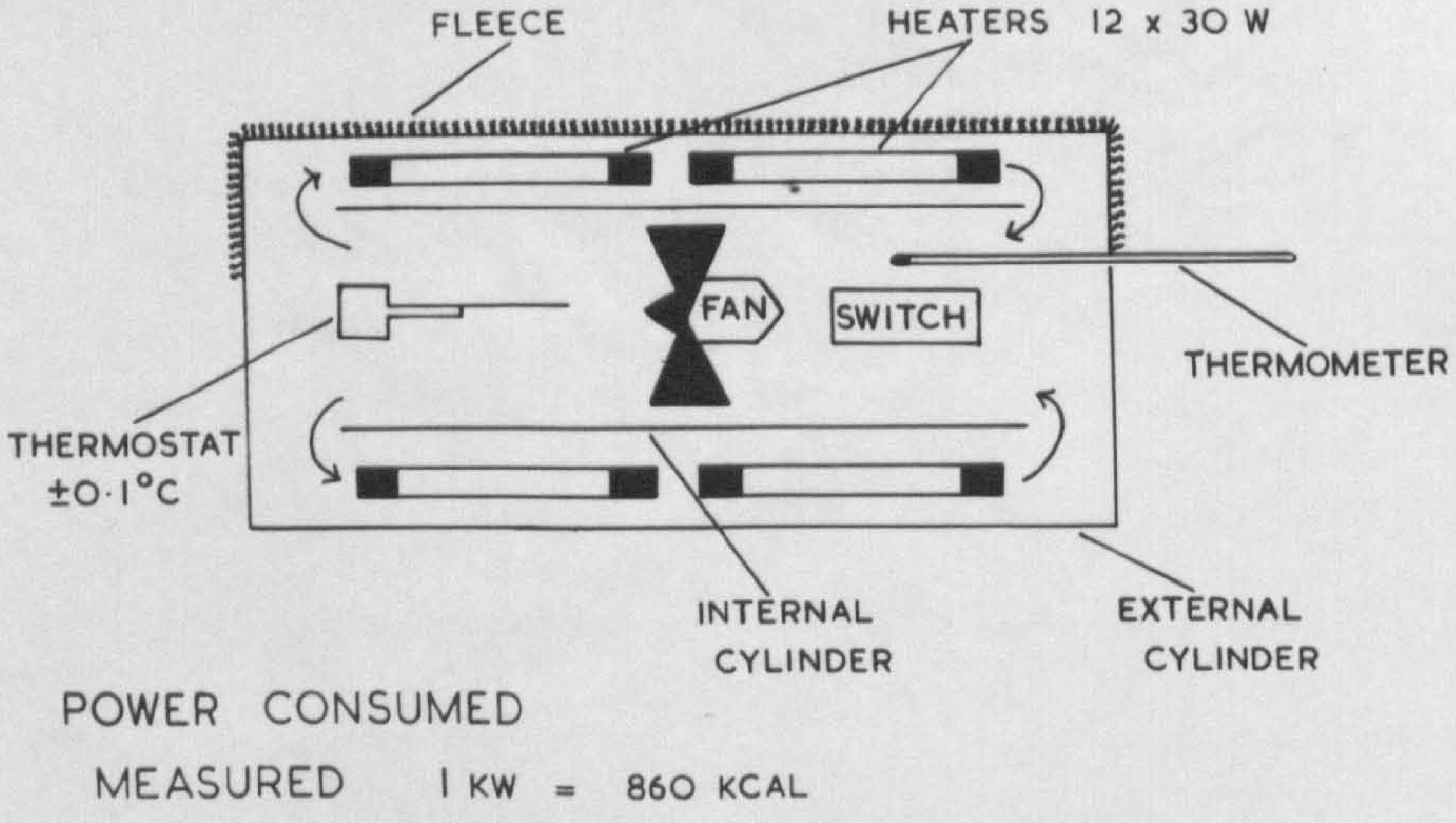


Fig. 2 A

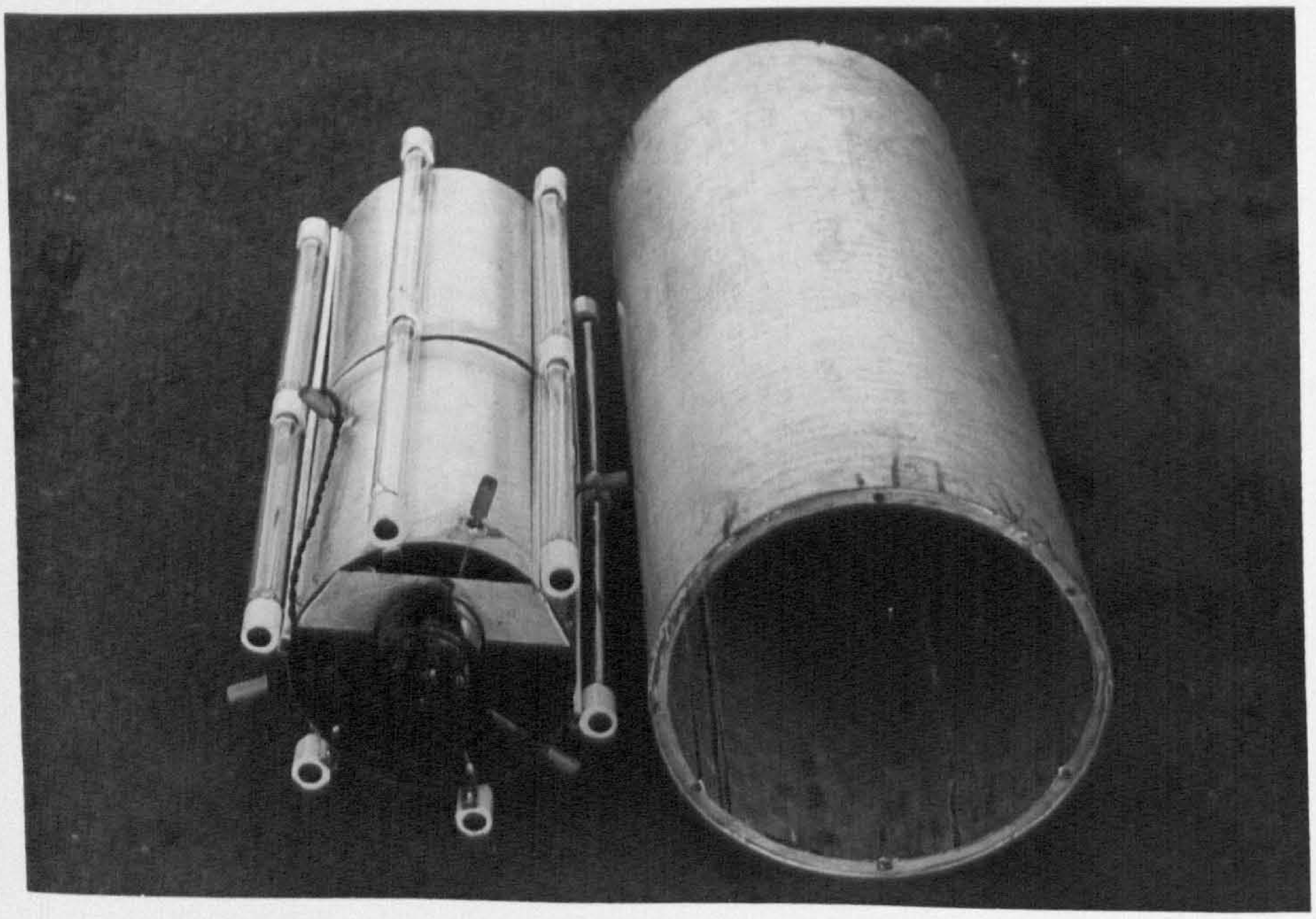


Fig. 2 B

Fig. 2. Diagram (A) and photograph (B) illustrating the construction of the artificial homeostatic sheep.

cylinder were six sets of two 30 W strip lights. Controlling the strip lights by means of a hot wire vacuum switch was a thermostat set to control the interior temperature at 39°. The wall thickness was adjusted inside by sticking brown corrugated cardboard to the internal wall, so that the temperature gradients from the inside to the "skin" surface were the same as those in the living animal. The internal insulation was adjusted to 2.9 insulation units as measured in the controlled climate room which has been described by Findlay et al. (1959), using thermocouples cemented to the surface. The whole unit was air-tight and rested on four wooden legs so that the centre of the "sheep" was approximately 12 in. above ground level. It is shown diagramatically and photographically in Fig. 2. The power consumed to maintain the internal temperature was measured on a wattmeter and this measurement was converted into the form kcal/m^2/24 h for comparative purposes as will be described later.

(vi) Reflectance of solar radiation. To measure the reflectance or albedo of the terrain to solar radiation one solarimeter was used to measure the incoming radiation incident on a horizontal surface and the other inverted so that the receiving face was parallel to the surface being measured. The difference in incident radiation between the two solarimeters was a measure of the amount of radiation absorbed by the terrain. For smaller objects, such as sheep skins and cattle hides, the shielded solarimeter was used. The object being measured was placed on a sheet of plywood which in turn was mounted on an adjustable framework. The solarimeter was mounted 15 in. above the skin so that the receiving face of the instrument was receiving the radiation reflected from a circle of skin of 36 in. diameter. Usually the board was adjusted so that readings were taken when the face of the solarimeter was at angles of 0°, 15°, 30° and 45° to the surface of the skin. The incoming radiation on a horizontal surface was measured on a second solarimeter. Solar radiation reflectance measurements were made on closely clipped grass, on 10 in. and 16 in. high ryegrass swards, and also on dry tar macadam, ten freshly slaughtered fleeced sheep pelts, three freshly slaughtered shorn sheep pelts and one Aberdeen Angus cattle hide (summer coat).

(vii) Measurement of the amount of solar radiation incident on the model sheep. The use of a cylinder to approximate the dimensions of a sheep for calculating the incident heat load due to solar radiation has been used previously by Priestley (1957), who calculated the theoretical incidence of the direct, diffuse and reflected solar radiation on a cylinder, assuming that the height of the cylinder above ground level was such that the shadow cast by it was infinitely small and could be neglected so that all the reflected radiation received by the cylinder came from a terrain subject to total hemispheric radiation. This assumption is not valid for an animal with relatively short legs, and to obtain more realistic estimates the following experiments were made.

The first involved the construction of two sheep models to simulate fleeced and shorn sheep and measurement of the actual solar radiation incident on them. The second involved measurement of the albedo or reflectance of terrains and fleeces to determine the amount of radiation reflected from various terrains to which sheep might be subjected, and the proportion of the incident radiation on the sheep that would be reflected and would thus not contribute to the heat load received by the sheep.

The cylinder used as a model to determine radiation incident on a sheep with fleece was 91 cm long and 46 cm in diameter. Its exposed surface area was 1.65 m^2, side profile 0.42 m^2 and end profile 0.17 m^2. These dimensions approximate very closely to measurements of live sheep made by Clapperton & Blaxter (1964) although the end area tended to be

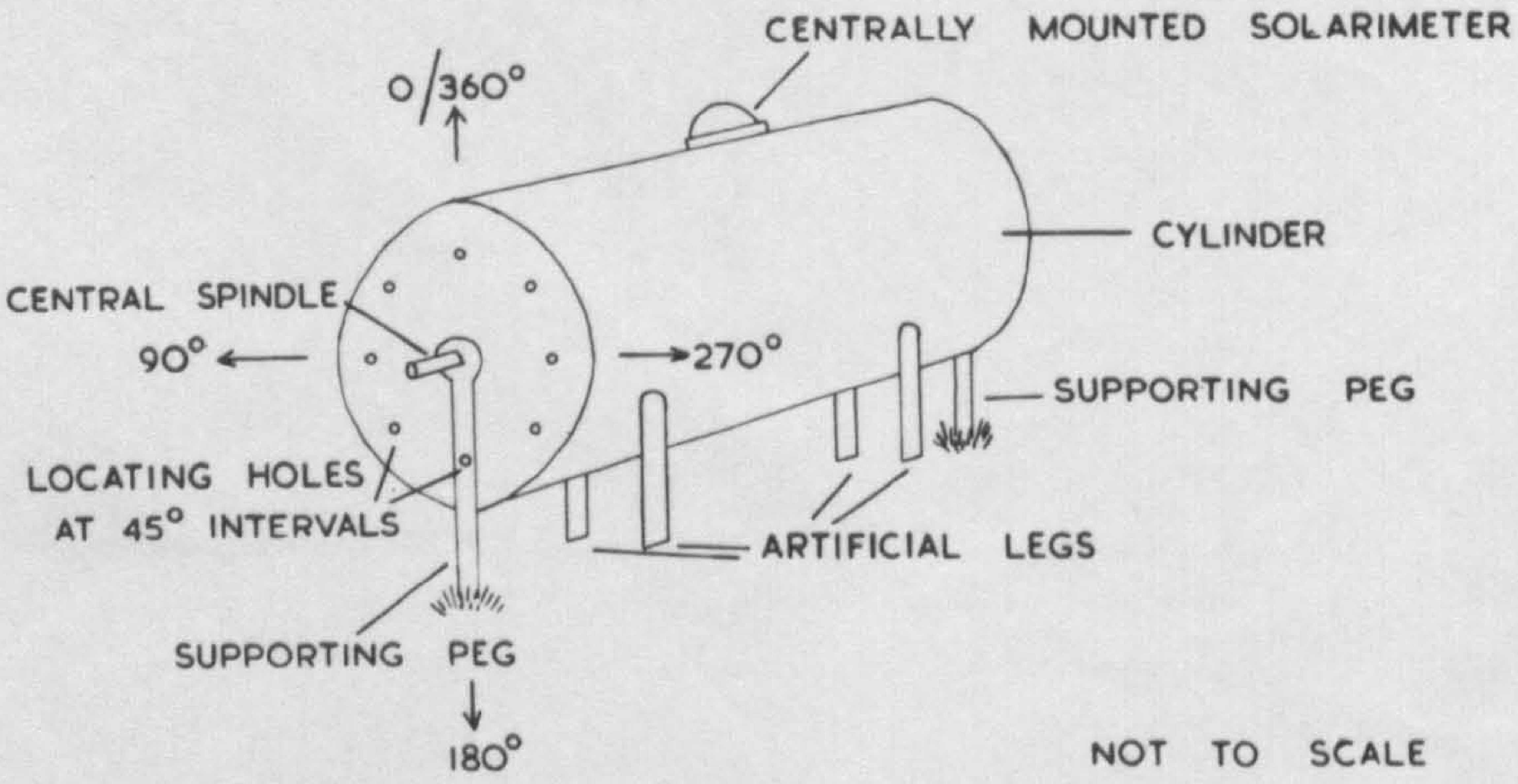


Fig. 3 A

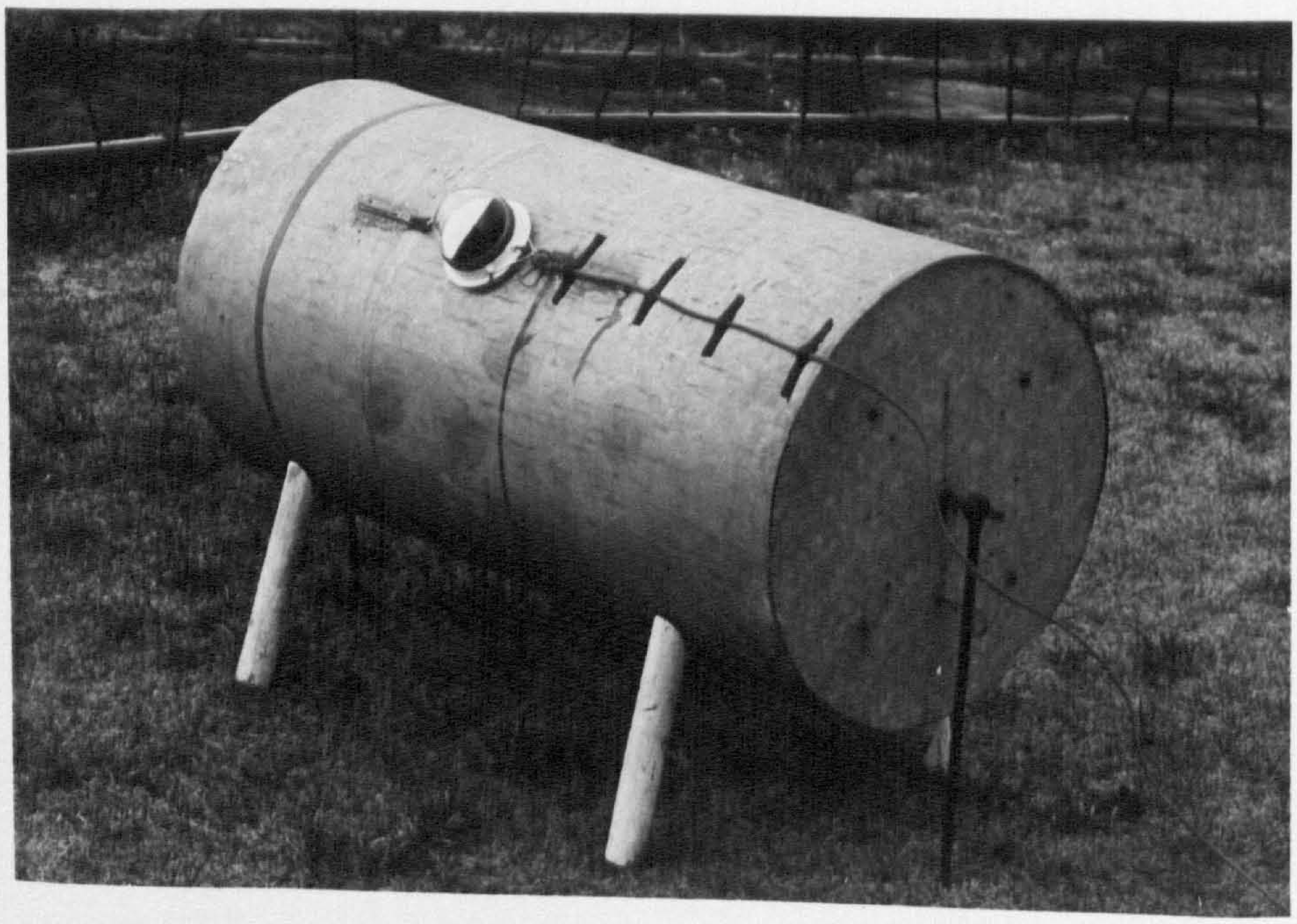


Fig. 3 B

Fig. 3. Diagram (A) and photograph (B) illustrating the design of the artificial sheep models used to measure solar heat loads.

slightly smaller on the model. The cylinder approximating to the shorn sheep was 76 cm long and 31 cm in diameter. Its exposed surface area was 0.89 m^2, side profile 0.24 m^2 and end profile 0.075 m^2. These values were calculated by assuming that the fleeced sheep model bore a fleece of 7.5 cm in depth.

Each cylinder was able to revolve around a central spindle located through the axis of the cylinder. The model was mounted between two pegs, one at either end of the spindle and each peg was set into the ground and adjusted to keep the centre-line of the sheep 38.5 cm above ground level. At one end of each cylinder were eight locating holes which corresponded with another hole drilled in one of the supporting pegs. In the centre of the side a hole was drilled and two brackets positioned to accommodate a solarimeter. Four small cylindrical pegs were used to simulate legs and provide a slight modification of the shadow area. This is shown diagramatically and photographically in Fig. 3.

The models were set up on a large flat grass area and aligned with the axis of the cylinder either at right angles or parallel to the solar beam, and the solarimeters attached. A separate solarimeter was used to measure the incoming solar radiation on a horizontal surface. Each cylinder was rotated through 360° and total hemispheric radiation measurements were made on each sheep at 45° intervals. Simultaneous incoming radiation on a horizontal surface was measured on the stationary solarimeter. After each revolution of the cylinder around its long axis the total incoming radiation received by both of the perpendicular ends of each sheep was measured. In all a total of eighty-seven 360° measurements were made using these sheep. Measurements were made under a variety of cloud cover conditions and solar elevations.

The reflectance of the terrain was measured using one solarimeter mounted so that it was pointing downwards at the terrain and at such a height

(36 in.) that the area of the shadow cast by it was negligible relative to the total area scanned. Simultaneous measurements were made with an upward pointing solarimeter to determine the incoming radiation.

B. Production of experimental environments. All indoor experiments were made in either of two places. In some experiments measurements were made in an air-conditioned building in which the lowest ambient temperature that could be maintained was 5° by the use of two cellar coolers (L. Sterne & Co. Ltd., Glasgow). A large number of experiments including all those at environmental temperatures below 5° was made in a controlled climatic room (Findlay *et al*. 1959).

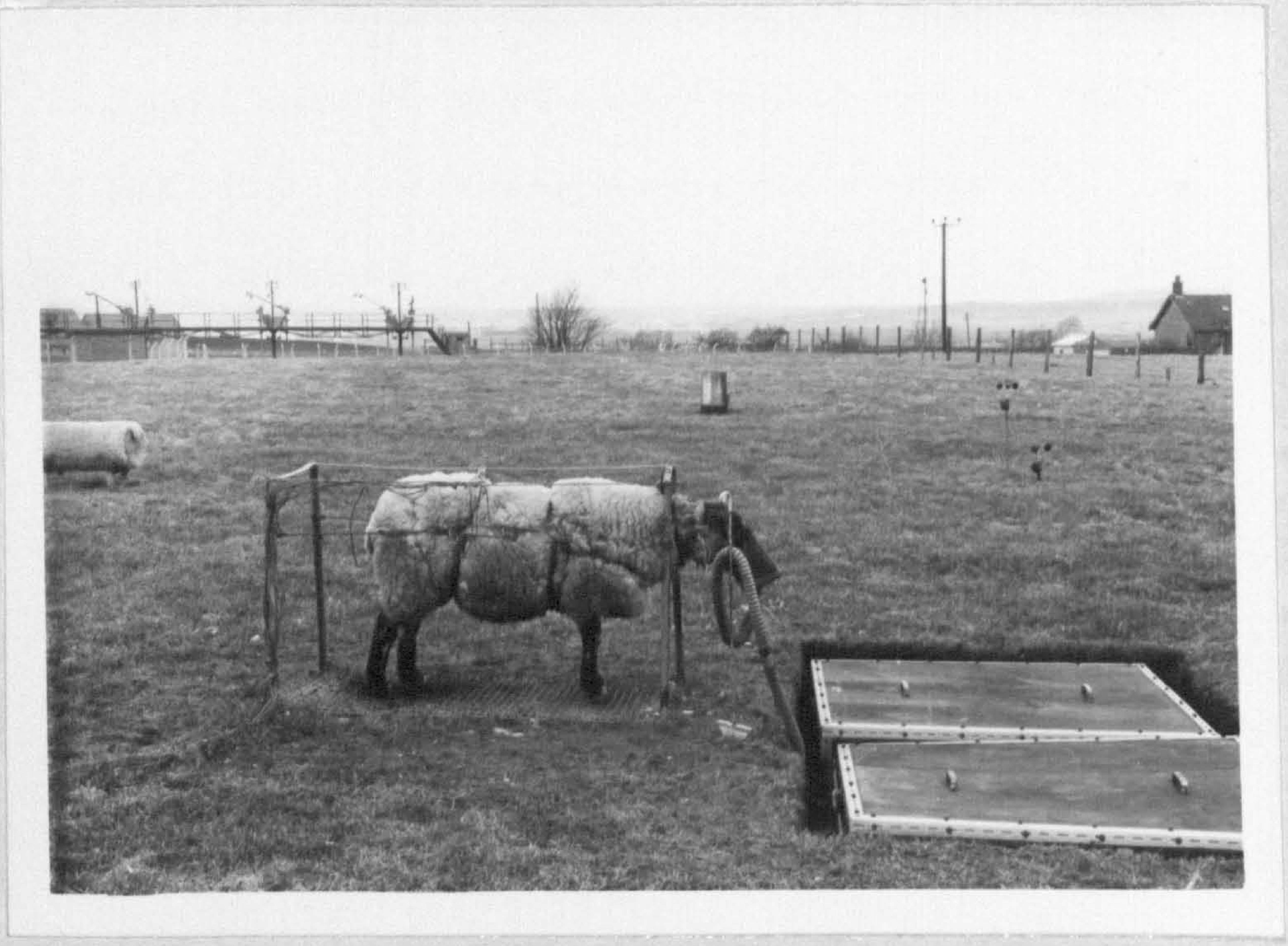
(i) Air velocity. In all experiments, except the artificial rain trial, the wind was produced by two 12 in. diameter fans activated by variable speed motors placed 5.5 ft from the sheep. The fans were mounted with their centres 19 in. apart and 21 in. from the ground and produced a steady flow of air around the sheep. The maximum air velocity attainable was 9.6 m.p.h. In the artificial rain trials an extra two fans were placed on top of the previous two fans and a small wind tunnel built to concentrate the air flow around the sheep, the air velocity in this instance being 9.9 m.p.h.

(ii) Ambient temperature. It was only possible to make sudden changes in ambient temperature by changing the location of the sheep. Sheep were therefore kept in the anteroom of a climatic room (Findlay *et al*. 1959) which was controlled at 15° ± 2° at the time of these experiments, and they were transferred in 2 - 3 min into the main climatic room which was maintained at temperatures as low as -3° for long periods.

(iii) Infrared radiation. The infrared radiation environment was altered by the use of infrared heaters. The object was to simulate the effect of solar radiation under artificial conditions using these infrared radiators. Eight 250 W infrared lamps in series were placed equidistantly around the animal, each at a distance of 3 ft from the nearest part of the sheep. It was not possible with this apparatus to measure the total radiant flux incident on the sheep.

(iv) Artificial rain. An attempt was made to produce a spray of water onto the animal which would be similar to natural rain. Two large drums were filled with water and by means of a suitable cock system, any one drum of water could be constantly presurized by connecting it to the outlet of a vacuum pump. The pressurized water was then led to an upward facing atomizer spray set 8 ft above and 8 ft to the side of the sheep and which gave an upward directed spray. The spray then fell by natural gravitation onto the sheep at a rate equivalent to 0.4 in./h of rainfall - a rate commonly experienced in Great Britain (British Rainfall, 1958).

(v) Outdoor site layout. In the experiments made out of doors the sheep were restrained and could not behave as normal free-grazing animals. The experimental site was in a flat grass paddock with herbage kept at 2 - 3 in. in height by mowing and was free from nearby obstructions which could alter the air flow over the site. The sheep was restrained using a light harness attached to a skeleton framework of 1 x 1 in. angle iron set into the ground. The skeleton framework was orientated permanently to lie parallel to the prevailing wind, i.e. east-west in direction and thus the sheep normally presented its hindquarters to the prevailing wind. A large pit 9 ft x 4 ft x 1 ft 6 in. was dug just in front of the skeleton framework and was lined with wood. This pit acted as a guard for the two large Douglas bags when they were being filled by the animal and prevented them from blowing away. Placing the Douglas bags below ground level also ensured that they did not act as a wind shelter for the sheep, especially when the bags were filled with expired air. Thermocouple



<u>Fig. 4 A</u>. Photograph of the outdoor experimental site demonstrating the collection of expired air from sheep By when wearing a face mask.

leads ran from the site to the potentiometric recorder 50 yd away. Ambient temperature was measured on a shielded thermometer, solar radiation on the actinograph and rainfall on the automatically recording rain gauge. Wind speeds were measured at 12 in., 30 in. and 10 ft heights using three sensitive cut anemometers (contact type) recording the total miles of wind run, and short term variations in wind speed on a three-channel special purpose recorder designed and built by Mr. W. Nisbet of the Physiology Department, The Hannah Dairy Research Institute. The 12 in. and 30 in. anemometers were approximately at the heights of the belly and back of the sheep, and the 10 ft. recordings could be related to the standard Meteorological Office height of 10 m (33 ft) by adding a correction of 20% (Handbook of Meteorological Instruments, 1956). Wind direction was indicated by a swinging vane. A photograph of sheep By on the outdoor site is given in Fig. 4A.

C. Experimental design

1. Comparison of the respiratory exchange of tracheostomized sheep given constant rations as measured in the respiration chamber and by the Douglas bag technique. Two series of experiments were made, one using sheep Ct and Cs on a constant level of dry matter and the other using sheep Cs, Yl and Se on four different planes of nutrition. The experimental design is described in Appendix I.

2. Equilibration experiments. The time taken to attain equilibrium of body and skin temperatures and of O_2 consumption following changes in air velocity, ambient temperature, infrared radiation (sheep Cs and Yl) and artificial rain (sheep By and Fr) were measured in the following experiments, which were designed to measure the time needed to obtain a steady state in energy metabolism. This was necessary before any measurements of the

effects of varying levels of air velocity, ambient temperature and artificial rain could be made under repeatable conditions.

In all these experiments and in the steady state series of experiments (excluding all artificial rain experiments) to be described later, each sheep was given a ration of 750 g of artificially dried grass daily in two meals. This amount was calculated to provide sufficient energy to maintain body weight in a thermoneutral environment. The analysis of the dried grass, which contained 85.1% dry matter, was 2.77% nitrogen, 46.6% carbon and 4.530 kcal/g of the dry matter.

(i) Ambient temperature. Four experiments were made to study the time taken to reach an equilibrium when the ambient temperature was changed. Each sheep was kept in a transportable pen at a temperature of 15° in the anteroom of the climatic room. After allowing 45 - 60 min for an equilibrium to be established, initial measurements were made for 1 h. The pen and sheep were then carried into the climatic room in which the ambient temperature was 0°. Measurements were made in the cold for 2 h 20 min, when the sheep were returned to the warm anteroom and measurements continued for another 2 h. Two experiments were made in which the temperature of the cold room was the same as that of the anteroom, to find whether the act of carrying the sheep and their transfer to new surroundings affected their metabolism.

(ii) Air velocity. At least 1 h was allowed to establish an initial equilibrium under the conditions of undisturbed air. Measurements of the initial values then began and lasted for 1 h. Air velocity was increased by means of the fans from that of undisturbed air in the room to 6.2 or 8.9 m.p.h. The fans were switched off after 2 h 20 min but measurements continued for a further 2 h to trace the re-establishment of an equilibrium in undisturbed air. Eight experiments of this type were made with sheep Cs, four with the side of the sheep at right angles to the wind flow and four with the hindquarters at right angles to the wind. Four experiments were made with sheep Yl, two with the side and two with the hindquarters presented to the wind.

(iii) Infrared radiation. Using ambient temperature of 0^{o} and after an initial adjustment period of 45 min, measurements were made on sheep Cs of the initial values for 1 h. The infrared lamps were then switched on and measurements taken for 2 h 20 min after which the lamps were switched off and measurements continued for another 2 h. For sheep Yl the corresponding times for no radiation, radiation and no radiation were 40, 110 and 60 min.

(iv) Artificial rain. After an initial adjustment period of 1 h at ambient temperatures of 5 - 8^{o}, measurements were made on sheep By and Fr for 1 h. The rain sprayer was then switched on and measurements made for 2 h 20 min, after which it was switched off again and measurements continued for another 2 h 20 min. Sixteen experiments were made with different fleece lengths ranging from 3 - 40 mm.

3. Steady state experiments. As discussed later, it was found that a steady state of O_2 consumption and surface temperature was reached in much less than 60 min after a change in climate (excluding infrared radiation and rain). Therefore, in all the steady state experiments described here, at least 30 min, and normally 45 - 60 min, were allowed as periods of metabolic adjustment before measurements were made under the altered environment.

(i) Air velocity. In 112 experiments air velocity was varied. Measurements were made of O_2 consumption, skin and body measurements. Each experiment consisted of three or four consecutive periods of observation each lasting 20 min. Sheep Ct and Zk were both used in eight experiments when each had a full fleece. Sheep Yl was used in 38 experiments during the course of which its fleece was allowed to grow from 6 mm to 20 mm. Sheep Cs was used in 58 experiments during which its fleece grew from 19 - 50 mm. Wind velocity varied from a minimum of 0.2 m.p.h. to a maximum of 9.6 m.p.h. Air temperature varied in these experiments from -3° to +10° and was kept constant in any one experiment to within ±0.2°. Four of the experiments on air velocity made with sheep Cs and Yl were designed to find the effect of body position on metabolism. The positions were as in the equilibrium experiments, side on or hindquarters on to the wind.

(ii) Joint effect of infrared radiation and wind. Sheep Cs and Yl were each used in two series of experiments in which the following sequence of experimental treatment was imposed at an ambient temperature of 0°, no wind and no radiation, infrared radiation and no wind, infrared radiation and wind, and wind with no radiation. The wind used was 9.6 m.p.h. and after an adjustment period of 30 min to each treatment, measurements were made continuously for 1 h 20 min. Undisturbed room air movement was 0.6 m.p.h.

(iii) Joint effects of artificial rain and wind. Two sheep, By and Fr, were used in a series of twelve experiments in which the fleece length of sheep By ranged from 3 to 40 mm and that of Fr from 4 to 40 mm. The following sequence of treatments was imposed on each sheep: wind, no rain; no wind, no rain; rain, no wind; and rain, wind. The sequence was altered in that the wind period might or might not precede the no wind period in each of the rain or no rain treatments but the no rain treatment always preceded the rain treatment. This was necessary to ensure that the fleeces of the sheep were dry when the no rain treatment was imposed. An arbitrary fixed preliminary period of 2 h of rain on the sheep was used prior to the measurement of the effect of rain. Ambient temperatures ranged from 4 to 8° but did not vary by more than ±0.5° in any one sequence of treatments. The wind speed imposed on the sheep was 9.9 m.p.h., and air movement in the room with the fans switched off was 0.6 m.p.h. This high speed was due to the strong convection caused by the fans of the cellar coolers.

(iv) Respiration chamber experiments for basic heat loss measurements. Using the methods previously described, the minimal heat production of each sheep, being fed its own ration, was determined in the respiration chambers. Care was taken that whatever the fleece length carried by the sheep, the ambient temperature of the chamber was adjusted so that the animal was within its zone of thermoneutrality. The minimal heat production was determined for each sheep. The measurement of the heat production and minimal water vapour loss was measured also under cold stress conditions (i.e. at an ambient temperature below the animal's critical temperature) for the following sheep only, Ct, Cs, Yl, By, Fr, Jr, and Re. From these results and from the carbon-nitrogen measurements, the energy retention by each sheep was determined.

(v) Outdoor trials. Using the outdoor site and techniques described earlier, sheep By, Fr, Jr and Re were used to measure heat production and skin and body temperature changes in relation to the natural environment and its changes. This trial was intended to assess what portion of the results gained in the previous section could be taken as applying to single sheep isolated in a natural outdoor environment. It was also intended that it should measure the effects of solar radiation and natural rain on metabolism. Each sheep was fed a ration of 800 g of artificially dried grass daily in two meals throughout the whole series of experiments and also in the artificial rain experiments. The grass contained 83.5% dry matter, and the dry matter contained 2.81% nitrogen, 45.0% carbon and gave 4.636 kcal/g on combustion. All the experiments done during the day lasted for 1 h and normally five such experiments could be done on one sheep in one day, and 120 experiments were made over the whole experimental period. At least 1 h was allowed outside for the animal to come into metabolic equilibrium with the environmental conditions.

In an attempt to integrate the various components of the environment into a single variable, the artificial sheep, covered with a fleece of 38 mm in depth, was positioned nearby the live sheep, and hourly records were taken for comparison with those obtained with the live sheep.

CHAPTER III

Table 2. The recovery of N_2 from tracheostomized and masked sheep as an index of air leakage

Sheep	Inspired volume of N_2	Expired volume of N_2	% recovery of N_2
		Tracheostomized sheep	
Cs	262.1	262.9	100.3
Cs	251.9	247.9	98.5
Zk	244.6	236.5	96.7
Zk	249.0	248.0	99.6
Ct	248.3	248.1	99.9
		mean	98.8 ± 1.4
		Sheep with face masks	
Fr*	228.4	230.6	101.0
Fr*	198.5	200.2	100.9
Fr	159.6	158.8	99.5
Fr	164.9	164.0	99.5
By	206.1	207.2	100.5
By	213.0	210.1	98.6
		mean	100.0 ± 0.3

* Hair clipped from around middle third of face

RESULTS

A. The accuracy of the primary estimates of metabolism and the assumptions involved

1. Accuracy of mask and tracheal measurements in terms of gas leakage.

For the face-mask and tracheostomy methods to be accurate it is essential that there should be no leakage of expired air. Shown in Table 2 is the percentage recovery of N_2 used as an index of air leakage. The percentage recovery from the tracheostomized sheep tended to be slightly lower (98.8%) than that from the sheep wearing face masks (100.0%). However, neither method showed serious leakage and both methods can be considered to be satisfactorily leak-proof procedures. With the masked sheep clipping of the face did not have any appreciable effect.

2. Repeatability of measurements of minimal water vapour loss from sheep.

The loss of heat caused by evaporation of water (minimal water vapour loss) had to be determined for each sheep so that the sensible heat loss per unit area of the skin surface could be calculated from the total heat production under conditions of zero heat storage. The results obtained on seven sheep are given in Table 4. These results fall into two categories 359 - 379 kcal/24 h and 201 - 238 kcal/24 h, each seeming to be associated with the level of intake. Within each group the range of loss of heat as water vapour was remarkably constant. The mean minimal water vapour heat loss of 371 kcal/24 h for sheep Cs, Ct, and Yl was comparable to results obtained for sheep by Blaxter et al. (1959 b) but the mean of 219 kcal/24 h for sheep Fr, Jr, Re and By was much lower than expected. The reason for the low minimal level of water vapour loss for these last four sheep is not known.

3. Repeatability of measurements of O_2 consumption and CO_2 and CH_4 production made in the respiration chamber and when using the Douglas bag technique. The repeatability of measurements of the respiratory

exchange of sheep was high irrespective of which technique was used. Table 3 of Appendix I (p. 530) shows the standard errors attached to measurements of the same sheep on the same ration measured in both ways. The standard error attached to a series of nine observations in the respiration chamber ranged from ±0.24 - ±0.35 l. O_2/h when the mean O_2 consumption ranged from 14.07 - 22.19 l./h. Similar ranges for CO_2 and CH_4 production were ±0.29 - ±0.38 l./h for CO_2 production and ±0.06 - ±0.10 l./h for CH_4 production when the range of mean productions for CO_2 and CH_4 were respectively 12.06 - 24.06 l. CO_2/h and 0.66 - 2.04 l. CH_4/h. Measurements made by the Douglas bag technique tended to have slightly lower standard errors than those observed in the respiration chamber method. The means for O_2 consumption and CO_2 production by the two methods were similar, but CH_4 production was only 0.11 - 0.44 l./h by the Douglas bag method compared with 0.66 - 2.04 l./h by the respiration chamber method.

4. <u>Comparison of respiratory measurements and respiration chamber measurements</u>. Appendix I (pp 528 - 532) gives the results of O_2 consumption and CO_2 and CH_4 production measured on tracheostomized sheep using the respiration chamber and Douglas bag methods. In the first series of experiments the results showed that the Douglas bag method for determining O_2 consumption gave values which agreed with those determined by hourly measurements in the chamber, the means being 16.23 l./h for the Douglas bag method and 16.13 l./h for the respiration chamber method. These values were very similar to those determined over the 24-h period in the respiration chamber (16.41 l./h). Douglas bag determinations of CO_2, however, were 4.0 l./h lower for sheep Ct and 4.2 l./h lower for sheep Cs than the values computed from the 24-h respiration chamber experiments. Less than one-tenth of the CH_4 found in the respiration

chambers over the hourly periods was recovered using the Douglas bag method. Similarly, hourly respiration chamber measurements of CH_4 made during the intervals between meals, were lower than the value obtained for the 24-h chamber mean, the latter including the effects of two meals. It is considered that belching of CO_2 and CH_4 accounted for most of these discrepancies.

Results of the second series of experiments where different levels of feeding were used are shown in Table 3 of Appendix I. The mean O_2 consumption measured in the chamber was 0.02 l./h lower than that measured by the Douglas bag method and this difference was not statistically significant and was negligible compared with the mean O_2 consumption of 17.3 l./h. As in the first series of experiments considerably less CO_2 and CH_4 were collected in the Douglas bags than was measured in the chamber and the extent of this loss was to a large extent dependent on the level of feeding.

As shown in Appendix I regression equations were calculated for the amount of CH_4 belched (calculated as the difference between the respiration chamber results and those obtained by Douglas bag collection) and the total amount of CH_4 produced, and also for the CO_2 belched against the total CH_4 produced. These were:-

$$\underset{(\text{l./h})}{CH_4 \text{ belched}} = 0.833 \underset{(\text{l./h})}{CH_4 \text{ produced}} - 0.03 \; . \; . \; . \; . \; . \; . \; . \; . \quad (7)$$

$$(P < 0.001)$$

$$\underset{(\text{l./h})}{CO_2 \text{ belched}} = 1.579 \underset{(\text{l./h})}{CH_4 \text{ produced}} - 1.38 \; . \; . \; . \; . \; . \; . \; . \; . \quad (8)$$

$$(0.01 > P > 0.001)$$

As shown in equation (7) the CH_4 loss on belching was proportional to the amount of CH_4 produced, and approximately 83% of the CH_4 produced was lost by belching irrespective of the feeding level. Conversely 17% of the CH_4 was absorbed into the blood from the intestinal tract and excreted by the lungs. With CO_2 production, however, equation (8) shows that little CO_2 was belched until the CH_4 production exceeded 0.87 l./h and then the loss of CO_2 by belching increased rapidly. When CH_4 production was 1 l./h, the belched gas consisted of 0.80 l. CH_4/h and 0.20 l. CO_2/h, and when CH_4 production was 2.5 l./h, 2.05 l./h of CH_4 and 2.5 l./h of CO_2 were lost by belching. These figures for belched CH_4 are slightly different from those given on p. 532 of Appendix I where a constant of -0.27 instead of -0.03 was mistakenly used in equation (7).

5. Measurement of calorific value of oxygen increment above thermoneutral zone values. As will be brought out in the discussion it was decided to estimate the heat production of the tracheostomized and masked animals from the O_2 consumption only. This necessitated the measurement of the heat production of each animal for each ration used, under thermoneutral environmental conditions, and the simultaneous determination of the minimal water vapour loss under cold stress conditions. The basis of these determinations for the calculation of the total and sensible losses of heat has been discussed in the introduction. From the simultaneous determination of O_2 consumption, CO_2 and CH_4 production and urinary-N excretion made at hourly intervals during the day using the respiration chamber, operated at temperatures well above the critical temperature, the hourly heat production in a thermoneutral environment was calculated. If exactly the same ration was given and the animal kept, during a similar period of the day, in an environment which elicited a metabolic response to cold, then heat production in that cold environment could be regarded as consisting of this normal heat production plus an additional amount of heat arising from the additional combustion of body fat (Graham et al. 1959). The number of kcal of heat

Table 3. Constants in the equations used to estimate heat production and the sensible heat loss from oxygen consumption

Sheep	Heat production in a thermoneutral environment (Constant A) (kcal/h)	Oxygen consumption in a thermoneutral environment (Constant B) (l./h)	Minimal loss of heat by vaporization of water (kcal/h)
Cs	75.0	15.21	14.98 ± 0.19*
Ct	75.8	15.31	15.78 ± 0.19
Yl	80.2	16.16	15.60 ± 0.30
Zk	72.2	14.28	-
By	76.1	15.16	8.58 ± 0.74
Fr	66.4	13.42	8.90 ± 0.78
Jr	65.2	13.33	8.46 ± 0.79
Re	69.4	14.22	9.90 ± 0.85

* Standard error of mean.

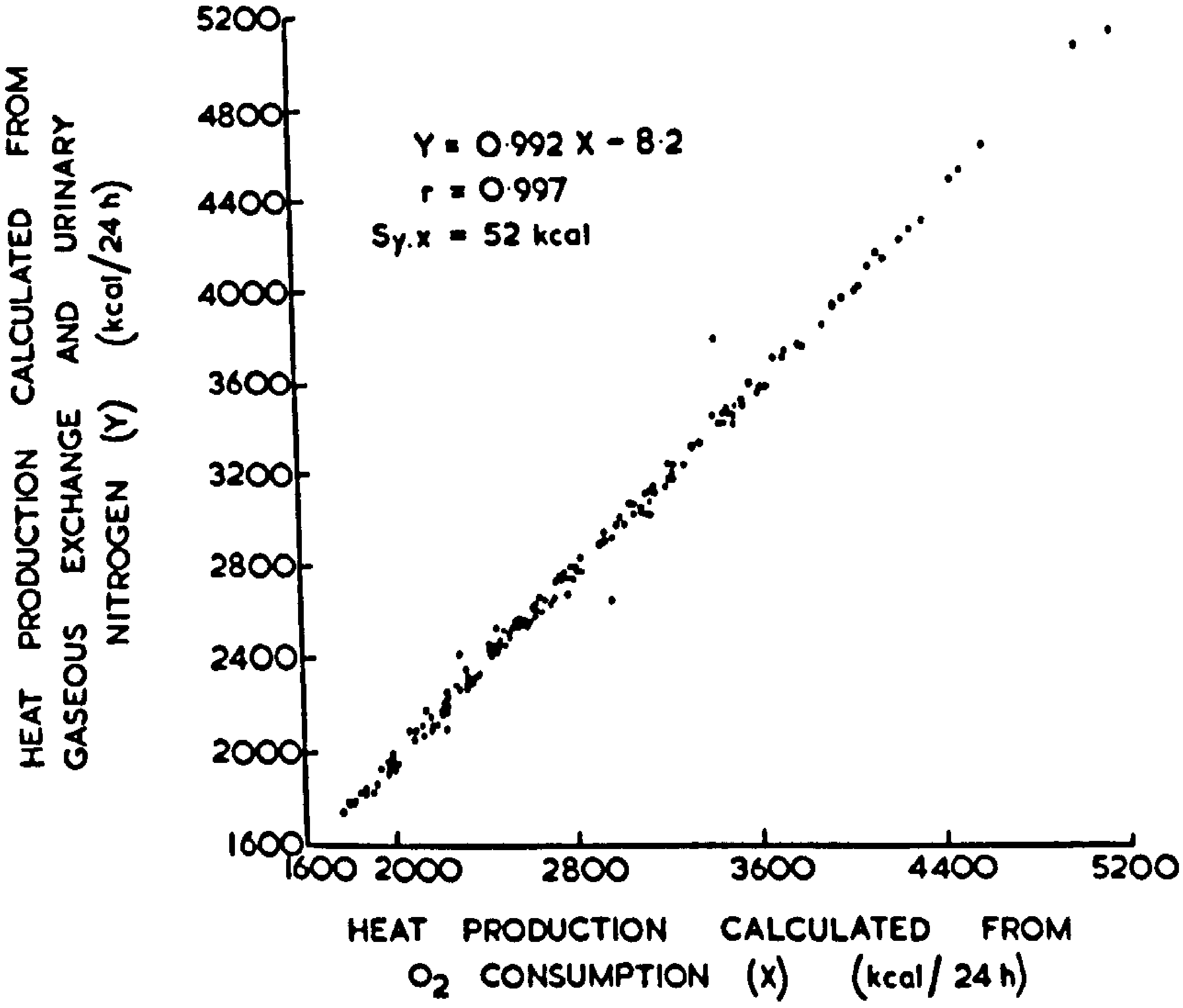


Fig. 4 B. Comparison of two methods of estimating heat production from either the total gaseous exchange or only O_2 consumption.

produced for every litre of O_2 consumed when body fat is being catabolized is 4.68 kcal assuming an R.Q. of 0.70 (from Zuntz & Schunberg's tables quoted by Brody, 1945). Heat production in an experiment can therefore be calculated from the expression:

$$\begin{array}{l}\text{Total heat}\\ \text{produced/h}\\ \text{in an}\\ \text{experiment}\end{array} = \begin{array}{l}\text{Heat produced/h}\\ \text{in a thermoneutral}\\ \text{environment}\\ \text{(A)}\end{array} + 4.68 \left\{ \begin{array}{l}\text{l. } O_2 \text{ consumed/}\\ \text{h in the}\\ \text{experiment}\end{array} - \begin{array}{l}\text{l. } O_2 \text{ consumed/}\\ \text{h in a thermo-}\\ \text{neutral environ-}\\ \text{ment}\\ \text{(B)}\end{array} \right\}$$

If the experimental environment evoked no metabolic response, the term in parenthesis was zero and heat production was then the same as that measured in the respiration chamber under thermoneutral conditions.

Table 3 summarizes the equations and constants used for each sheep to calculate heat production and the sensible heat loss; they were determined from the respiration chamber experimental results given in Table 4.

When using face masks it is presumed that all the expired gases, both from respiratory and eructed sources, are collected, and heat production can then be calculated from the total gaseous exchange. The factors used to convert O_2 consumption and CO_2 and CH_4 production and urinary-N loss to levels of heat production when using face masks were 3.815 kcal/l. O_2, 1.232 kcal/l. CO_2, -1.419 kcal/l. CH_4 and -0.578 kcal/g N_2 in urine (Brouwer, 1961). It was thus possible to compare the calculated heat productions on the same sheep over the same period using the incremental O_2 method and the total gaseous exchange factor method. Results for the face-mask method in the outdoor experiment are shown in Fig. 4B. Heat productions calculated by either of these methods showed very little difference. The regression equation relating them was $Y = 0.992\ X - 8.2$ where Y was the heat production calculated from total gaseous exchange and X was the heat production calculated from O_2 consumption. The

Table 4. Metabolic results in eighteen experiments with eight sheep given constant rations in different environments in the respiration chamber

Sheep	Fleece length (mm)	Temperature of chamber (°)	No. of 4-day trials	Energy metabolism (kcal/24 h)						Loss of heat as water vapour (kcal/24 h)
				Intake	Faeces	Methane	Urine	Heat	Retained	
Cs (1)	64	18	1	2891	677	214	132	1801	+67	359
	9	6.7	1	2891	705	222	201	3504	-1741	
Ct (1)	90-92	18	3	2891	754	255	206	1831	-155	379
	6	7.6	1	2891	758	283	194	3630	-1974	
Yl (1)	60	18	2	2891	649	244	175	1892	-69	374
	24	5.4	1	2891	684	218	159	2924	-1094	
Zk (1)	98	18	1	2891	648	232	169	1842	0	-
Fr (2)	40	21.5	1	3106	869	145	183	1615	+294	232
	18	5.3	1	3106	784	142	202	2205	-227	
Jr (2)	12	28.2	1	3106	721	137	191	1656	+401	201
	13-14	6.0	1	3106	831	138	205	2197	-265	

Table 4 (continued)

Sheep	Fleece length (mm)	Temperature of chamber (°)	No. of 4-day trials	Energy metabolism						Loss of heat as water vapour (kcal/24 h)
				Intake	Faeces	Methane (kcal/24 h)	Urine	Heat	Retained	
Re (2)	44	21.2	1	3106	764	151	217	1650	+324	238
	9	6.7	1	3106	770	127	208	2965	-964	
By (2)	37	20.5	1	3106	761	153	217	1843	+132	206
	11	6.4	1	3106	753	134	196	2843	-820	

(1) Ration 750 g of dried grass/day

(2) Ration 800 g of dried grass/day

regression coefficient of 0.992 was not significantly different from unity and the standard deviation was ±52 kcal/24 h. The errors associated with both these methods of computing heat production were independent of the level of heat production. From these results it may be postulated that both tracheostomy and face-mask methods are equally effective for computing heat production, and the method chosen would depend on the type of investigation being made and not on any difference in accuracy between the two methods.

6. Metabolic experiments in the respiration apparatus. The results of eighteen experiments made in respiration chambers are shown in Table 4. Sheep Cs, Ct, Yl and Zk were fed only 750 g dried grass/day compared with the 800 g/day given to the other four sheep. At environmental temperatures of 18° or above, all the sheep except Ct, Yl and Zk stored energy in the body. The smaller ration was closer to a maintenance ration than the larger one. Heat production varied from a minimum of 1615 kcal/24 h to a maximum of 1892 kcal/24 h for sheep Yl.

When the sheep were shorn and the environmental temperature was reduced to $5 - 8^{\circ}$, heat production increased without any significant change in the loss of energy in the faeces, urine or methane. Considerable losses of energy from the body then occurred varying from 227 kcal/24 h for sheep Fr at a fleece length of 18 mm to 1974 kcal/24 h for sheep Ct with a fleece length of 6 mm. The final column of Table 4 shows the determined losses of heat in terms of water vapour at a temperature of $5 - 8^{\circ}$. For the first three sheep on the smaller ration, heat losses were 360 - 380 kcal/24 h which are in good agreement with previous estimates for sheep (Blaxter et al. 1959 b). The values obtained with the last four sheep were much lower than expected (200 - 240 kcal/24 h); the reason for this is not known.

Table 5. Urinary nitrogen losses of sheep given constant rations in warm and cold environments

Sheep	Fleece length (mm)	Temperature of chamber (°)	Energy retained (kcal/24 h)	Urinary N loss (g/24 h)
Cs	64	18	+67	16.0 ± 1.3*
	9	6.7	-1741	14.0 ± 1.0
Ct	90 - 92	18	-155	13.1 ± 1.2
	6	7.6	-1974	13.1 ± 2.1
Yl	60	18	-69	12.3 ± 2.2
	24	5.4	-1094	11.4 ± 2.0
Fr	40	21.5	+294	12.5 ± 2.8
	18	5.3	-227	13.0 ± 3.1
Jr	12	28.2	+401	11.2 ± 1.8
	13 - 14	6.0	-265	14.0 ± 4.5
Re	44	21.2	+324	13.3 ± 2.0
	9	6.7	-964	14.1 ± 1.9
By	37	20.5	+132	13.9 ± 3.1
	11	6.4	-820	13.8 ± 2.6

* Standard deviation from mean.

Table 6. Pooled regressions of O_2 consumption and CO_2 and CH_4 production (l./h) on standing time (h)

Series of experiment	d.f.	Mean values (l./h) O_2 consumption	 CO_2 production	 CH_4 production	Increase on standing (l./h) O_2 consumption	 CO_2 production	 CH_4 production
1st* (1 h measurements)	53	15.26	-	-	0.79 ± 0.85	-	-
2nd (3 h measurements)	36	17.31	17.33	1.34	1.07 ± 1.34	2.44 ± 1.27	-0.83 ± 0.31

* Results of an additional two experiments in which hourly collections were made have been included together with those of the two in series I.

Table 5 shows the urinary-N losses of the sheep for the same experiments as are recorded in Table 4. In the incremental O_2 consumption method it was assumed that the increase in heat production in the cold resulted from the combustion of fat and not protein. If there had been an increase in the protein catabolism of the sheep in the cold environments, then the amount of N excreted in the urine would have risen. Table 5 shows, however, that no systematic increase in N excretion in the urine occurred.

7. Extraneous circumstances that could cause errors in assessing the level of metabolism. There are a number of activities of the sheep that could possibly cause errors in assessing normal levels of heat production. The most important onces that could affect the results in this thesis are changes of posture (standing or lying down), locomotion, eating, training and fear.

(a) Changes of posture. When in the respiration chamber the sheep were unrestrained except for a chain attached to the collar and they could lie at will and usually did lie for long periods. With the Douglas bag technique, in spite of being able to lie at will, the sheep invariably stood. Thus in view of Pullar's (1962) observations on sheep in a gradient layer calorimeter, that standing can increase heat emission by up to 70%, any comparison of chamber measurements with Douglas bag measurements must take into account any significant variations of respiratory exchange that may occur on standing.

In Appendix I (p. 528) it is shown that standing resulted in an increase in O_2 consumption in both series of experiments. The pooled regression analysis of O_2 consumption on standing time given in Appendix I is also shown in Table 6 together with the corresponding regressions for CO_2 and CH_4 production. The results indicate that standing resulted not only in slight increases of O_2 consumption and CO_2 production, but also in a slight decrease in CH_4 production. This decrease in CH_4 production on standing may possibly have been associated with more frequent belching by the sheep when lying. The value of one litre O_2/h, corresponding to about 5.0 kcal/h or 1.7 kcal/kg body weight/24 h, is in reasonable agreement with observations of Hall & Brody (1933) that the increase in metabolism as measured from O_2 consumption in cattle was 2.1 kcal/kg body weight/24 h. Forbes et al. (1927) found 3.6 kcal/kg body weight/24 h and Mitchell et al. (1932) 2.9 kcal/kg body weight/24 h, both sets of results being based on cattle experiments. More recently McLean (1963) using face-mask methods on calves has obtained results in which the levels of O_2 consumption while the calves were lying were 6 - 10% lower than when they were standing. The effect of standing in these experiments was much smaller than that noted by Pullar (1962), and since the effect on O_2 consumption was not significant, it has been ignored in subsequent calculations.

(b) Locomotion. In all the experiments described in this thesis the sheep were compelled to be stationary and hence locomotion effects did not enter into the calculation of results.

(c) Eating. As shown in Appendix I (pp 532 - 535), O_2 consumption and CO_2 production were elevated during periods of eating, and the magnitude of the increment appeared to be related to the level of feeding. However, as shown in Table 4 of Appendix I, when the sheep were on a constant level of feeding, as in all the experiments described here, the increment in O_2 consumption had disappeared by the third hour after the last meal, and then O_2 consumption levels measured in a thermoneutral zone were stable until the next meal was given. All the experiments described in this thesis were made during the period 4 - 12 hours after the last meal, so no correction was necessary for variations in respiratory exchange caused by eating.

(d) Training and fear. These two are necessarily related; once the animal was sufficiently trained and accustomed to the respiration apparatus no trace of fear was noticeable. All the sheep, whether they were being used for tracheostomy or face-mask methods, were trained for at least 10 days before experimental measurements were made. Usually this period of training appeared quite adequate and it is considered, especially since O_2 consumption results from the respiration chamber and those from the Douglas bag technique under thermoneutral conditions were very similar, that the measurements made on these sheep were unaffected by inadequate training or fear. The only instances of fear reported here are those found in the temperature equilibration experiments when the animals were transported manually from one room to another.

8. Discussion and conclusions

Comparison of tracheal, mask and chamber results. Tracheostomized sheep and sheep wearing face masks were equally useful for determining the rate of O_2 consumption. However, with the tracheostomized sheep measurements of the respiratory exchange, while easy to make, were difficult to convert to estimates of heat production. As was realized by Klein (1915) the gaseous exchange from the lung differs from that of the whole animal. Large amounts of CO_2 and CH_4 are not recovered (especially at higher levels of feeding) and are presumed to be belched by the sheep. With the face mask technique this problem was obviated since all the CO_2 and CH_4 belched were collected and losses by other means of excretion, e.g. anal and skin, were considered to be negligible. However, with the tracheostomized sheep the O_2 consumption as measured by respiratory exchange was the same as that measured in the respiration chamber. The experiments conducted showed that the amount of CH_4 collected from the lung varied with the level of feeding and presumably with the amount of fermentation elicited. About 83% of the methane produced by tracheostomized sheep was not excreted by the lungs and was presumably lost by belching. This value of 83% is slightly higher than the one of 70% found in cattle by Klein (1915). A correction could be made for this loss of CH_4 when using respiratory gas exchange results for heat production estimates, by multiplying the level of CH_4 measured by a factor of six to account for the CH_4 lost by belching since only about one-sixth of the total CH_4 was collected in the Douglas bags from the tracheostomized animals.

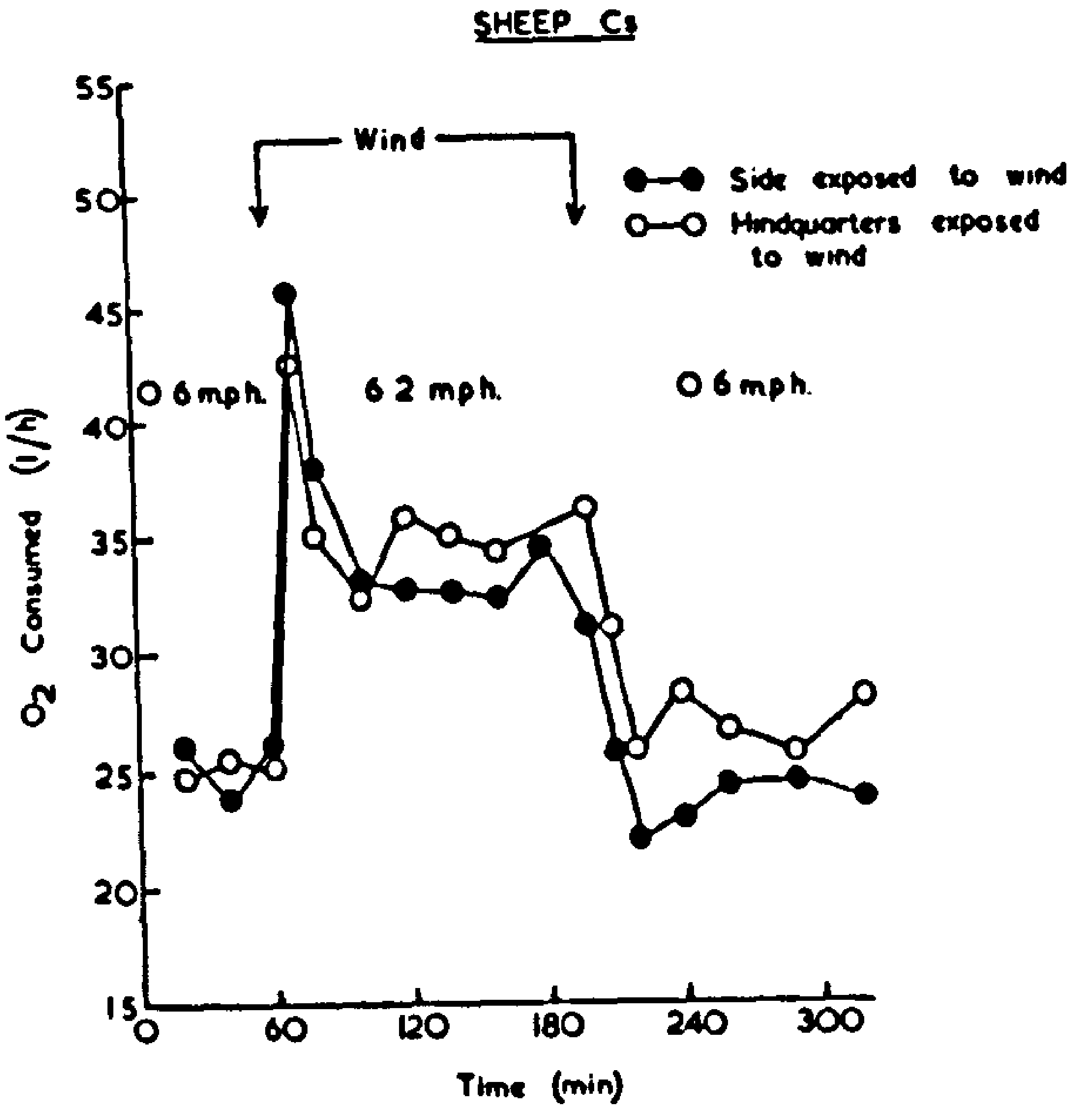
The method of correcting for methane could not be applied to carbon dioxide. The discrepancy between the total CO_2 production and pulmonary collection was small when small amounts of food were given but the difference increased markedly when the level of feeding was increased. Furthermore, indirect evidence from the measurement of gaseous exchange in tracheostomized sheep while eating suggests that during feeding the loss of CO_2 is greater than it is between meals. On the basis of the results of these experiments it is difficult to see how this discrepancy in the value for CO_2 consumption could be corrected. Perhaps from equations (7) and (8) on p. 38 a prediction of total CO_2 production from the pulmonary gas levels of CO_2 and CH_4 could be derived which would apply to conditions operating during the 9-h period between meals. However, it does not appear possible that such a correction could be applied to pulmonary exchange measured during and immediately after feeding, and it might not apply to rations and sheep other than the ones used in these experiments.

There are several alternative methods available for estimating heat production when the total CO_2 and CH_4 production levels are not available and a true respiratory quotient cannot be calculated. One method is to multiply the observed O_2 consumption by some average calorie equivalent/l. O_2 and a usual one is 4.80 kcal/l. O_2 corresponding to an R.Q. of 0.80. However, the R.Q. is unlikely to be 0.80 under all experimental conditions. If the animal is fasting and metabolizing fat rather than carbohydrate, the R.Q. will be close to 0.70 and the calorific equivalent/l. of O_2 will be 4.68, but if the animal is synthesizing large amounts of fat the calorific equivalent of the O_2 will be close to 5.05, that is when the true R.Q. is 1.00. Under these conditions to assume an R.Q. of 0.80 would overestimate heat production by 6.2% when the animal was fasting and underestimate it by 3.0% when the sheep was synthesizing large amounts of fat. An alternative method is to measure the calorific equivalent of O_2 in a respiration chamber over a similar period and with the same ration as that used in the experiments in which the pulmonary gas exchange is to be measured. This would undoubtedly reduce errors compared with the first method but it must be emphasized that any estimation of heat production over short periods, even when the total CO_2 and CH_4 produced and O_2 consumed can be measured, could lead to errors particularly if the determinations were made during a meal. From the comparison of the results of the collection of gas from the lungs and from the respiration chamber, it appears that large amounts of CO_2 can be lost during feeding by belching, with a subsequent elevation of the R.Q. The incremental R.Q.'s during feeding are so large, on some occasions being over 2.0, that they indicate that complete dissimilation of the substrate being oxidized has not occurred and the conditions for estimating heat production from O_2 consumption and CO_2 production have not been met. In the method used in the environmental experiments a constant calorific value of 4.68 kcal/l. O_2 above the thermoneutral levels of O_2 consumption was assumed. It appears from the results of the face-mask experiments that estimating heat production levels by this incremental O_2 consumption method, when compared with the normal method using the usual calorific values for the O_2 consumed and CO_2 and CH_4 produced was quite accurate and little difference was found between the two methods for transposing the respiration data to heat production values.

A difficulty encountered in measuring the respiratory exchange of tracheostomized sheep was that such surgical preparations were difficult to maintain for long periods. Only one animal out of seven survived for over 11 months without a stenosis of the trachea. In some sheep stenosis occurred only a matter of weeks after the operation. Undoubtedly the use of a rigid material such as "Perspex" for the cannula contributed to the stenosis. This could be overcome if a suitable material for constructing the cannula could be found which was soft enough not to cause irritation in the trachea and yet rigid enough to maintain its shape without distortion at body temperatures. Since these experiments were made such a material has been used by Young & Webster (1963) but no mention was made of the survival periods for the animals thus tracheostomized.

The face-mask method was easier to use than the tracheostomy method and had the additional advantage that the animal was not interfered with surgically. Except in those experiments where it was imperative that the face and mouth should not be occluded by the use of a mask, the face-mask technique was superior to tracheostomy as a routine method of collecting expired air from sheep. The comparison of the external insulation as measured using masked sheep and that predicted from the tracheostomized sheep data, showed that the correlation coefficient was 0.99which suggests that there was little difference between the two methods as a means of measuring heat production.

In all the short term experiments described the animals were always



	Air temperature	Fleece length
Side exposure	12°	11mm
Hindquarter exposure	6 5°	12mm

Fig. 5 A

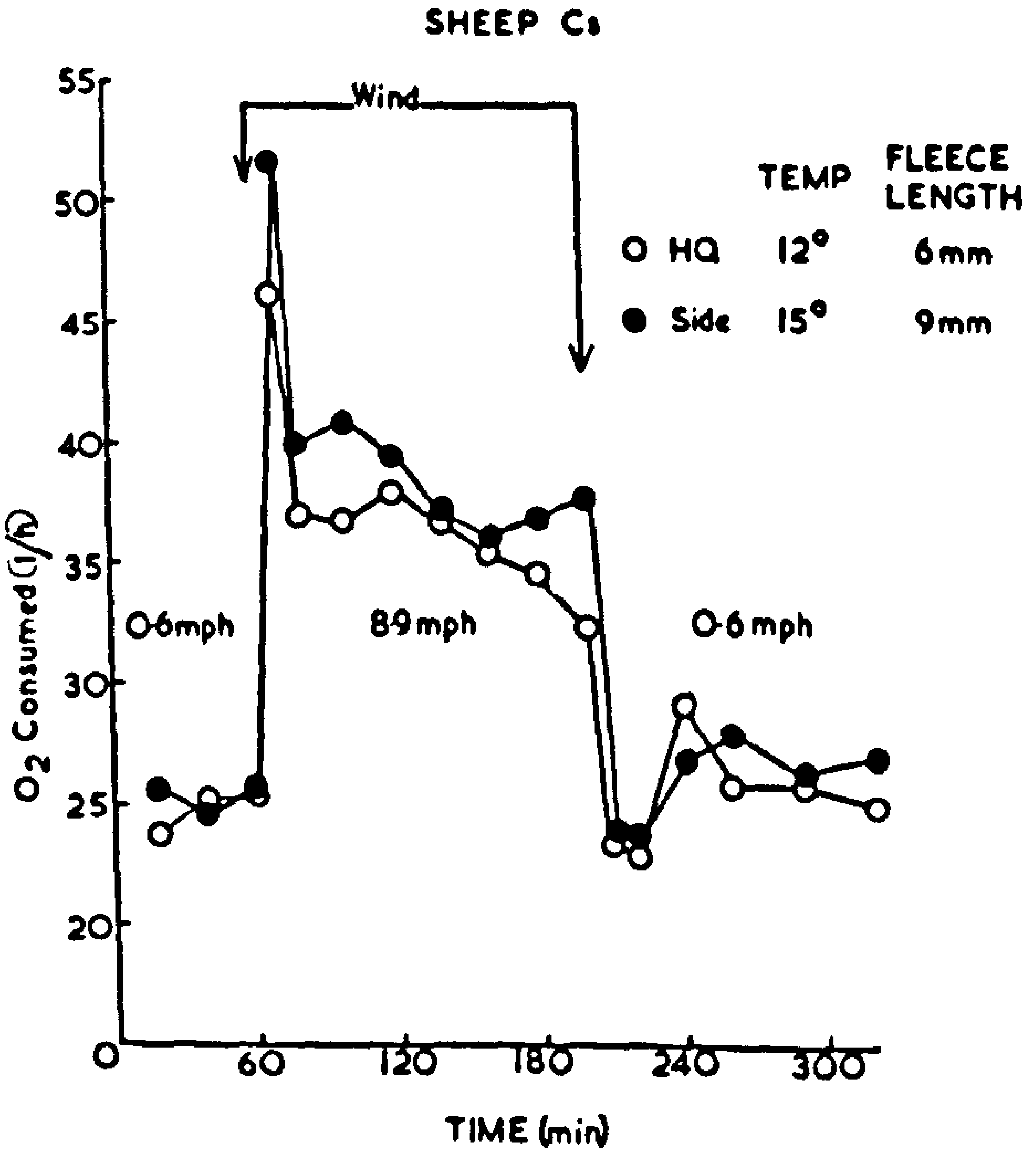


Fig. 5 B

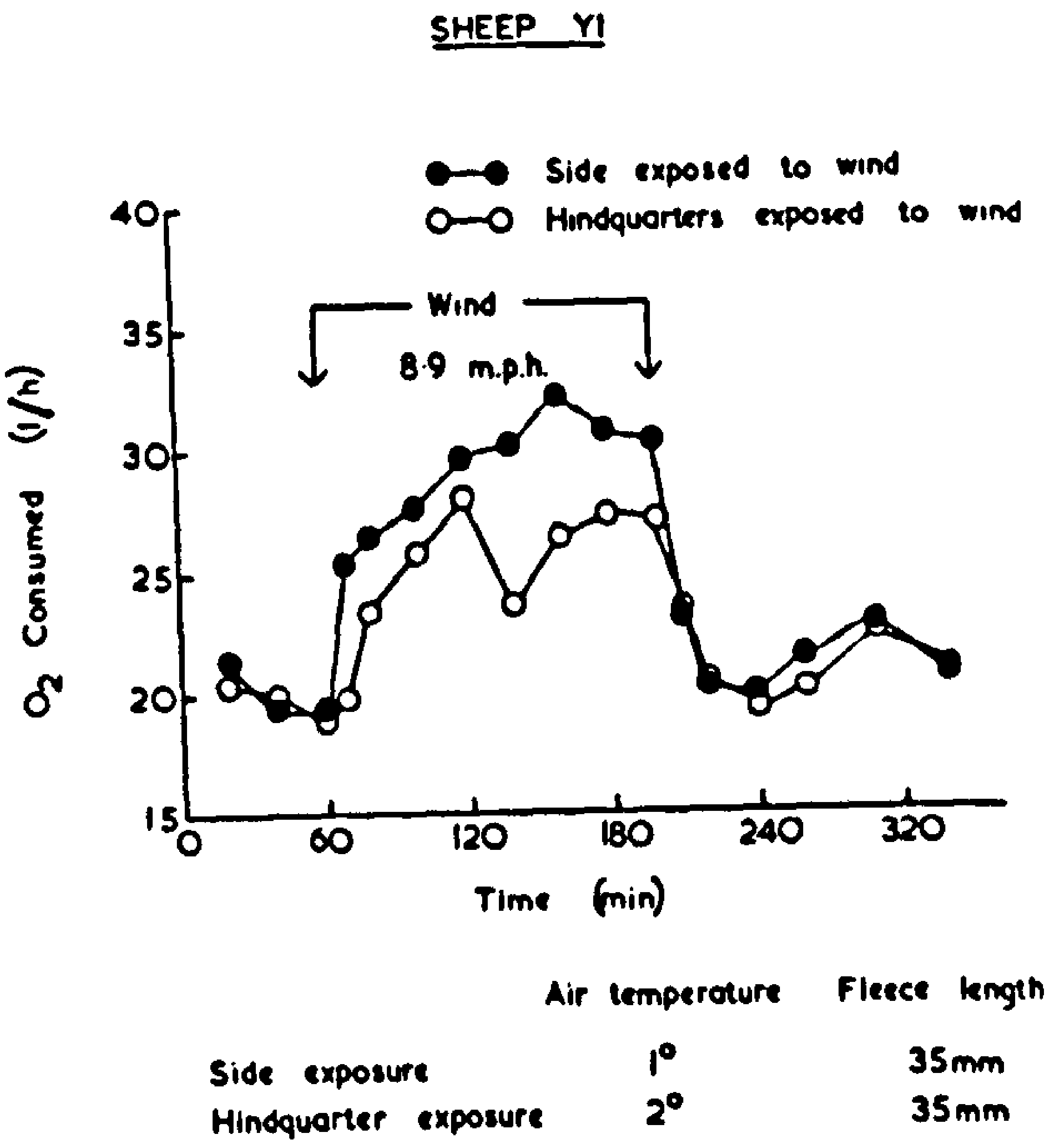


Fig. 5 C

Fig. 5. The variations in O_2 consumption on changing the wind speed when either the side (●) or hindquarters (O) of the sheep were facing the wind source.

(A) O_2 consumption of sheep Cs at wind speeds of 0.6 and 6.2 m.p.h.

(B) O_2 consumption of sheep Cs at wind speeds of 0.6 and 8.9 m.p.h.

(C) O_2 consumption of sheep Y1 at wind speeds of 0.6 and 8.9 m.p.h.

standing, but in the respiration chamber experiments to determine the thermoneutral heat production the amount of time spent lying was considerable. The increase in O_2 consumption of 1 l. O_2/h measured on standing corresponded to an increase of 5.0 kcal/h or 1.7 kcal/kg body weight/24 h which is in agreement with the observations of Hall & Brody (1933) that in cattle the increase in metabolism as measured from O_2 consumption was 2.1 kcal/kg body weight/24 h. It is also similar to results reported by McLean (1963) with calves and also to the level of 2.4 kcal/kg body weight/24 h observed by Benedict & Johnson (1919) in young women. It is much smaller than the large increases noted by Pullar (1962) using direct calorimetric methods. The reason for the disparity between the direct and indirect calorimetric estimates of the energy cost of standing compared with that of lying is not known. The energy cost of standing was thus considered to be small and was always ignored when calculating the results.

B. Equilibration experiments of O_2 consumption and rectal and body surface temperatures. The results in this section were obtained from experiments designed to determine the minimum and maximum times for the body to become metabolically adjusted to changes in the environmental surroundings.

(1) Air velocity. Changes that occurred in the O_2 consumption of sheep Cs when exposed to a wind of 6.2 m.p.h. are shown in Fig. 5 a. The results for sheep Cs and Yl at a wind speed of 8.9 m.p.h. are shown in Figs. 5 b and 5 c. Each plot is the mean result of two experiments. The environmental temperature was below the critical temperature of each sheep in each experiment when the fans were switched off and the air was still. In each of the graphs, therefore, an additional litre of O_2 consumed was equivalent to 4.68 kcal heat production, and increases in heat production could be calculated from the O_2 scale.

Table 7. Effect of wind on the mean skin temperature of the windward and leeward side of the trunk and of the legs of two sheep with their side presented to the wind. Each observation is the mean of two exposures

Skin temperature	Animal	Fleece length (mm)	Wind speed (m.p.h.)	Air temperature (°)	Skin temperature (°) - minutes after exposure to the wind						
					Before	5	10	20	40	80	140
Windward sites on trunk	Cs	11	6.2	12	29.0	25.5	25.4	24.6	25.3	25.1	24.9
	Cs	6	8.9	15	31.1	25.0	24.9	24.4	24.0	23.4	23.7
	Yl	35	8.9	1	35.0	29.4	28.4	27.6	27.3	27.1	27.6
Leeward sites on trunk	Cs	11	6.2	12	29.7	26.9	26.5	26.0	26.4	26.7	26.2
	Cs	6	8.9	15	31.3	27.5	27.7	28.1	27.7	27.6	27.5
	Yl	35	8.9	1	35.2	35.1	35.0	34.7	35.2	35.1	35.1
Fetlock, both sides	Cs	11	6.2	12	17.2	16.8	16.1	15.6	14.6	14.5	13.8
	Cs	6	8.9	15	16.8	16.1	16.5	16.2	15.8	15.8	16.2
	Yl	35	8.9	1	7.0	1.7	1.5	1.4	1.1	1.1	1.1

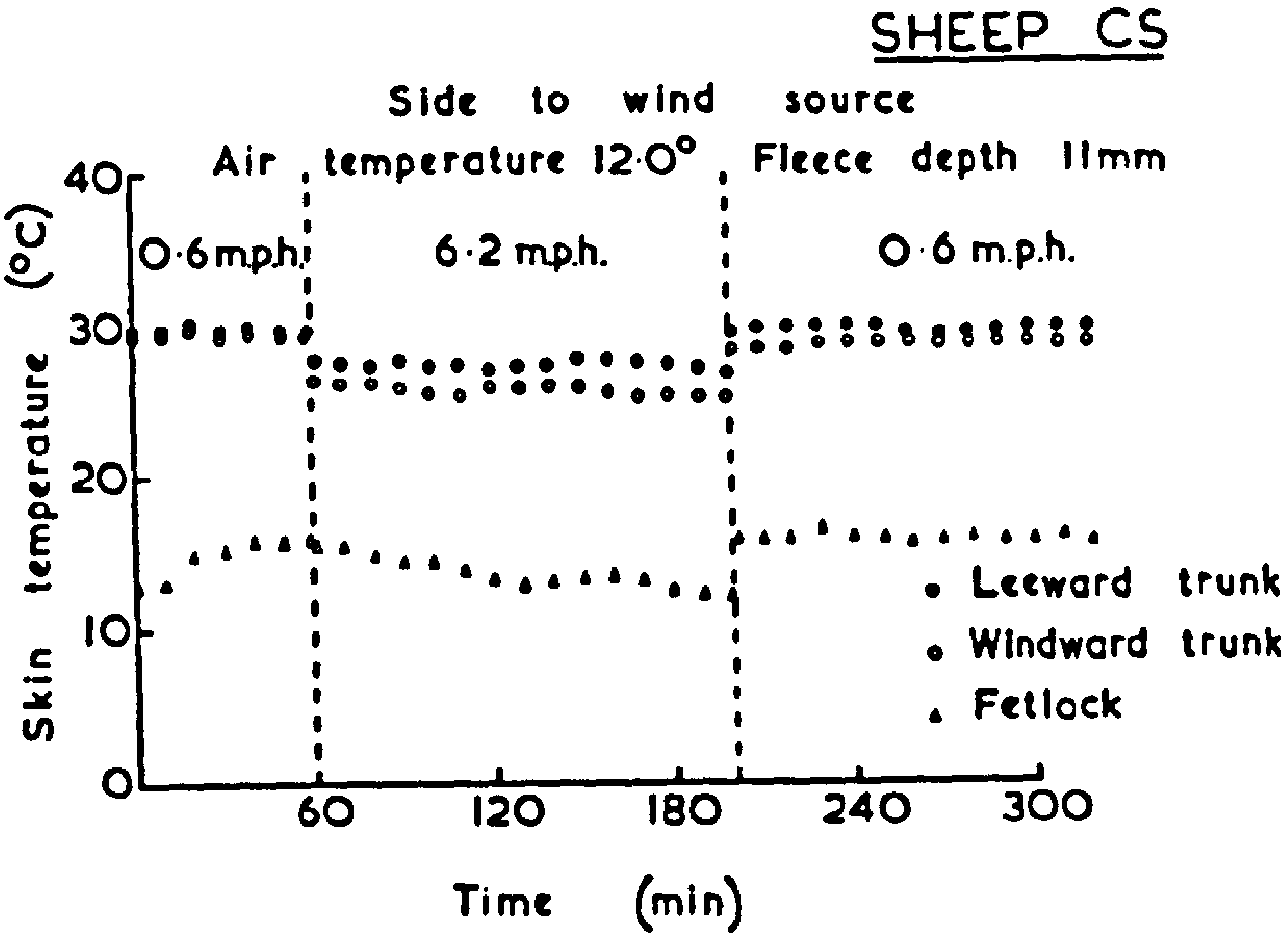

SHEEP CS
Side to wind source
Air temperature 12·0° Fleece depth 11mm
0·6m.p.h.
6·2 m.p.h.
0·6 m.p.h.
Skin temperature (°C)
40
30
20
10
0
60
120
180
240
300
Time (min)
• Leeward trunk
∘ Windward trunk
▴ Fetlock

Fig. 6 A

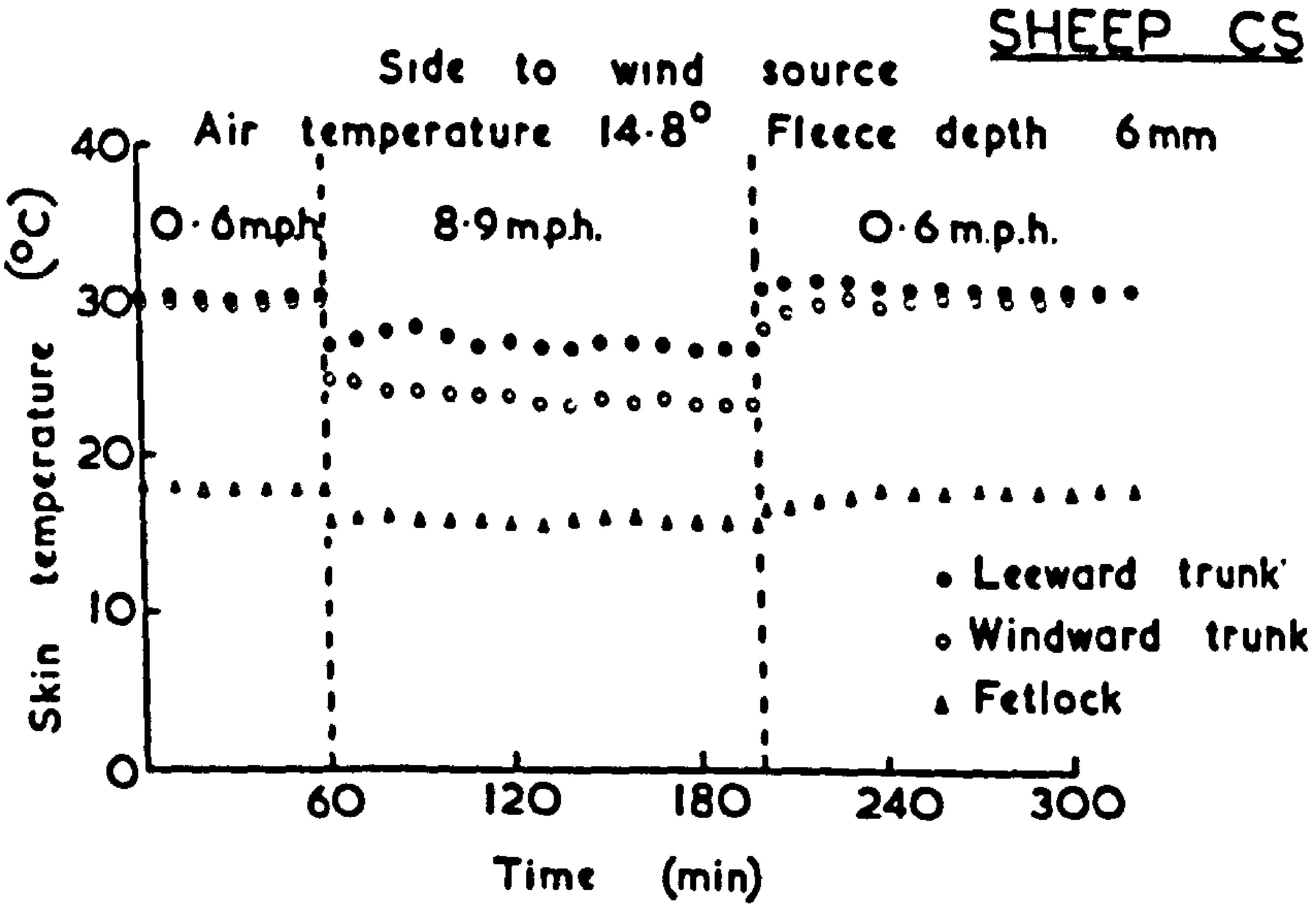

SHEEP CS
Side to wind source
Air temperature 14·8° Fleece depth 6mm
0·6mph
8·9m.p.h.
0·6 m.p.h.
Skin temperature (°C)
40
30
20
10
0
60
120
180
240
300
Time (min)
• Leeward trunk
∘ Windward trunk
▴ Fetlock

Fig. 6 B

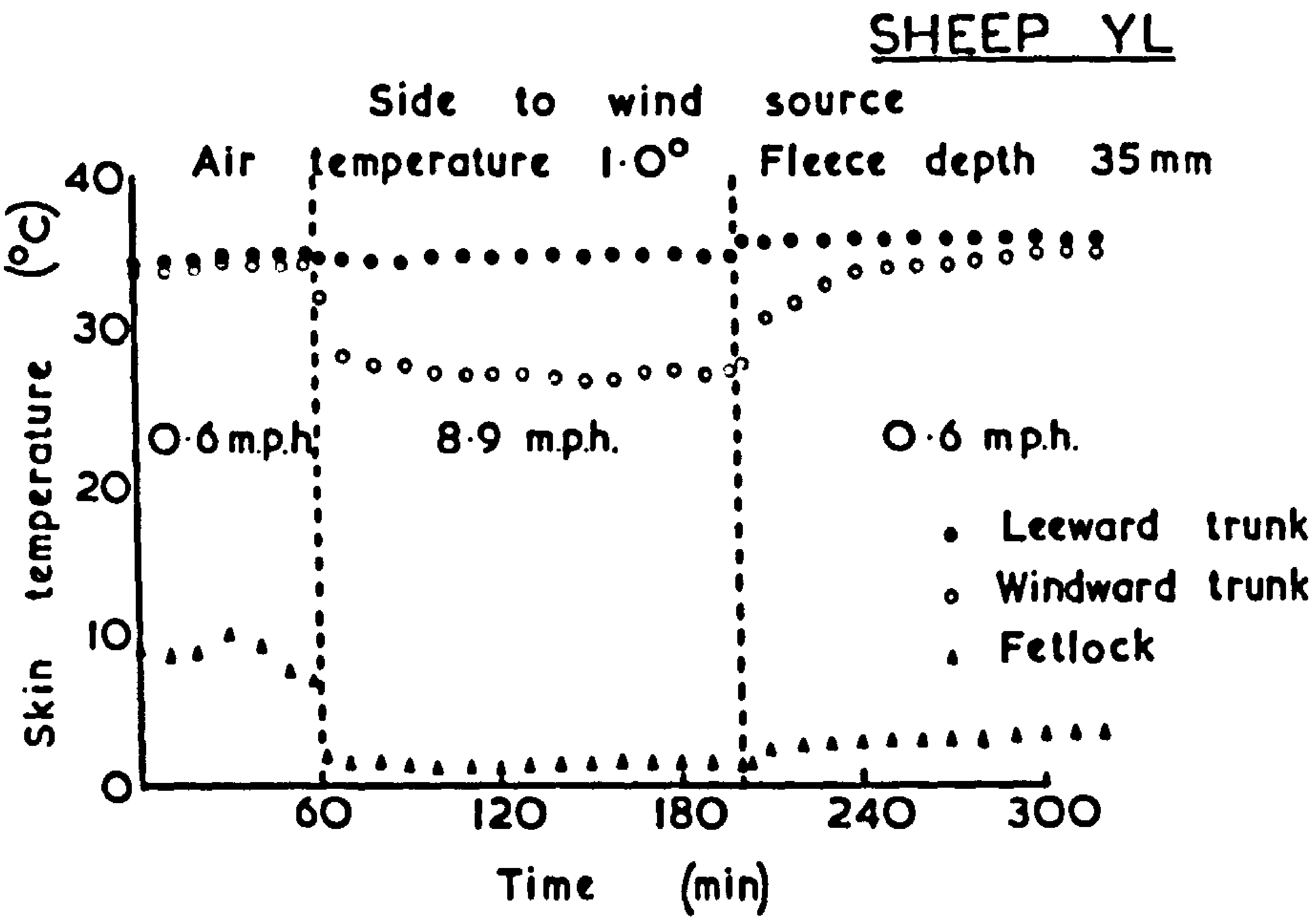


Fig. 6 C

Fig. 6. The changes in skin temperatures of sheep with variations in wind speed when the side of the sheep was presented to the wind source.

(A) Skin temperature of sheep Cs at wind speeds of 0.6 and 6.2 m.p.h.

(B) Skin temperature of sheep Cs at wind speeds of 0.6 and 8.9 m.p.h.

(C) Skin temperature of sheep Yl at wind speeds of 0.6 and 8.9 m.p.h.

With sheep Cs in both sets of experiments switching on the fans led to a large rise in O_2 consumption during the first 5 min. This fell in the following 15 min and then became either virtually constant (Fig. 5 a) or fell slightly (Fig. 5 b). The fall in O_2 consumption after the 15th minute in the results shown in Fig. 5 b, may have been due partly to a slight increase in air temperature from 11.4° to 12.2° when the hind-quarters were presented to the wind source and from 14.3 to 14.8° when the side was exposed. When the fans were switched off O_2 consumption immediately fell to values below those observed initially but subsequently rose to steady values 20 min after the wind had stopped. With sheep Yl, bearing a longer fleece, as recorded in Fig. 5 c, the early peak in O_2 consumption did not occur but the short depression of O_2 consumption on stopping the wind was again noticed. The O_2 consumption of sheep Yl reached an equilibrium within ±2 l. O_2/h after 60 min of exposure to the wind and also after stopping the wind. The comparable time for sheep Cs on a change of air velocity to attain an equilibrium within 1 l./h was 20 - 40 min.

Table 7 summarizes measurements of skin temperatures made in the experiments with one side of the sheep exposed to the wind. The temperatures for the windward and leeward sides of the trunk recorded in Table 7 are each the mean of temperatures taken on three sites on each of the two sides. These results are shown graphically in Fig. 6. The fall in the temperature of the skin of the trunk on both the windward and leeward sides was initially very rapid but after the first 5 min the fall was slow. The increase in skin temperature on stopping the wind was equally rapid. In all the experiments the temperature of the skin on the windward side of the trunk fell more than that of the leeward side, indeed with sheep Yl, with 35 mm fleece depth, no change in the surface temperature of the

Table 8. Mean temperatures of skin of two sheep after exposure of their side or hindquarters to wind for more than 2 h

Sheep	Fleece length (mm)	Wind speed (m.p.h.)	Site	Mean temperature (°) when:			
				Left side to wind		Hindquarters to wind	
				Left side	Right side	Left side	Right side
Y1	3 - 5	8.9	Air	1.0		1.8	
			Shoulder	31.3	35.5	33.4	33.0
			Midside	28.5	35.2	32.5	31.2
			Hip	23.0	34.6	29.2	29.6
			Hind fetlock	1.1		3.7	
Cs	11 - 12	6.2	Air	12.0		6.4	
			Shoulder	24.1	29.4	25.1	25.1
			Midside	24.9	26.3	24.2	25.2
			Hip	24.8	26.1	23.8	23.6
			Hind fetlock	13.8	14.9	8.0	7.7
Cs	6 - 9	8.9	Air	14.8		12.0	
			Shoulder	24.4	31.6	25.5	25.4
			Midside	23.2	25.8	21.5	21.1
			Hip	24.2	25.8	20.3	19.8
			Hind fetlock	15.4	16.9	15.6	15.6

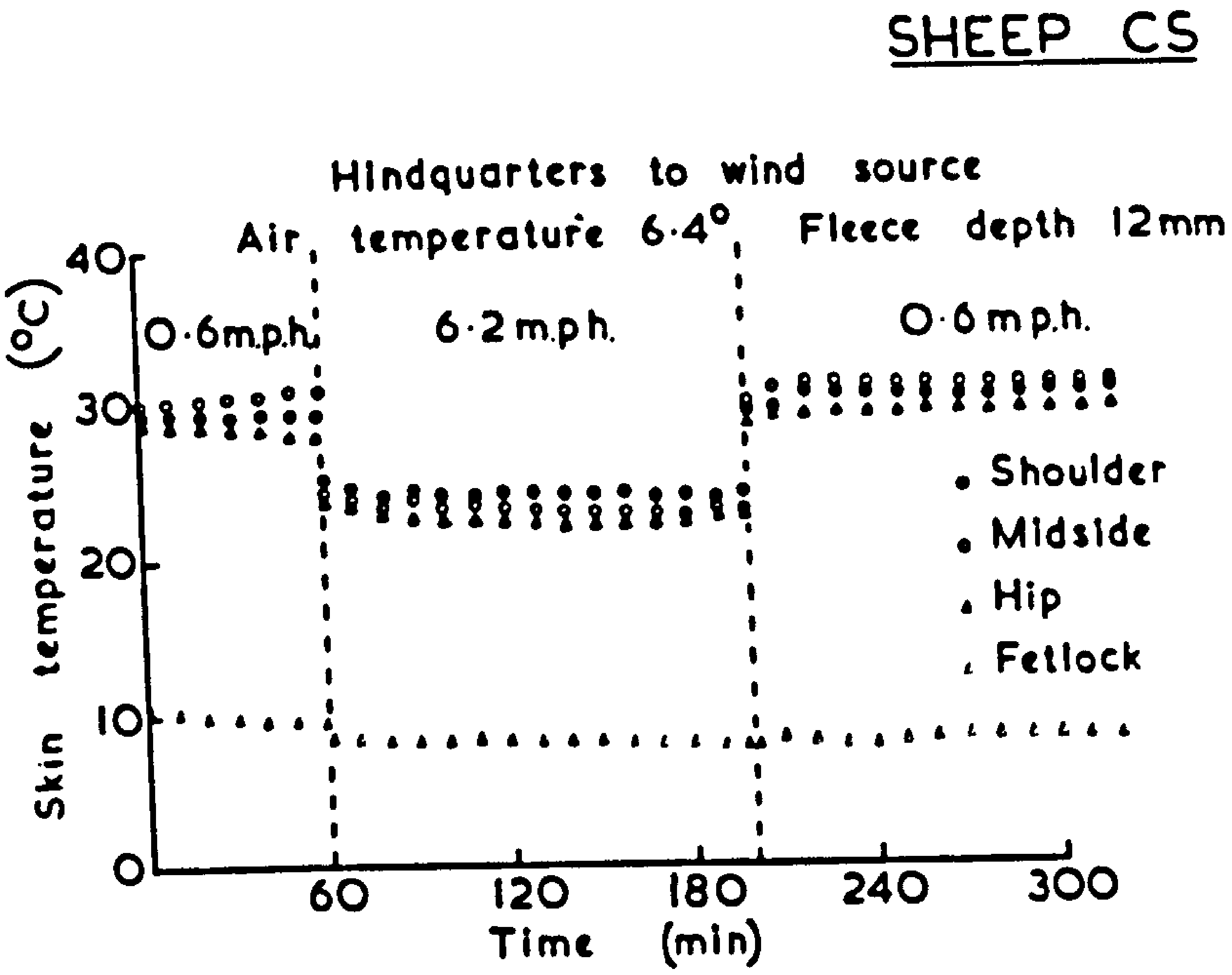

SHEEP CS
Hindquarters to wind source
Air temperature 6·4°
Fleece depth 12mm
0·6m.p.h.
6·2 m.p.h.
0·6 m.p.h.
Skin temperature (°C)
40
30
20
10
0
60
120
180
240
300
Time (min)
Shoulder
Midside
Hip
Fetlock

Fig. 7 A

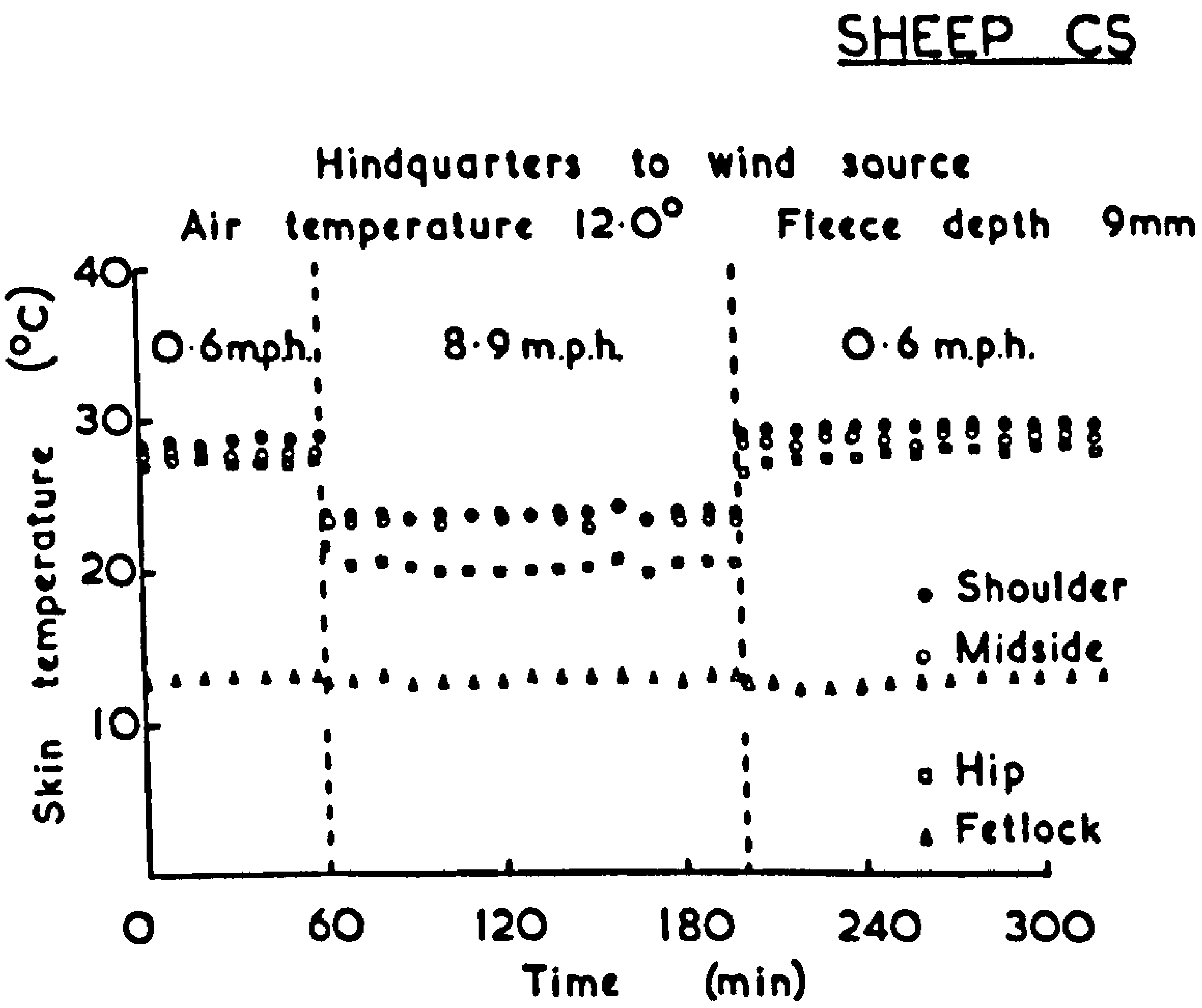

SHEEP CS
Hindquarters to wind source
Air temperature 12·0°
Fleece depth 9mm
0·6mph.
8·9 m.p.h.
0·6 m.p.h.
Skin temperature (°C)
40
30
20
10
0
60
120
180
240
300
Time (min)
Shoulder
Midside
Hip
Fetlock

Fig. 7 B

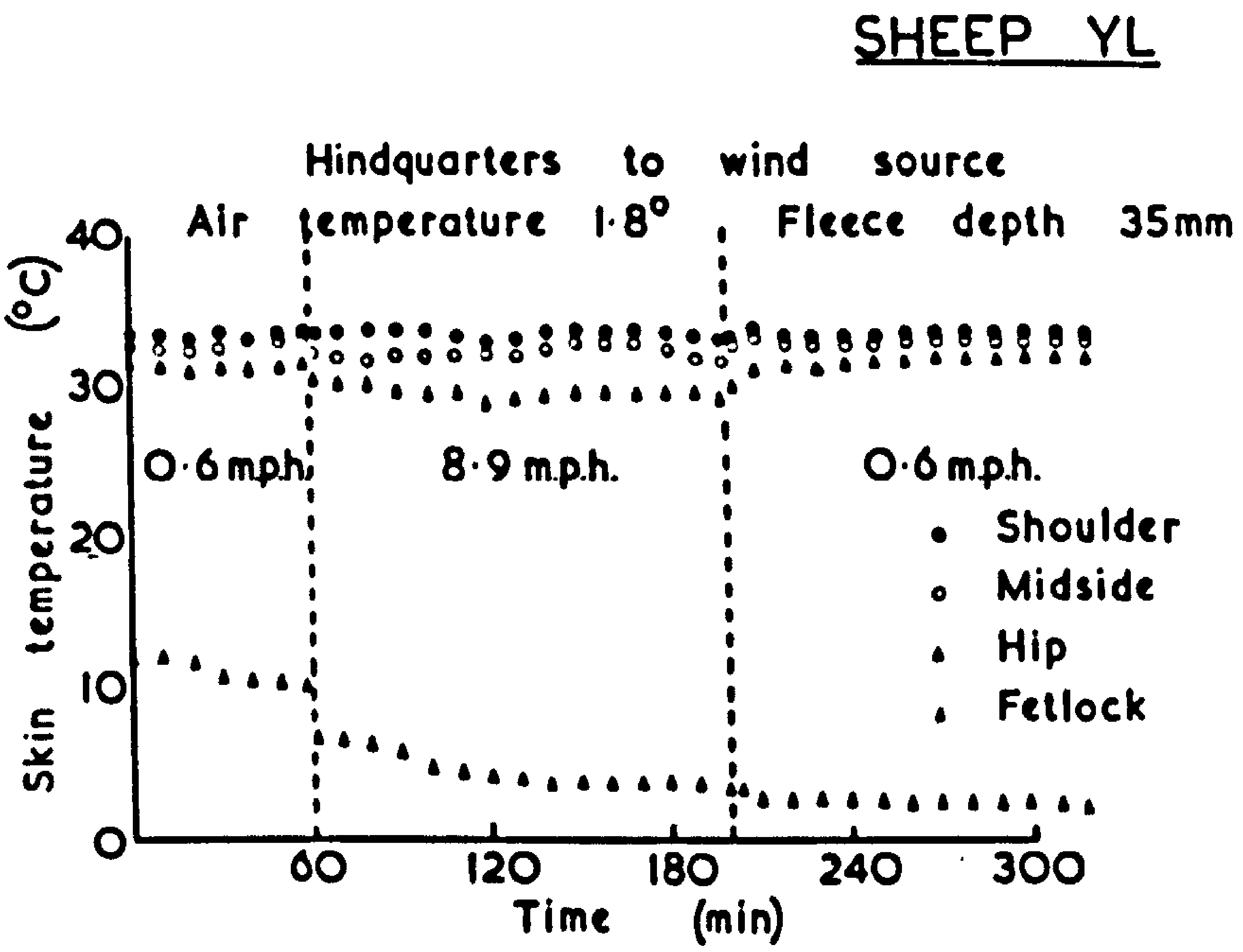


Fig. 7 C

Fig. 7. The changes in skin temperature of sheep with variations in wind speed when the hindquarters of the sheep were presented to the wind source.

(A) Skin temperatures of sheep Cs at wind speeds of 0.6 and 6.2 m.p.h.

(B) Skin temperatures of sheep Cs at wind speeds of 0.6 and 8.9 m.p.h.

(C) Skin temperatures of sheep Y1 at wind speeds of 0.6 and 8.9 m.p.h.

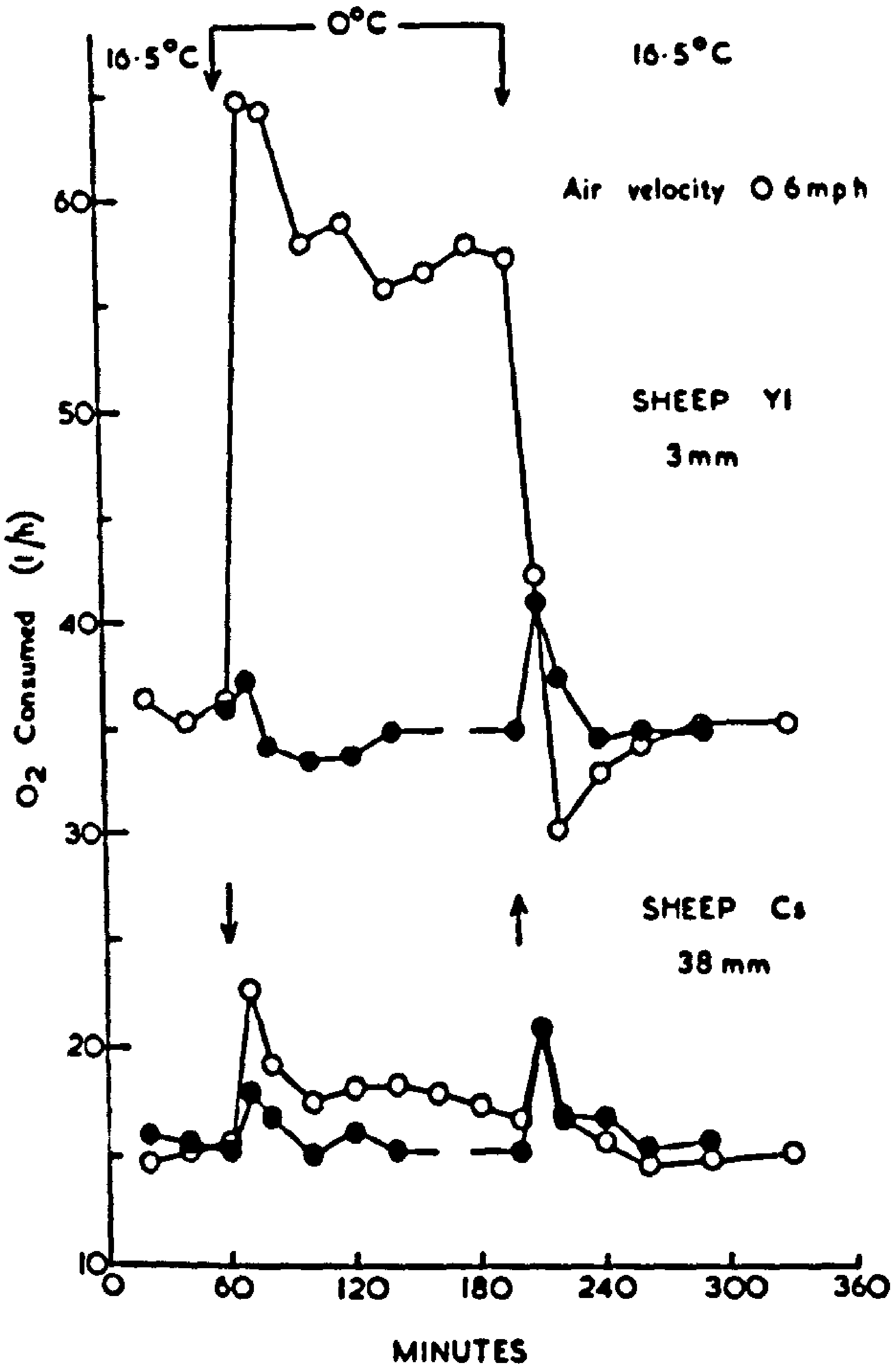


Fig. 8. Changes in O_2 consumption of sheep Cs and Y1 in response to changes in air temperature from 16.5° to 0° and back to 16.5°. The fleece depth was 38 mm for sheep Cs and 3 mm for Y1. (O) Environments of 16.5° and 0°.

(●) Both environments at 16.5°.

leeward sites occurred even though the temperature of the windward sites fell in temperature by 8^{o}. The fall in the temperature of the fetlocks was smaller than that of the trunk except when sheep Yl was exposed to a wind of 8.9 m.p.h. The rate of increase in the temperature of the skin of the fetlock on stopping the wind was also smaller than that noted for the trunk.

The temperature of the skin surfaces of the sheep when their hindquarters were presented to the wind were very different from those noted when their sides were presented. Table 8 shows the mean values obtained after exposure for 2 h, i.e. after an attainment of equilibrium. Results for each sheep are also shown graphically in Fig. 7. Whereas with side presentation a gradient of skin temperature from the leeward to the windward developed, hindquarter presentation intensified the small natural skin temperature gradient from the posterior to the anterior of the animal. In each experiment shown in Fig. 5, side exposure resulted in a greater O_2 consumption than hindquarter exposure. The air temperatures were not the same for the two presentations in any of the three sets of experiments and direct comparison of skin temperature for side and hindquarter presentation is not therefore possible.

(2) Ambient temperature. Fig. 8 shows the changes in O_2 consumption of sheep Cs and Yl when they were rapidly transferred from a room with an air temperature of 16^{o} to a room with an air temperature of 0^{o}. Each graph represents the mean values obtained in two experiments. The fleece depth of sheep Cs was 38 mm and of sheep Yl 3 mm. As expected the average response to cold was greater in the sheep with the shorter fleece. In the first 10 min following the transfer to the cold room, O_2 consumption was markedly increased, but after that both sheep attained lower O_2 consumption levels. When sheep Yl was transferred back from the cold into the warm

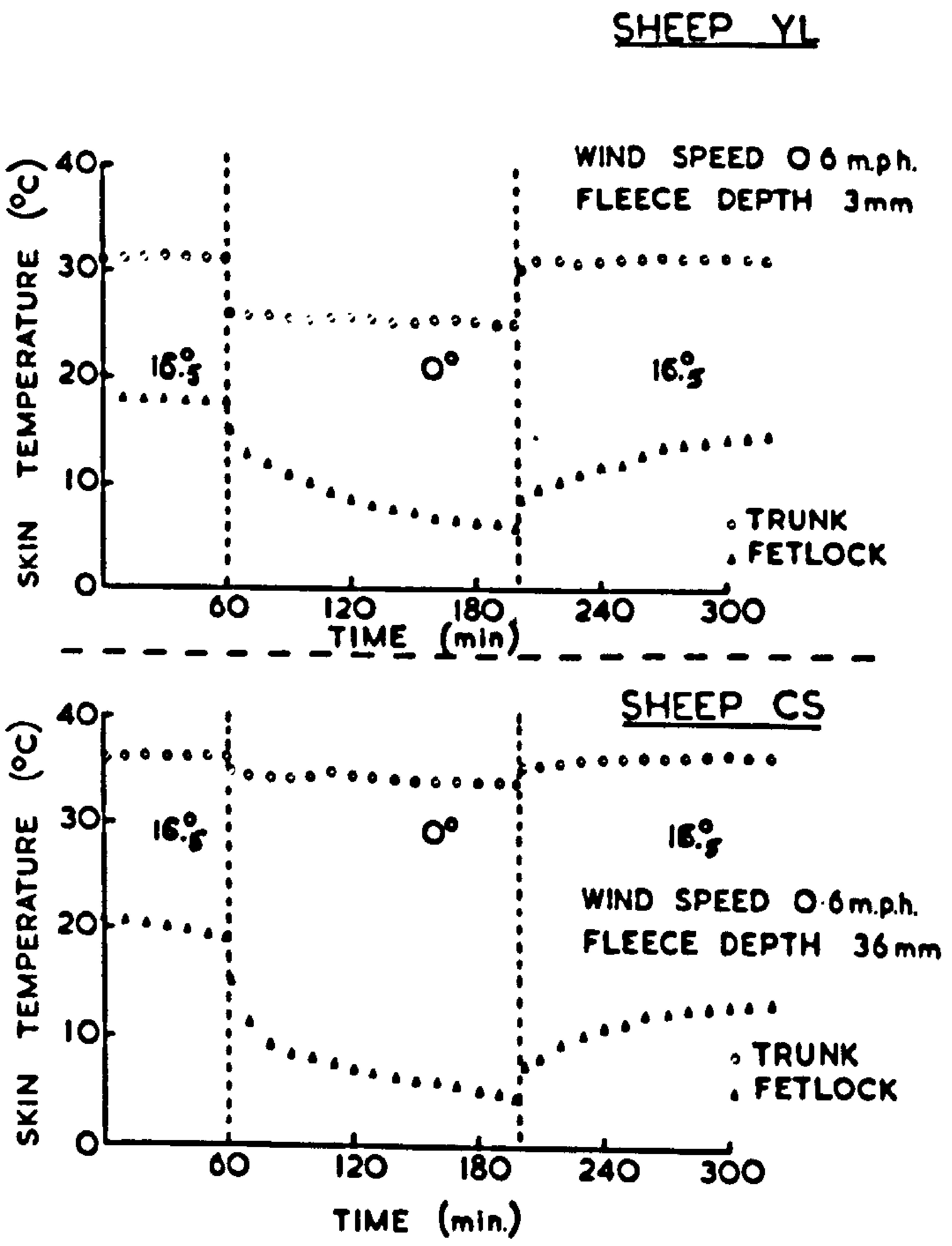


Fig. 9. Variations in the skin temperature of sheep Cs and Yl in response to changes in air temperature from 16.5° to 0° and back to 16.5°.

a transient period was recorded during which time O_2 consumption was lower than that measured when the same sheep was in the warm prior to being taken into the cold. The O_2 consumption of sheep Cs when transferred from the cold to the warm was elevated for 10 min after which time a rapid fall occurred. The act of transferring the sheep from one room to another obviously caused a disturbance to the animal's metabolism. The extent of this disturbance on O_2 consumption was measured in two control experiments in which each sheep was transferred from one room to another, both rooms being maintained at the same ambient temperature. The increases in O_2 consumption of both sheep during and immediately following the act of transference are shown in Fig. 8. This observation during transference may support the contention that the immediate transitory peak in O_2 consumption on subjecting a sheep to a sudden increase in wind may be due to disturbance caused by the tactile impact of the wind on the animal's body. However, it cannot explain the transitory depression or trough noticed on changing the animal Y1 from the cold to the warm room or on switching off the wind and the depression in O_2 consumption may be due to heat stored in the body, associated with a higher rectal temperature, being released on stopping the wind or raising the air temperature. The response of O_2 consumption to environmental temperature was completed very quickly, certainly within 40 min after the change in air temperature was made, no matter whether the temperature was raised or lowered. Skin temperatures on the trunk rapidly attained stable values, but this took longer for the fetlock (Fig. 9). The rate of temperature change of the skin of the extremities in response to a change in air temperature thus appears to be slower than that of the trunk.

(3). <u>Infrared radiation</u>. Although experiments were made with two sheep to find the time taken to obtain an equilibrium following a change in

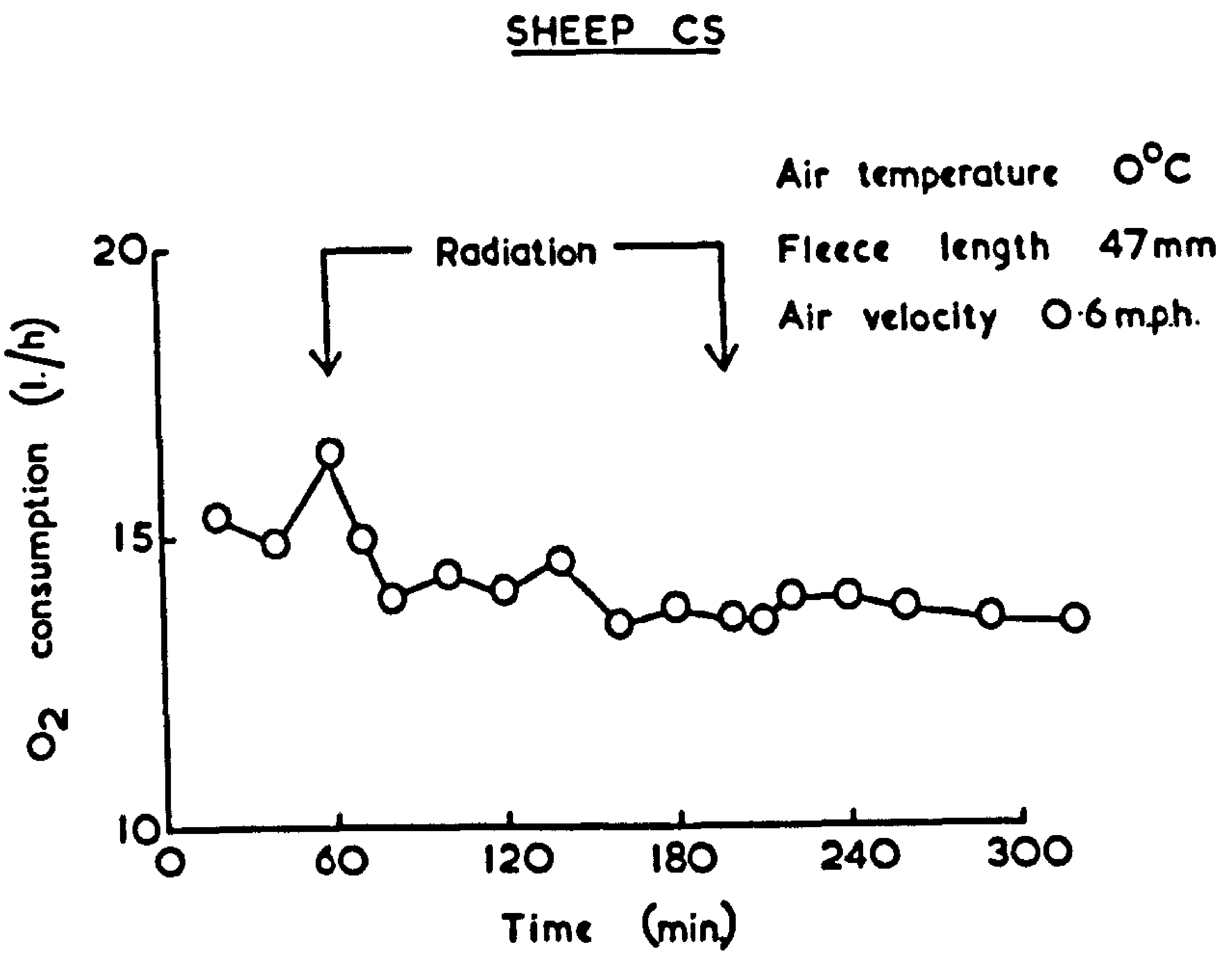


Fig. 10 A

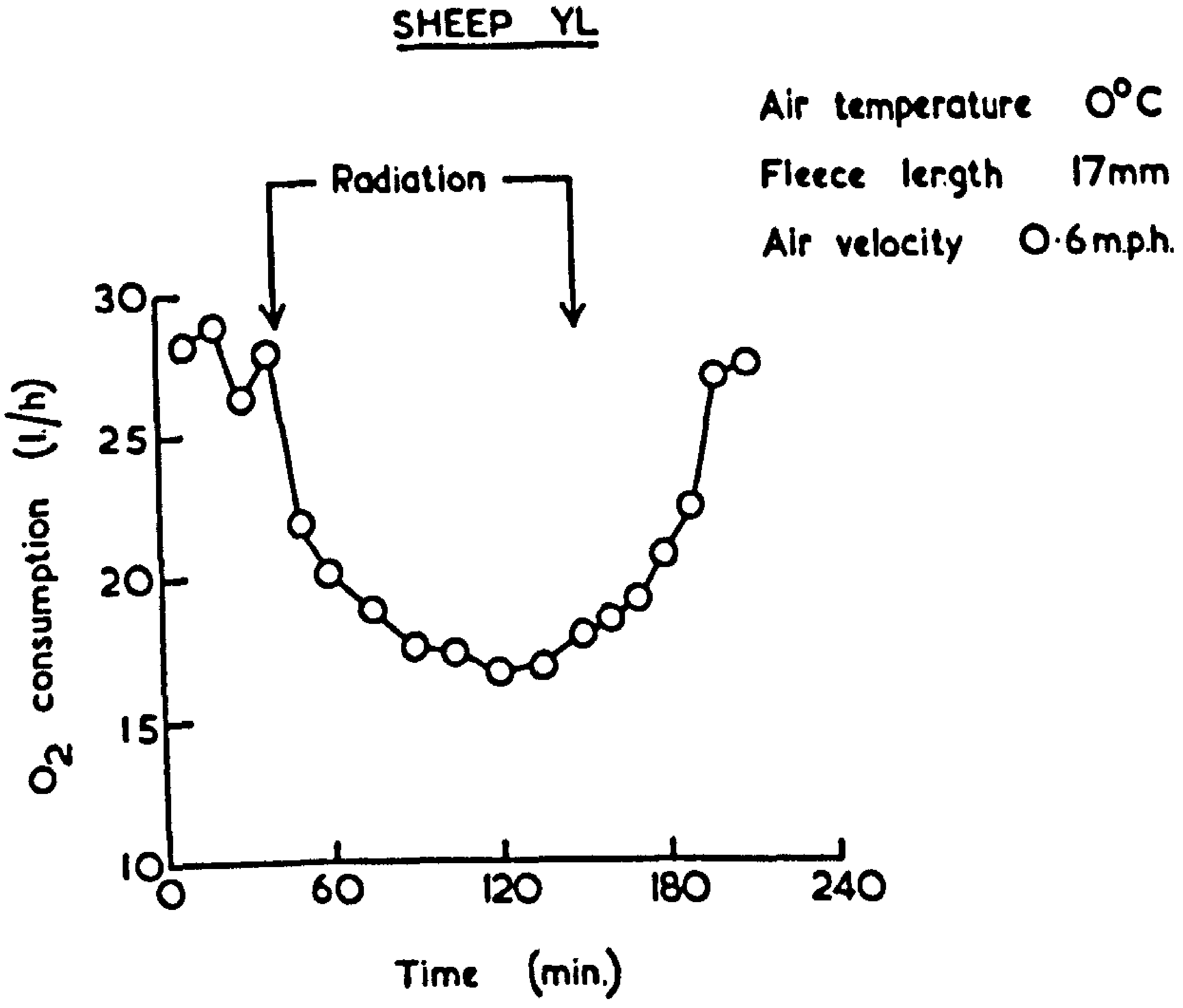


Fig. 10 B

Fig. 10. Changes in O_2 consumption of sheep Cs (A) and Yl (B) in response to the application of radiant heat.

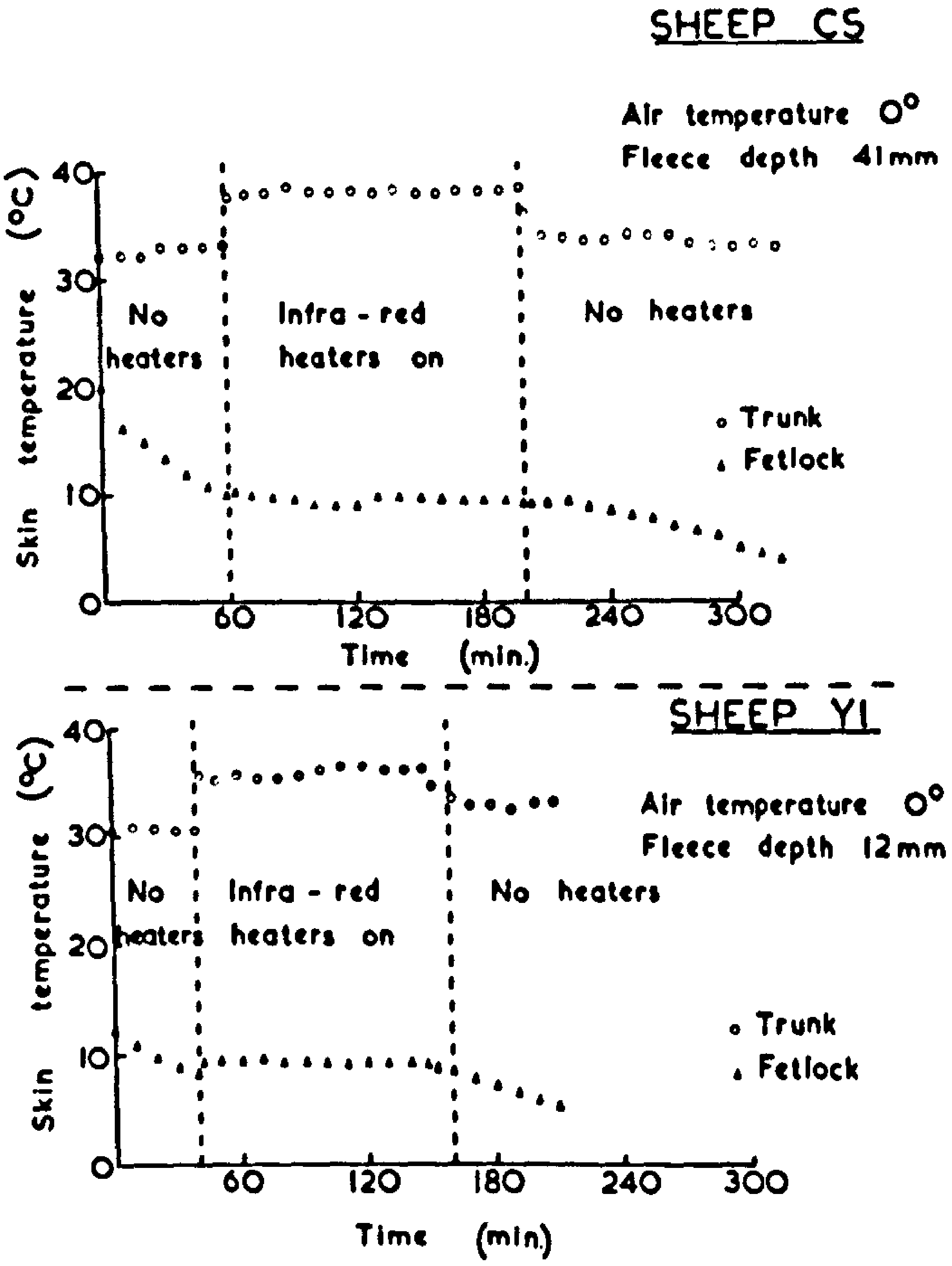


Fig. 11. Variations in skin temperature of sheep Cs (A) and Y1 (B) in response to changes in the radiant temperature.

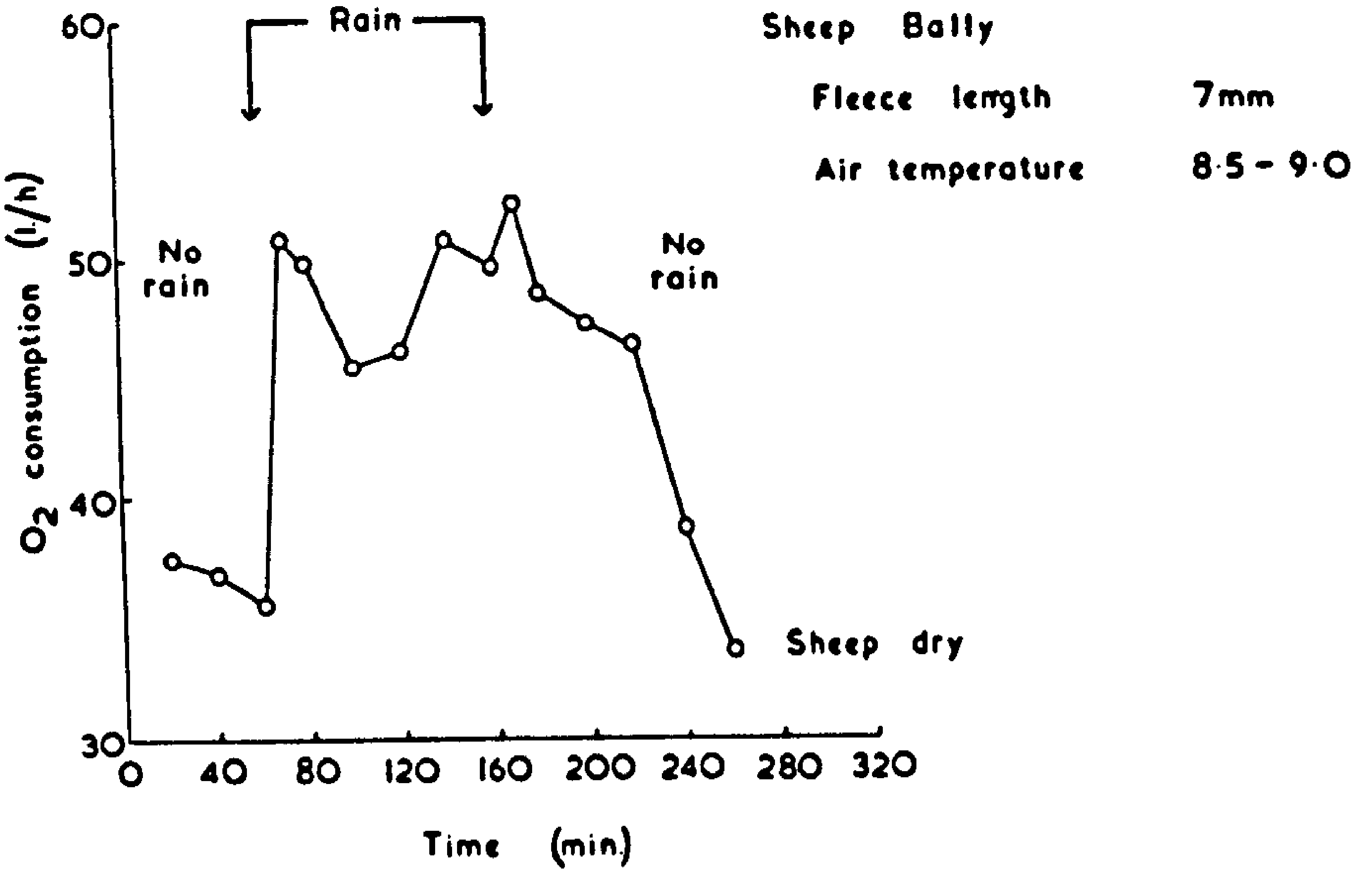


Fig. 12 A

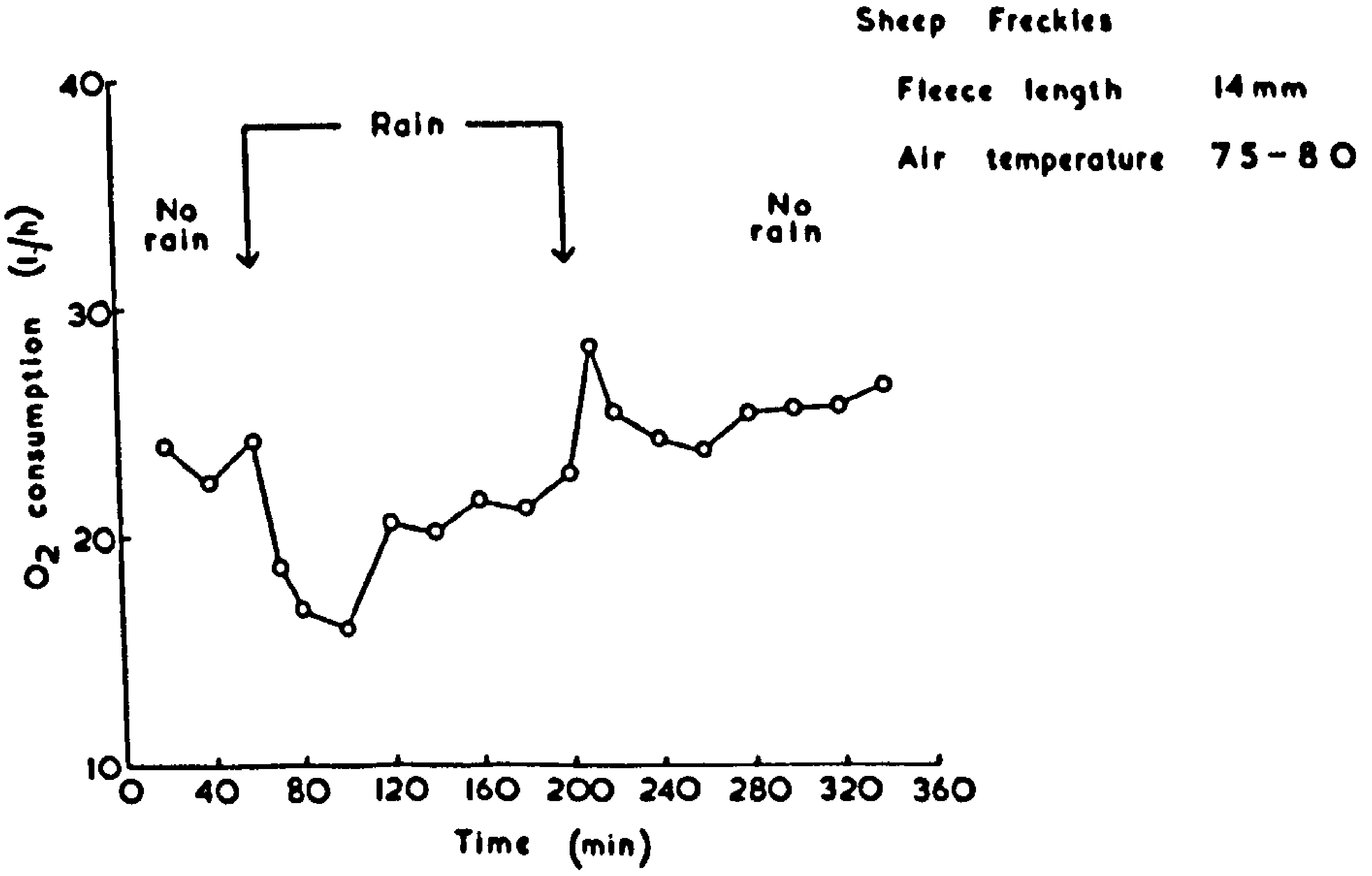


Fig. 12 B

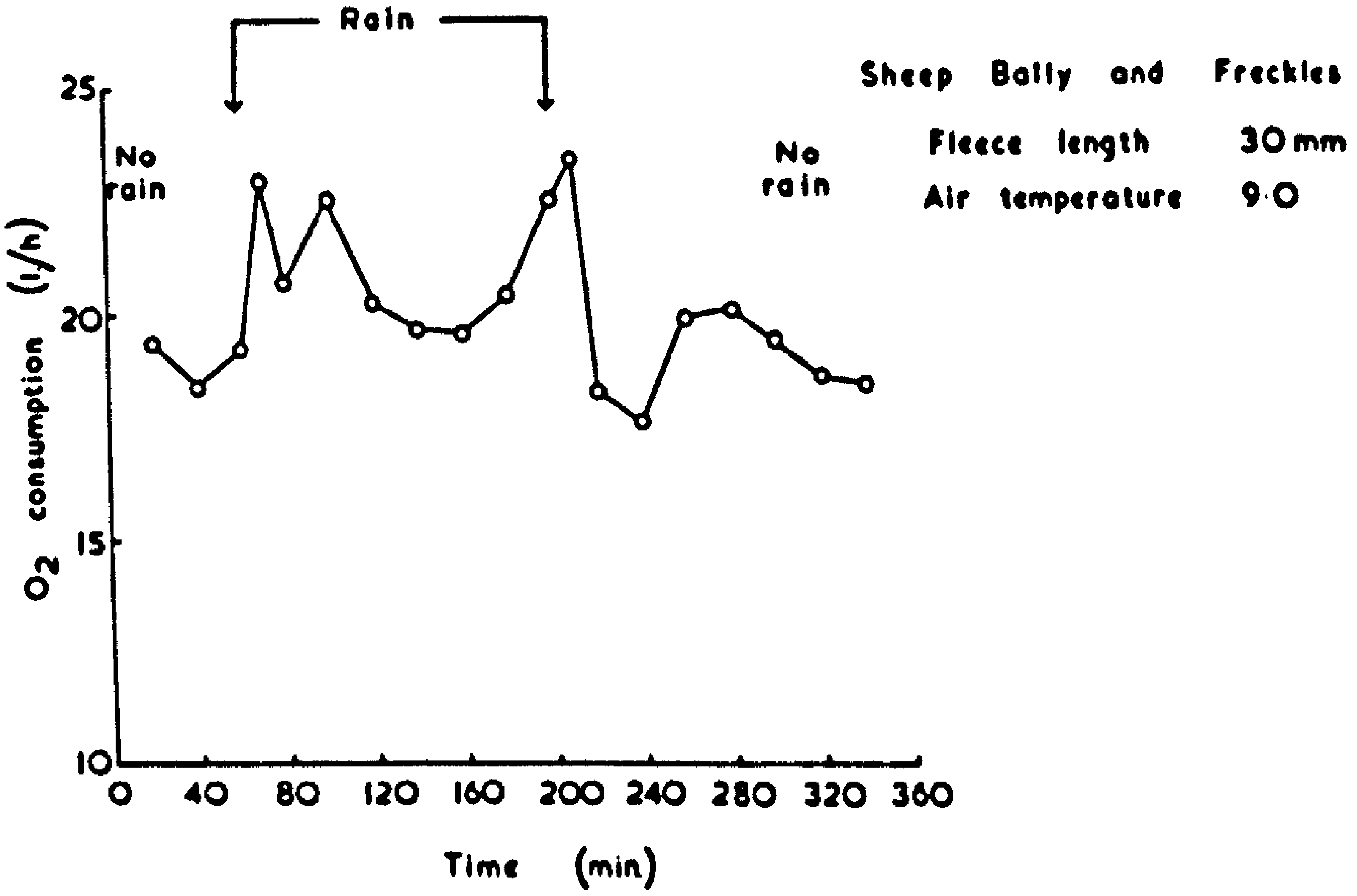


Fig. 12 C

Fig. 12. Changes in O_2 consumption of sheep By and Fr with fleece lengths of 7 mm (A), 14 mm (B) and 30 mm (C) in response to the application of rain at a rate of 0.4 in./h.

the intensity of infrared radiation, only the sheep Yl showed a response in O_2 consumption (Fig. 10 a). As shown in Fig. 10 b the environmental temperature was above the critical temperature for sheep Cs since there was no response in O_2 consumption. The response in O_2 consumption to changes in infrared radiation intensity were slow. In sheep Yl it took about 60 - 80 min to reach a minimal O_2 consumption when heat was applied and 50 min to return to initial values when heating was stopped. No true equilibrium O_2 consumption was ever reached although the values were reasonably steady from the 30th to the 80th min after radiation began. As expected from the previous equilibration experiments, trunk temperatures (Fig. 11) responded very quickly showing almost complete equilibrium within 5 min of the changeover. The skin temperature of the fetlock of both sheep, however, showed a slow fall during the periods before and after the infrared heaters were switched on (Fig. 11).

(4) Artificial rain. As shown in Fig. 12 it was difficult to determine any time period in which the sheep had reached an equilibrium value in O_2 consumption when it was wetted with artificial rain. Each plot in Fig. 12 is the mean of two experiments except for the results for 30 mm fleece length (Fig. 12 c) in which the plots are each a mean of four experiments. When sheep By had a fleece 7 mm long it showed an initial increase of O_2 consumption on exposure to rain from 35.6 to 50.8 l. O_2/h, and thereafter the O_2 consumption fell by 5 - 6 l./h and this was followed by a slight secondary rise in O_2 consumption. On stopping the rain O_2 consumption fell rapidly and 100 min after the rain stopped it was 33.7 l. O_2/h. This value was slightly below the initial value. Sheep Fr at a fleece length of 14 mm showed an initial decrease in O_2 consumption when the rain started. This decrease occurred during the

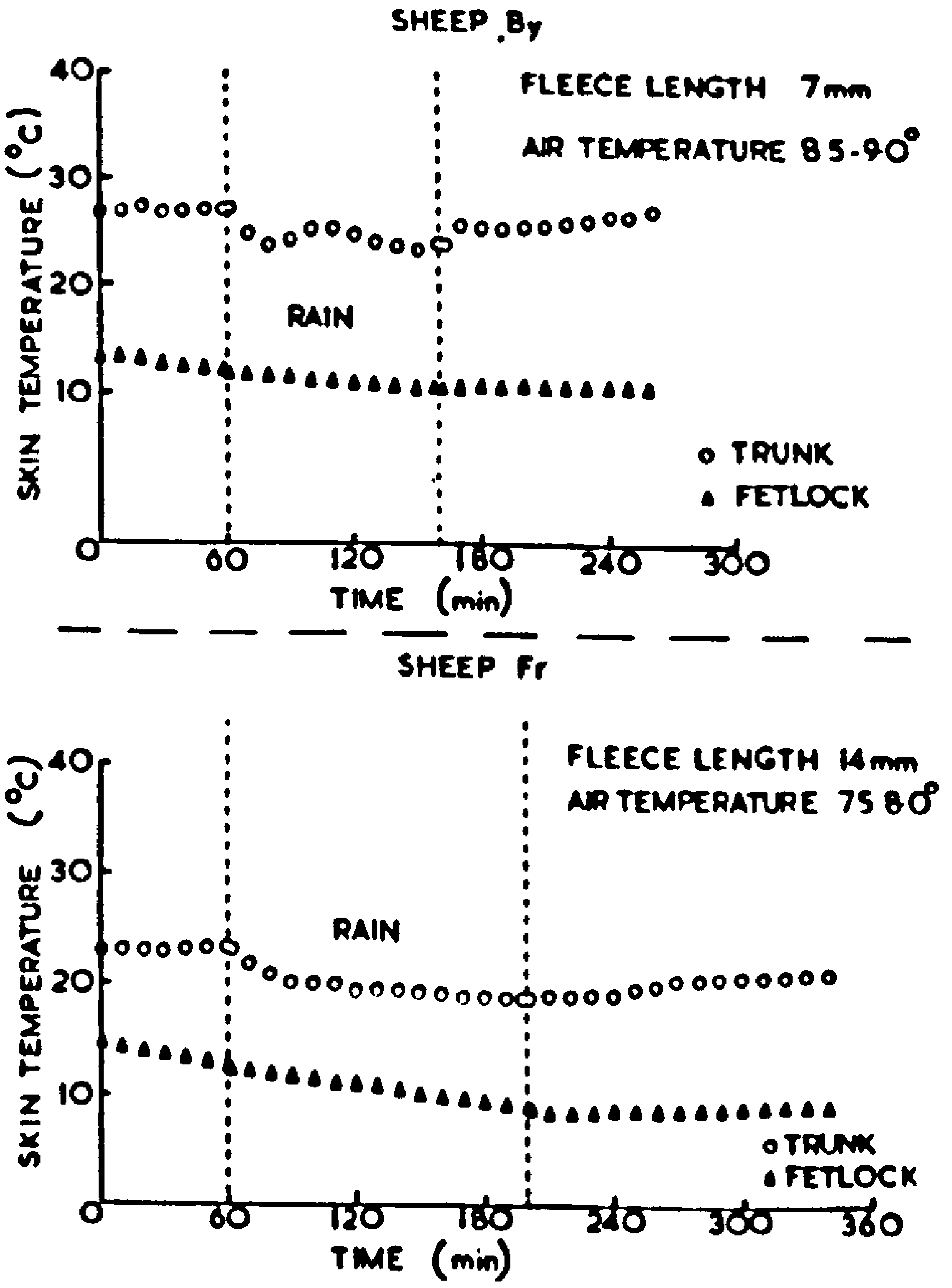


Fig. 13 A & B

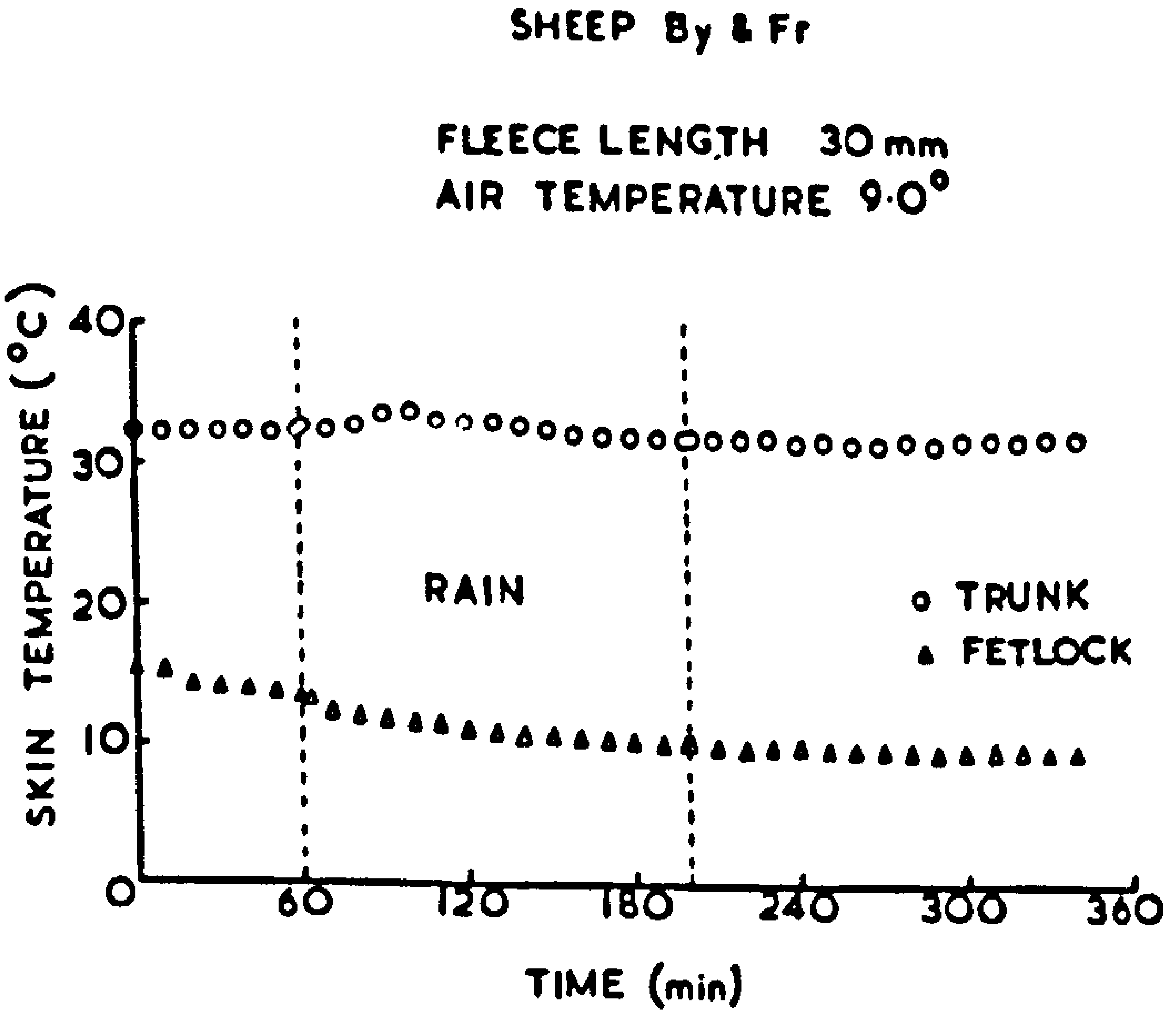


Fig. 13 C

Fig. 13. Changes in the skin temperatures of sheep By and Fr with fleece lengths of 7 mm (A), 14 mm (B) and 30 mm (C) in response to the application of rain at a rate of 0.4 in./h.

Table 8 a. The effect of artificial rain on the mean skin temperature of the trunk and of the legs of two sheep

(Each observation is the mean of two exposures)

Skin temperature	Animal	Fleece length (mm)	Wind speed (m.p.h.)	Air temperature (°)	Skin temperature (°) - minutes after exposure to artificial rain						
					Before	5	10	20	40	80	140
Sites on trunk	By	7	0.6	8.5 - 9.0	26.9	25.8	24.5	23.6	25.0	23.3	-
	Fr	14	0.6	7.5 - 8.0	23.5	22.6	21.8	20.9	20.0	19.5	19.1
	By & Fr	30	0.6	9.0	32.6	32.4	32.3	32.5	33.6	32.5	31.6
Fetlock, both sides	By	7	0.6	8.5 - 9.0	11.9	11.5	11.4	11.3	11.0	10.5	-
	Fr	14	0.6	7.5 - 8.0	12.5	12.1	12.0	11.8	11.5	10.5	9.0
	By & Fr	30	0.6	9.0	13.0	12.4	12.0	11.6	11.2	10.3	9.8

first 40 min and thereafter a slow increase in O_2 consumption occurred over the remaining 100 min during which rain was applied. On switching off the rain an increase of short duration was noted, and this was followed by a relatively steady O_2 consumption over the remaining 130 min of the experiment. Sheep By and Fr, both with 30 mm fleece lengths (Fig. 12 c) showed an initial increase in O_2 consumption when the rain was switched on followed by a decrease of 4.2 l. O_2/h extending over 90 min. After this decrease in O_2 consumption a rise of 2.9 l./h was noted over the remaining 40 min of wetting. On switching off the rain a very slight increase occurred in the next 10 min followed by a sudden decrease of 5.8 l. O_2/h, after which O_2 consumption values were fairly stable but with a slight tendency to decrease.

As will be shown later the level of O_2 consumption or heat production can be related to skin temperature levels. Using this relationship as a basis, O_2 consumption (Fig. 12), can be interpreted with reference to the skin temperatures for the same trials (Fig. 13 and Table 8 a). As shown in the results for sheep By when carrying 7 mm of fleece, a sudden increase in O_2 consumption at the onset of rain was associated with a decrease in mean trunk temperature. The decrease in O_2 consumption over the period 80 - 100 min of rain was associated with an increase in skin temperature (23.6 - 25.1°). The consequent increase in O_2 consumption was associated with a decrease in skin temperature. After the stopping of the rain O_2 consumption decreased and skin temperature rose.

Little relationship could be shown with sheep Fr at a fleece length of 14 mm between O_2 consumption and skin temperatures. In this experiment it was difficult to explain why O_2 consumption over the whole of the rain period was lower than in either the initial or final dry periods.

With both sheep By and Fr at a fleece length of 30 mm, little variation in skin temperature was noted although it was significant that the trough in O_2 consumption in the rain period was associated with a slight increase in skin temperature.

(5) Discussion and conclusions. From the equilibrium experiments it can be concluded that the responses in O_2 consumption to changes in wind and ambient temperature environments were virtually complete within 40 - 50 min. Metabolic changes in response to changes in the infrared radiation environment were slower than those for wind or ambient temperature but were virtually complete after 60 min. The results with artificial rain are difficult to interpret because contrary to results of experiments in which air velocity, air temperature and radiant temperature were changed, there appeared to be no period in which a stable O_2 consumption occurred. Any decrease in O_2 consumption on wetting could possibly result from two different causes. The rain droplets were very small and the outside of the fleece tended to become saturated with the interior remaining dry. The wetting of the outside of the fleece may have acted as a seal and have minimized convectional heat losses from the sheep. The second possibility is that heat was liberated in the fleece when water was applied. Hedges (1926), Speakman (1944) and Bligh (1963) have shown that when the humidity of a fleece is raised there is an exothermic effect. This exothermic effect can be quite considerable and its limits have been shown by Hedges (1926) to be 24 cal/g of wool when the relative humidity of the fleece is raised from 0 to 100%.

Trunk skin temperatures responded quickly to changes in environment and were normally stable within 10 min of the change except for the rain equilibration experiments in which a slight rise in trunk skin temperature occurred in some instance up to 20 min after the rain began. Fetlock skin temperatures only responded slowly and occasionally they did not appear to

Table 9. Errors attached to estimates of the O_2 consumption by four tracheostomized and two masked sheep obtained by the Douglas bag method

Animal	No. of experiments	Mean O_2 consumption (l./h)	No. of degrees of freedom within experiments	Estimated standard deviation of O_2 consumption (l./h)	Coefficient of variation (%)
Yl	44 T	40.5	112	±2.49	±6.17
Ct	7 T	18.9	14	±0.90	±4.77
Zk	9 T	16.2	19	±1.24	±7.70
Cs	69 T	20.6	178	±1.00	±4.68
Fr	24 M	33.6	48	±3.10	±9.23
By	24 M	44.5	48	±2.92	±6.55

T = tracheostomized sheep

M = sheep with face masks

be in a state of equilibrium.

From these observations it seemed that in making steady state experiments a period of 1 h following a change in the environment would suffice before beginning the measuring period. The exception to this was the work involving rain in which a 2-h wetting period was arbitrarily decided upon.

C. Measurement of the effects of steady state environments

1. Introduction. The results of 129 experiments with tracheostomized sheep and 48 experiments with sheep wearing masks, in which the animals were subjected to controlled environments for sufficient time for them to become accustomed to the environments are summarized in Table 9. In each of these experiments three or four consecutive determinations of O_2 consumption were made. The standard deviations given in the table represent the error attached to a single determination. The values ranged from ±0.90 to ±3.10 l. O_2/h, and the largest values tended to be for the sheep which on the average consumed most oxygen. Coefficients of variation ranged from about ±5 to about ±9%. The error attached to the mean of four consecutive determinations can be taken to be ±3% of the amount determined and the same error can be taken to apply to estimates of heat production made from the equations given earlier (Table 3).

2. Effect of air velocity on metabolism. Appendix II summarizes the results of sixty-six experiments made with sheep Cs, forty-six with sheep Yl, eight with sheep Zk and eight with sheep Ct in which the air velocity was varied. Most experiments were made with the side of the sheep presented to the wind, but where the hindquarters were presented the fact has been noted in Appendix II. The appendix also includes the results of experiments in which the effects of air velocity and of infrared radiation

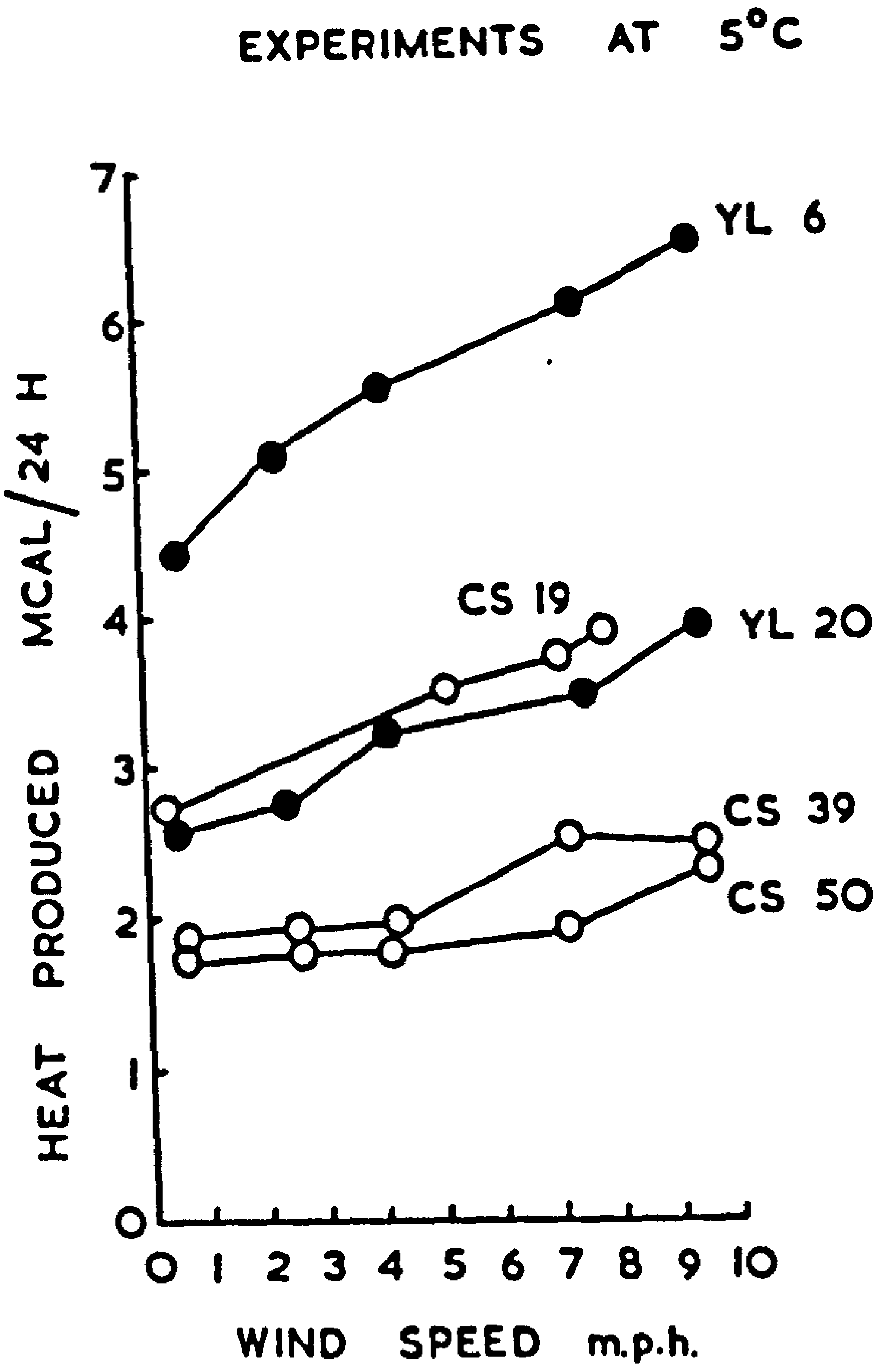


Fig. 14 A

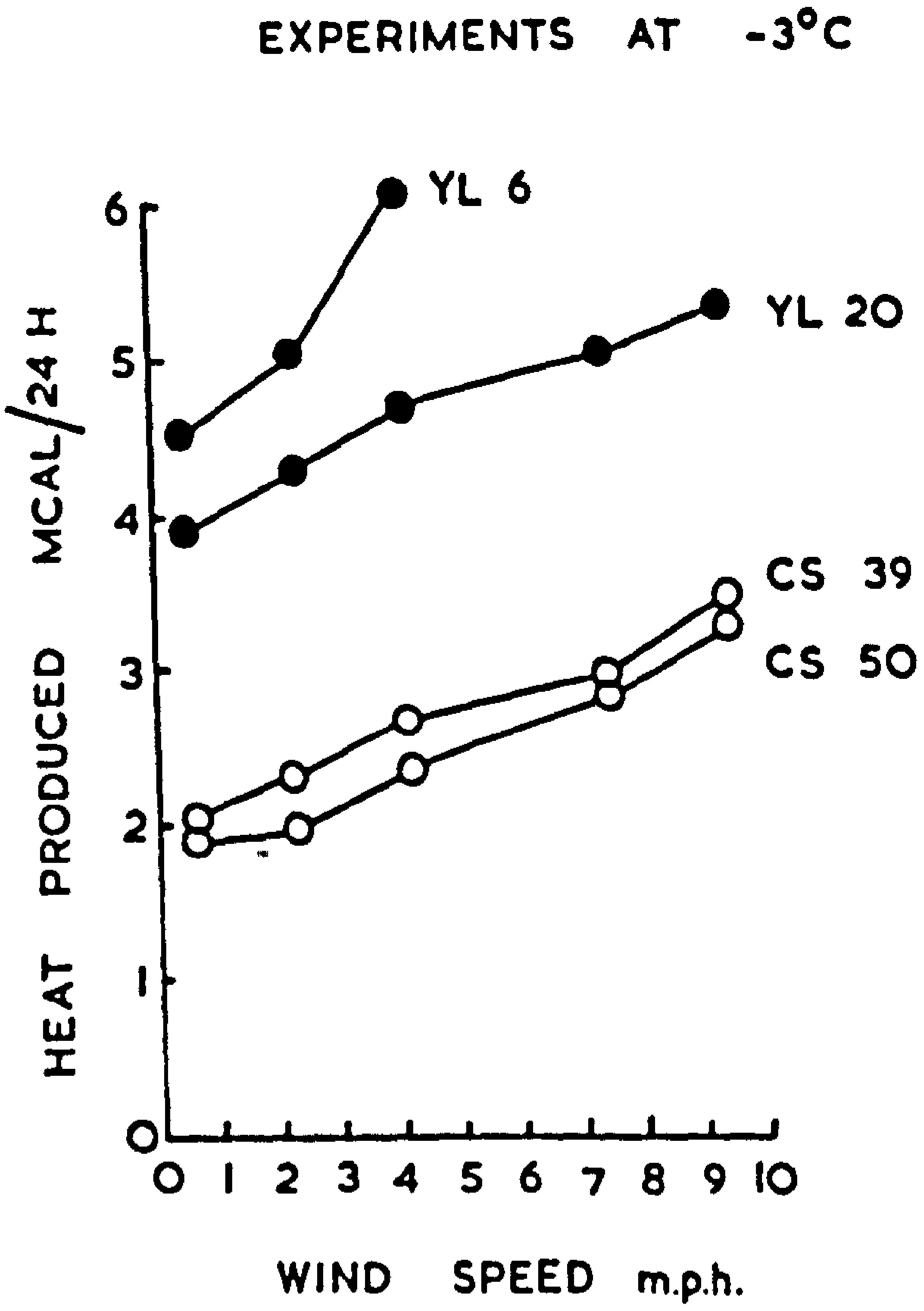


Fig. 14 B

Fig. 14. Changes in the heat production of sheep Cs (O) and Yl (●) with different fleece lengths on increasing the wind speed progressively from 0.6 to 9.6 m.p.h. at air temperatures of +5° (A) and -3° (B). Each line is labelled with the fleece length in mm carried by the sheep.

both together and separately were studied. Heat production has been expressed on a 24-h basis, although the measurements were in fact made over periods of 1 - $1\frac{1}{2}$ h.

(a) Heat production. The effects of air velocity on the heat production of sheep Cs and Y1 at air temperatures of $+5^{\circ}$ and -3° are shown in Figs. 14 a and 14 b. Each graph is labelled with the measured depth of fleece carried by the sheep when the experiments were made. For comparison Table 4 shows that the metabolism of sheep Cs in a thermoneutral environment was 1801 kcal/24 h and for sheep Y1, 1892 kcal/24 h. When the air temperature was 5° the metabolism of sheep Cs with a fleece depth of 39 - 50 mm was unaffected by the wind until the air velocity exceeded 4.2 m.p.h. It appears that this sheep was at or above its critical temperature at wind speeds lower than 4.2 m.p.h. When the fleece depth was 19 mm the total heat production was elevated to 2716 kcal/24 h at 5° even though the wind speed was only 0.2 m.p.h. At 5° sheep Y1 with shorter fleece lengths was never exposed to an environment which did not elicit a metabolic response, i.e. the heat production measured in each experiment was greater than that measured in the thermoneutral zone in a respiration chamber. With sheep Y1 at a temperature of -3°, when bearing a fleece 10 mm in depth, no observations were made at a wind speed greater than 4.2 m.p.h. At 4.2 m.p.h. and at -3°, this sheep produced 6271 kcal/24 h, i.e. 3.3 times that produced in a thermoneutral environment and 5.4 times the 1159 kcal/24 h which it produced when starved in a thermoneutral environment (Blaxter, 1962 b). This was probably not the maximal metabolism of which this sheep was capable for as shown in Appendix II, rectal temperature was maintained under these conditions. It was, however, thought at the time that the obvious strain

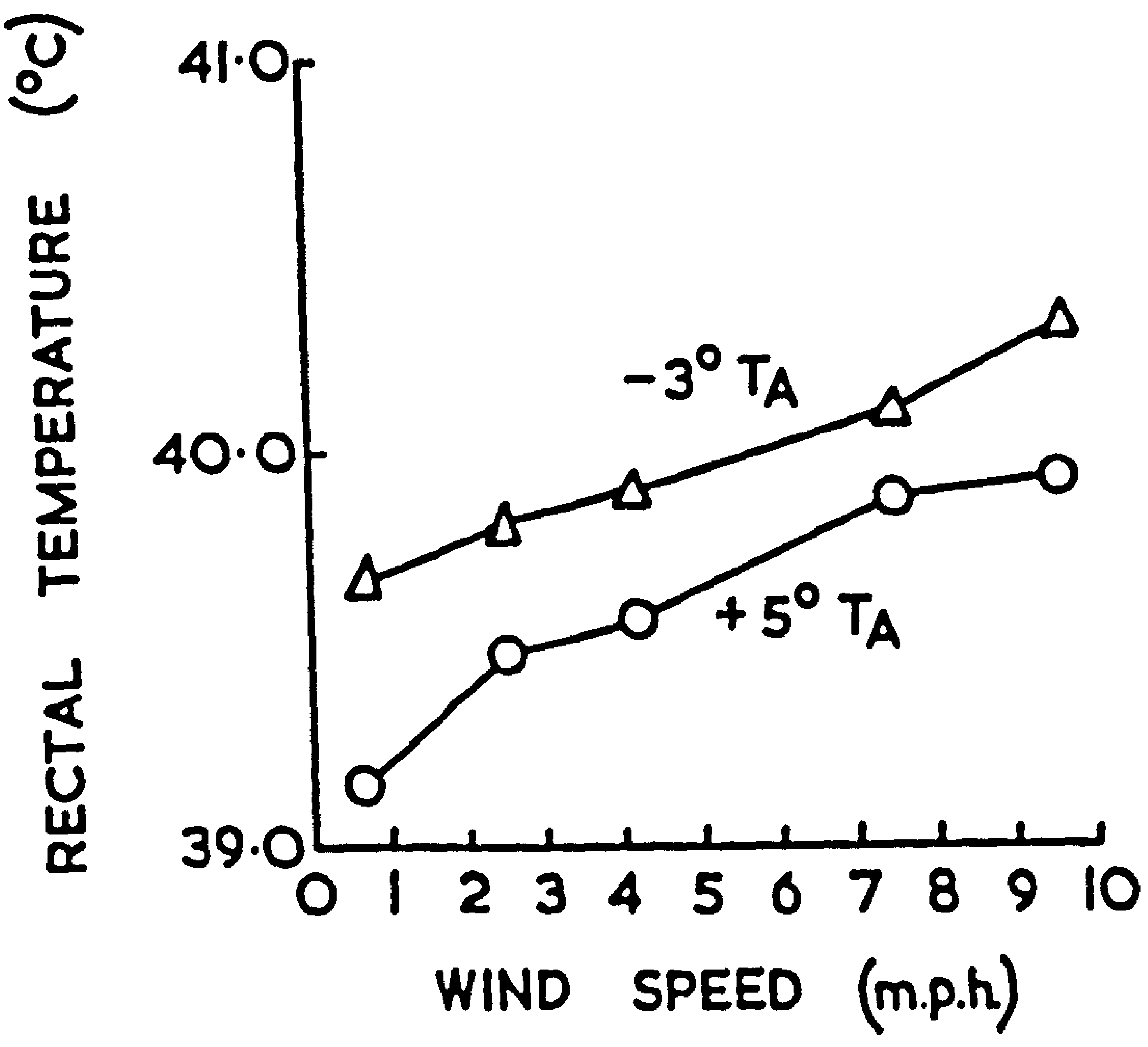


Fig. 15. The effect of increasing the wind speed progressively from 0.6 to 9.6 m.p.h. at air temperatures (T_A) of -3° (△) and +5° (O) on rectal temperature.

Table 10. Insulation values of the tissues of sheep at different wind speeds and air temperatures ($^{\circ}C \times 10^{-3}/kcal/m^2/24\ h$)

Sheep	Fleece thickness (mm)	Air temperature (°)	Wind speed (m.p.h.) 0.6	2.5	4.1	7.5	9.6
			($^{\circ}C \times 10^{-3}/kcal/m^2/24\ h$)				
Cs	39	5.0	5.1	4.6	6.1	5.2	6.9
	50	5.0	5.7	6.7	7.6	7.6	6.5
	39	-3.0	7.6	8.1	7.6	7.9	5.6
	50	-3.0	6.5	7.0	6.6	5.8	8.5
Yl	6	5.0	3.0	3.0	2.9	3.3	2.7
	20	5.0	4.1	4.3	4.1	4.2	4.0
	20	-3.0	3.4	3.3	3.3	3.5	3.7
	10	-3.0	3.8	3.6	3.4	-	3.9

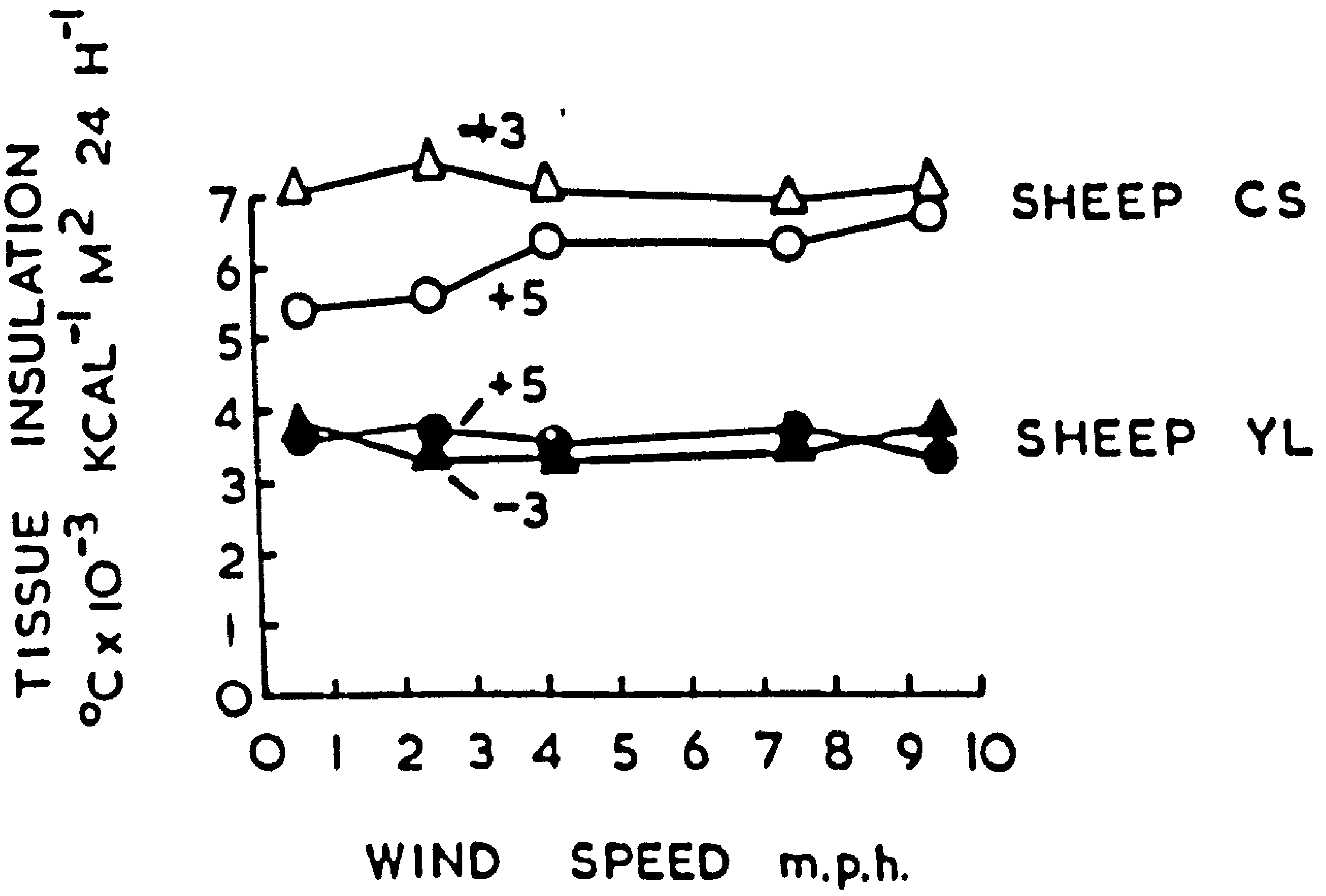


Fig. 16. The effect of wind speed on the tissue insulation of sheep Cs (△ O) and Yl (▲ ●) at air temperatures of +5°(O ●) and -3° (△ ▲).

On the recommendation of the external examiner, where the expression

$$°C \times 10^{-3}\ KCAL^{-1}\ M^{2}\ 24\ H^{-1}$$

is used it is preferable to alter this to the following -

$$°C \text{ per cal per } M^{2} \text{ per 24 h.}$$

on the animal was so great that it might not survive exposure to higher air velocities for any useful period. It is of interest that sheep By in experiments with artificial rain produced heat at the rate of 8432 kcal/24 h. In this experiment rectal temperature was not maintained but its heat production was 4.6 times its heat production in a thermoneutral environment.

(b) Effect of air velocity on rectal temperature. Appendix II shows that at a constant air temperature an increase in air velocity resulted in an increase in rectal temperature. Rectal temperatures were also elevated when the sheep were exposed to lower air temperatures (-3°). This effect of air velocity and air temperature is shown in Fig. 15. A similar increase in the rectal temperatures of lambs exposed in short term experiments to cold has been noted by Alexander (1961)a). The validity of this increase in rectal temperature in short-term exposure will be discussed later in relation to the effect of longer term exposure to cold.

(c) The insulation of tissues in winds. The insulation of the tissues was calculated in each experiment where there was evidence from temperature measurements that the limbs were vasoconstricted. Table 10 summarizes the data obtained in 39 experiments with sheep Cs and Y1 (see Appendix II). In these experiments wind speed was varied at each of two environmental temperatures (+5° and -3°). Fleece length had no apparent systematic effect on tissue insulation on either sheep in those experiments which elicited a metabolic response to cold. Table 10 and Fig. 16 also show that wind speed did not appear to affect tissue insulation except in sheep Cs when air speed was low and air temperature +5° and no metabolic response was obtained.

Table 11. The tissue insulation I_T of sheep in environments in which the temperature was lower than the critical temperature

Animal	Breed	No. of determinations	Tissue insulation (units)*	Reference
Cs	Cheviot	36	6.29	Present Douglas bag experiments
Cs	Cheviot	1	6.13	Present chamber experiments
Cs	Cheviot	3	6.26	1959 chamber experiments (1)
Jn	Cheviot	4	8.72	1959 chamber experiments (1)
Jr	Cheviot	15	7.34	Present mask experiments
Zd	Blackface	2	5.80	Present Douglas bag experiments
Zd	Blackface	4	5.35	1959 chamber experiments (1)
Dg	Blackface	3	5.90	1959 chamber experiments (1)
Ct	Blackface	3	5.87	Present Douglas bag experiments
Yl	Downcross	22	3.62	Present Douglas bag experiments
3	Downcross	11	3.40	1956 chamber experiments (2)
23	Downcross	12	3.33	1956 chamber experiments (2)
23	Downcross	2	3.90	1956 chamber experiments (3)

Table 11 (continued)

Animal	Breed	No. of determinations	Tissue insulation (units)*	Reference
By	Mixed**	45	5.03	Present mask experiments
Re	Mixed**	9	4.96	Present mask experiments
Fr	Mixed**	51	6.37	Present mask experiments

1. Armstrong et al. (1960).
2. Blaxter et al. (1959 b).
3. Blaxter et al. (1959 a).

* Unit I_T = $^{o}C \times 10^{-3}/kcal/m^2/24$ h

** Border Leicester x Cheviot with some Clun and Suffolk blood.

Table 12. The regression of external insulation (I_E) on fleece length (F) at different wind speeds determined with sheep Y1 and sheep Cs

Wind speed m.p.h.	No. of observations	Regression:* $I_E = a + b (F)$ (mm)	Standard error of regression coefficient (insulation units)	Standard deviation of estimated values (insulation units)
0.6	10	$I_E = 4.79 + 0.463 F$	±0.054	±1.55
2.5	7	$I_E = 4.05 + 0.397 F$	±0.078	±1.71
4.2	6	$I_E = 3.17 + 0.331 F$	±0.042	±0.90
7.5	9	$I_E = 2.92 + 0.348 F$	±0.050	±1.58
9.6	7	$I_E = 2.16 + 0.275 F$	±0.078	±1.21

* Unit I_E = $^\circ C \times 10^{-3}/kcal/m^2/24\ h$

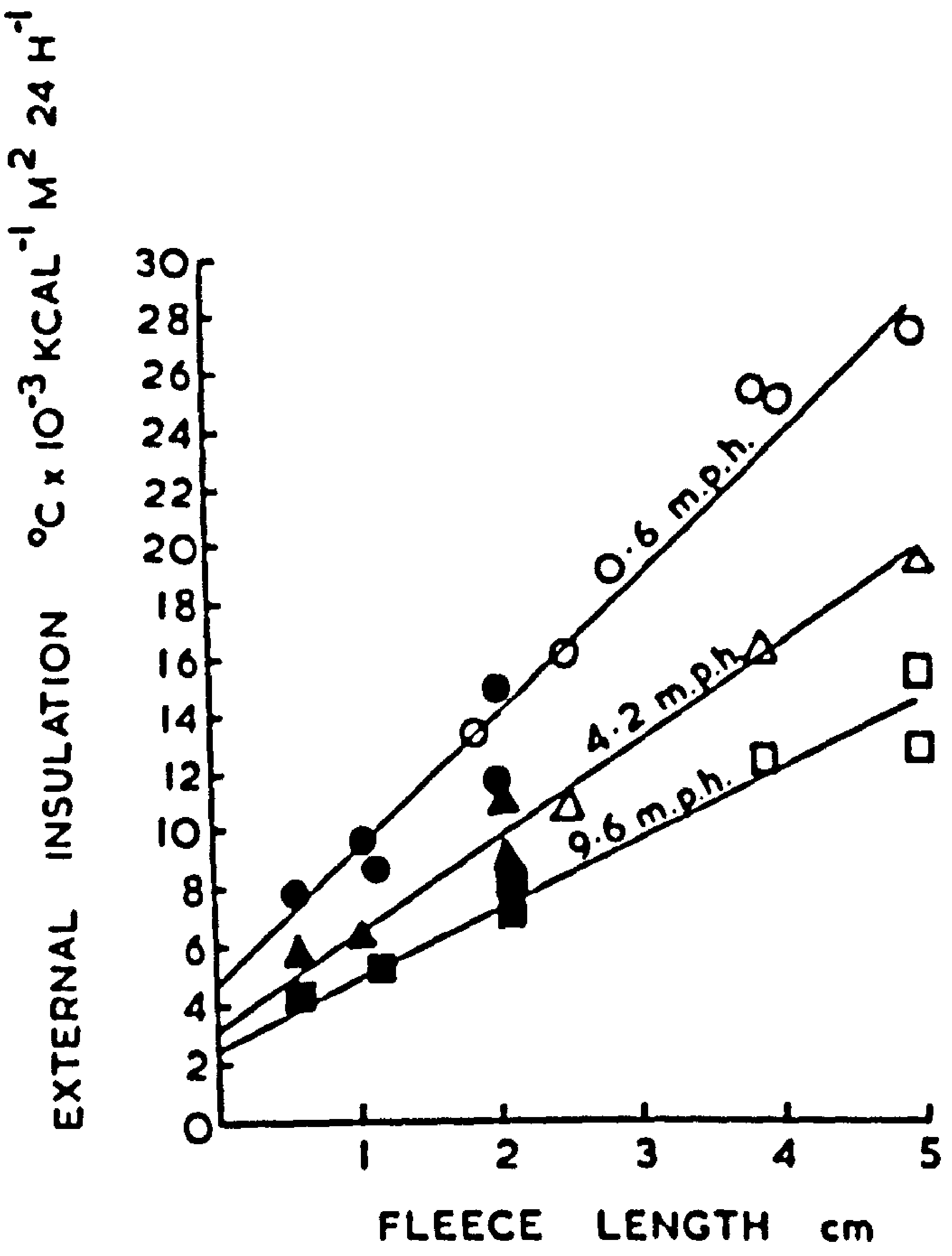


Fig. 17. The external insulation of sheep Cs (open symbols) and Y1 (closed symbols) with different fleece lengths at wind speeds of 0.6 (O ●), 4.2 (Δ ▲) and 9.6 (□ ■) m.p.h.

There was obviously a marked difference between the tissue insulations of the two sheep, the value for sheep Cs being 6.29 and that for sheep Yl being 3.62. The mean values for the tissue insulation of all the sheep used in these experiments and the results obtained by other workers are shown in Table 11. Together these results show that the tissue insulation of the Downcross sheep ranged from 3.3 to 3.9 insulation units, that of the Scottish Blackface sheep from 5.4 to 5.9 and of Cheviot sheep from 6.1 to 8.7 insulation units. Sheep By, Fr and Re could not be allocated to any breed type being obviously of mixed ancestry. Measurements made with the same individual at different times using different techniques gave similar values, even though the interval between measurements may have been a number of years. Although numbers of sheep were small, the values suggest real differences in the tissue insulation of different breeds. In this regard Ryder (1955) has shown that the Cheviot sheep has a poorly developed mid-dermal blood vessel plexus, whereas this is moderately well developed in the Down breeds. Ryder did not study the skins of Blackface sheep, and whether this arrangement of the plexus in relation to tissue insulation is a causal relationship or just fortuitous is not known.

(d) <u>The external insulation (I_E) in winds</u>. This section describes the effect of different wind velocities on the external insulation of the sheep. Table 12 summarizes the results of regression analysis of I_E on fleece length at five wind speeds, and individual results for three of these wind speeds are shown in Fig. 17. The results were obtained with sheep Cs and Yl in the controlled climatic room (Findlay <u>et al</u>. 1959), in which wall temperatures were the same as the air temperature and the infrared emissivity of the walls was 0.98. In the statistical analysis

Table 13. Linear regression of external insulation (I_E) on fleece length at wind speed 0.6 m.p.h.

Sheep	Fleece length (F) (mm)	External insulation (I_E) ($^{o}C \times 10^{-3}/kcal/m^2/24\ h$)
Y1	5.8	7.8
	10.4	9.6
	11.7	8.7
	20.4	11.7
	20.4	15.2
Sheep mean	13.74	10.60
Cs	18.8	13.4
	25.3	16.2
	39.0	25.6
	40.8	25.0
	50.3	27.2
Sheep mean	34.84	21.48
Mean of both sheep	24.29	16.04

Sum of squares

F^2	I_E^2	$F \times I_E$	Animal F^2	Animal $F \times I_E$	Animal I_E^2
7820.27	3058.82	4843.97	7013.07	4470.04	2868.75
5900.04	2572.82	3896.12	5900.04	3896.12	2572.82
1920.23	486.00	947.85	1113.03	573.92	295.93

Analysis of variance

Source of variation	d.f.	F^2	$F \times I_E$	I_E^2	b_{xy}
Total	9	1920.23	947.85	486.00	
Animals	1	1113.03	573.92	295.93	
Residual	8	807.20	373.93	190.07	0.46324

Table 13 (continued)

Regression analysis of residual variance

Source of variation	d.f.	Sum of squares	Mean square	F
Residual	8	190.07		
Regression	1	173.22	173.22	71.87^{***}
Deviations	7	16.85	2.41	

*** P 0.01

Regression $Y = \bar{Y} + b\,(X - \bar{X}) = \underline{4.79 + 0.463\,X}$

$$\text{S.E. of regression equation} = \pm\sqrt{\frac{2.41}{807.20}}$$

$$= \pm 0.054$$

Table 14. The external insulation (I_E) of sheep in winds which impinged on their sides or on their hindquarters

Sheep	Fleece length (mm)	Wind speed (m.p.h.)	External insulation (I_E) when the sheep presented to the wind	
			Left side	Hindquarters
			(Units)*	
Cs	6	8.9	3.7	3.8
Yl	6	9.6	4.9	4.5
Cs	11	6.2	5.3	6.2
Yl	35	8.9	12.1	13.1
Cs	39	9.6	9.9	13.6

* Unit insulation = $^{\circ}$C x 10^{-3}/kcal/m^{2}/24 h

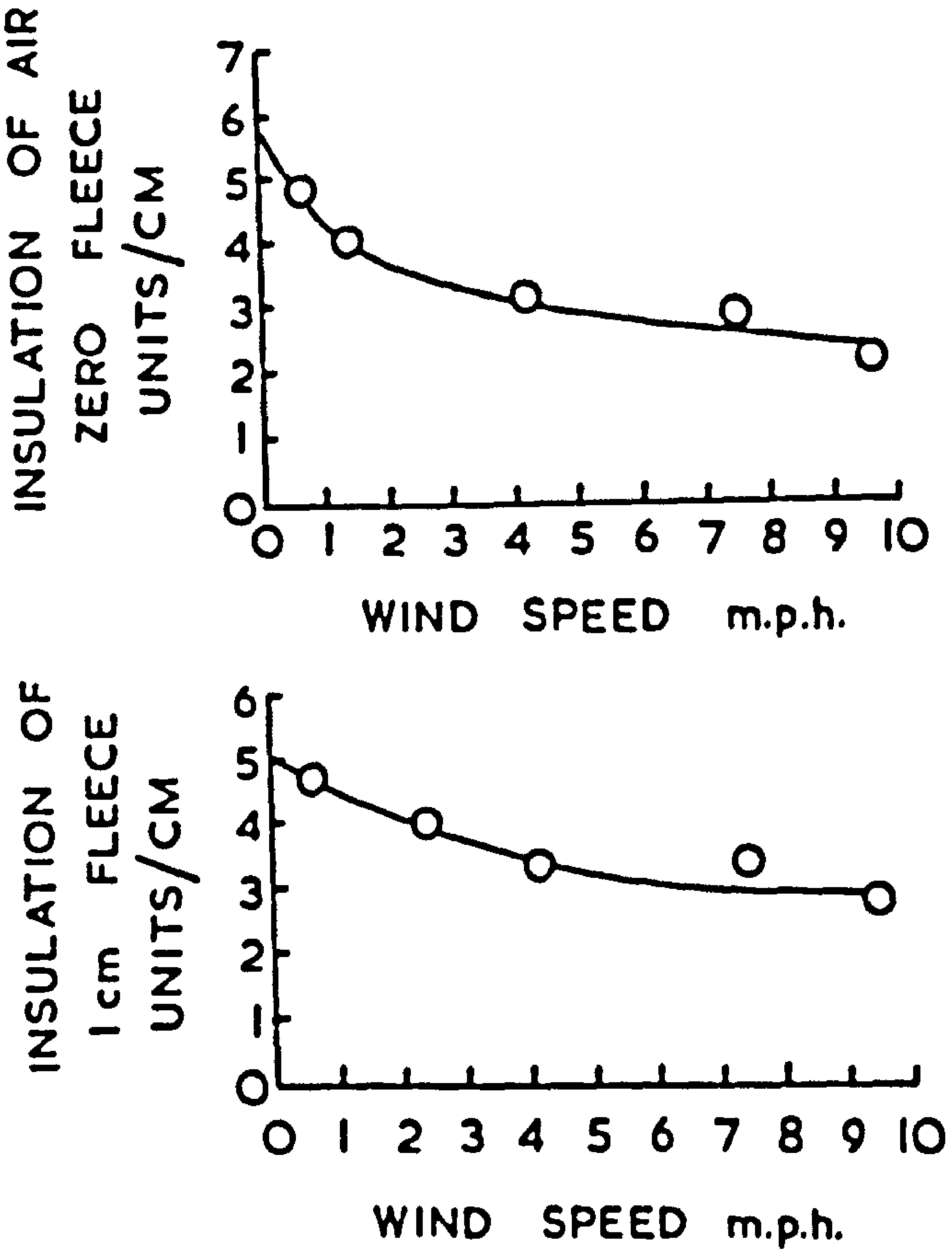


Fig. 18. The effect of wind speed on the calculated air insulation (A) and the calculated insulation of 1 cm fleece (B).

the within-sheep sum of squares and products were removed after taking out differences due to the individuality of sheep. An example of the statistical analysis used is given in Table 13. The results show that with a wind of 0.6 m.p.h. insulation increased by 0.46 units per mm increase of fleece length, whereas when the wind speed was 9.6 m.p.h., the external insulation increased by only 0.27 units. This means that the wind must have penetrated the fleece and that the destruction of insulation on increasing the wind speed from 0.6 to 9.6 m.p.h. was 42%. Fig. 18 shows the effects of wind speed on the calculated insulation of the air and on the insulation of 1 cm of fleece. There was no indication that the relationship between external insulation and fleece length was other than linear over the fleece lengths and wind speeds used in this experiment.

(e) The effect of body position on external insulation in winds. The results of the five comparisons which were made between the external insulations of sheep when winds impinged on their sides and on their hindquarters are summarized in Table 14. These experiments include the two shown in Appendix II and the three shown in Figs. 5 a, 5 b, and 5 c. When the fleece was very short the external insulation was much the same whether the hindquarters or the side were presented to the wind. At 6 mm fleece length the maximum difference in external insulation between the two was only 0.4 insulation units. With longer fleeces, hindquarter presentation resulted in a higher external insulation, being maximal in sheep Cs with a fleece length of 39 mm and the difference being 3.7 insulation units. The greater external insulation for hindquarter presentation than for side presentation when the fleece was long, suggests that less destruction of fleece insulation occurred in the former position.

Table 15. The heat production, external insulation and fleece surface temperatures of sheep Cs and Yl at wind speeds of 0.6 and 9.6 m.p.h. and when modified by infrared radiation

Sheep	Fleece length (mm)	Air temperature* (°)	Wind speed (m.p.h.)	Infrared radiation	Total heat production (kcal/ 24 h)	External insulation (Units)**	Fleece surface temperature (°)
Cs	41	0.0	0.6	No radiation	2114	25.0	0.1
			0.6	Radiation	1625	39.1	31.9
			9.6	No radiation	2500	21.0	-0.2
			9.6	Radiation	1675	35.1	16.7
Yl	12	0.0	0.6	No radiation	4630	8.7	8.1
			0.6	Radiation	3020	16.0	32.6
			9.6	No radiation	6200	5.2	2.2
			9.6	Radiation	3684	10.1	13.5

* The temperature of the climatic room was controlled within $\pm 0.5^{\circ}$ 2

** Units of external insulation = $^{\circ}C \times 10^{-3}/kcal/m^{2}/24\ h$

The profile presented to a wind when the hindquarters are diverted towards it is clearly less than when the sheep is side-on to the wind, and this suggests a causal relationship between the profile of the sheep exposed to the wind and the decrease in external insulation although this might be expected to operate irrespective of fleece length.

3. The effect of simulated radiation loads on metabolism. The results of the series of experiments with sheep Y1 and sheep Cs, in which the effect of infrared radiation on heat production and external insulation at wind speeds of 0.6 and 9.6 m.p.h. were studied, are given in Table 15, and Appendix II. With sheep Cs (41 mm fleece depth), when the wind increased from 0.6 to 9.6 m.p.h. heat production increased by 386 kcal/24 h in the absence of radiation and by 50 kcal in its presence. Radiation increased the external insulation by 14 units at both wind speeds. With sheep Y1 bearing a 12 mm depth of fleece, a wind of 9.6 m.p.h. compared with one of 0.6 m.p.h. increased heat production by 1570 kcal/24 h in the absence of radiation and by only 664 kcal/24 h in its presence. External insulation increased by 5 - 7 insulation units. As shown in Appendix II, the tissue insulation of sheep Y1 increased slightly when the wind increased, irrespective of radiation, but with sheep Cs tissue insulation fell markedly when radiation was applied at a wind speed of 0.6 m.p.h. and the values for this sheep suggest that it was partially vasodilated throughout the series of experiments.

These results show that variation in the infrared radiation intensity modify appreciably the animal's metabolism in wind. The precise amount of radiation impinging on the sheep was impossible to assess, but fleece surface temperature measurements were made using a radiometer. The results are shown in Table 15, and they emphasize the high fleece temperatures that

Table 16. The effect of rain on the heat production per unit area of sheep at wind speeds of 0.6 and 9.9 m.p.h.

Sheep	Fleece length (mm)	Air temperature (°)	Heat production (kcal/m²/24 h) Dry 0.6 m.p.h. (1)	Dry 9.9 m.p.h. (2)	Rain 0.6 m.p.h. (3)	Rain 9.9 m.p.h. (4)	(3) - (1)*	(4) - (2)**
By	2-3	6.8 - 8.5	3443	5007	5533	-	(2090)	-
Fr	3	7.6 - 10.0	3145	4169	4210	6100	1065	1931
By	4	9.1 - 9.9	3294	3811	4701	5413	1407	1602
Fr	4	6.9 - 8.2	2526	3641	3436	5015	910	1374
Fr	6	8.4 - 9.2	1898	2787	3154	3480	1256	693
Fr	6	8.7 - 9.4	1953	3202	2771	3629	818	427
By	9	6.8 - 8.4	2442	3251	3462	4471	1020	1220
By	9	6.5 - 7.7	2698	3095	3630	4425	932	1330
Fr	12	7.8 - 8.5	1241	1971	2531	2734	1290	763
Fr	12	7.4 - 8.0	1342	2013	2233	2748	891	735
By	14	7.5 - 8.3	1810	2383	2914	3363	1104	1280
By	14	7.2 - 7.6	1929	2507	2503	3472	574	965
						Mean	1024	1120

* Increase in heat production due to rain under still air conditions

** Increase in heat production due to rain under wind conditions

Table 17. The effect of rain on the external insulation of sheep at wind speeds of 0.6 and 9.9 m.p.h.

Sheep	Fleece length (mm)	External insulation units (I_E)*					
		Dry 0.6 m.p.h. (1)	Dry 9.9 m.p.h. (2)	Rain 0.6 m.p.h. (3)	Rain 9.9 m.p.h. (4)	(1) - (3)**	(2) - (4)***
By	2-3	5.42	2.06	1.80	-	3.62	-
Fr	3	5.45	2.38	2.77	0.96	2.68	1.42
By	4	4.09	2.32	2.28	1.25	1.81	1.07
Fr	4	6.52	2.76	3.12	1.51	3.40	1.21
Fr	6	7.86	3.17	3.25	1.78	4.16	1.39
Fr	6	7.00	2.50	3.65	1.27	3.35	1.23
By	9	6.83	3.57	4.16	1.66	2.67	1.91
By	9	6.73	3.86	4.13	2.52	2.60	1.34
Fr	12	12.41	5.72	5.66	2.95	6.75	2.77
Fr	12	13.42	6.16	6.28	2.94	7.14	3.22
By	14	9.60	5.18	4.04	2.16	5.56	3.02
By	14	9.03	5.21	5.34	3.09	3.69	2.12
	Mean‡	8.09	3.89	4.06	2.01	3.98	1.88

* External insulation units = $^{o}C \times 10^{-3}/kcal/m^{2}/24\ h$

** Decrease in external insulation due to rain under still air conditions

*** Decrease in external insulation due to rain under wind conditions

‡ Mean excludes results with sheep By with fleece length 2 - 3 mm

can arise under high radiation heat loads. The type of experiment described here, while difficult to transfer to natural environmental conditions, may well reflect what happens out-of-doors when solar radiation is absorbed and liberated as heat at the fleece surface.

4. The effect of artificial rain on energy metabolism. The results of the series of experiments with sheep By and sheep Fr in which the effect of artificial rain, falling at the rate of 0.4 in./h, on the heat production and external insulation at wind speeds of 0.6 and 9.9 m.p.h. are given in Tables 16 and 17. With both the sheep large increases in heat production were found when rain was applied irrespective of the rate of air movement. The largest increase was with sheep By at a fleece length of 2 - 3 mm. With this sheep at a wind speed of 0.6 m.p.h. rain increased heat production from 3443 to 5533 kcal/m^2/24 h. When, however, the wind speed was increased to 9.9 m.p.h. under rain conditions, the metabolism rose to 5762 kcal/m^2/24 h during the first 15 min of the collection period, but dropped rapidly thereafter to 4644 kcal/m^2/24 h whereupon the sheep showed signs of collapse and had to be removed and revived. Under these conditions rectal temperature fell rapidly to 36.7° from the initial value of 39.0°, and possibly higher rates of metabolism may have occurred in the period just before the measurements were made, although this is doubtful since the maximum recorded level of heat production (5762 kcal/m^2/24 h) was very close to the summit metabolism of lambs (4800 - 6000 kcal/m^2/24 h) as recorded by Alexander (1962 b). In the remaining experiments increases in heat production with rain ranged from 574 to 1407 kcal/m^2/24 h in the low air movement environment and from 427 to 1931 kcal/m^2/24 h with high speed air movement. The greater increases were associated with the shorter fleece lengths. Whether the effect of rain and wind on heat production were additive in their effects cannot be deduced from the means

in Table 16, because there was a tendency for higher air temperatures to occur at higher rates of air movement. The results given in Table 17 in the form of external insulations enable the effects of wind and rain to be separated. As shown in Table 17, the mean decrease in external insulation due to rain under still air conditions (0.6 m.p.h.) was 3.98 insulation units, whereas under windy conditions (9.9 m.p.h.), the insulation decrease was only 1.88 insulation units. The fact that these two values (3.98 and 1.88) were different shows that the effect of rain was less under windy conditions and wind and rain were apparently non-additive in their effect in decreasing the external insulation. This non-additive effect may have been due in part to the greater binding effect of a wet fleece preventing full penetration of the wind into the fleece. The mean percentage decreases in insulation for wind, rain and wind plus rain over the mean still air external insulation were 51.9, 49.8 and 75.2% respectively. The extent to which wind and rain together can destroy the insulation of the fleece is quite apparent, the lowest recorded insulation, 0.96 insulation units, was recorded under these conditions and represented a decrease of 82% from the insulation value obtained in still air conditions with no rain.

5. Discussion and conclusions. Levels of metabolism of the sheep used were greatly increased by low air temperatures and increased air velocity. The extent to which high wind speeds increased metabolism was dependent on the air temperature. The metabolism of sheep Cs with fleece lengths of both 39 and 50 mm was unaffected by wind speeds up to 4.2 m.p.h. at 5° but when the air temperature was reduced to -3° an increased metabolism was noted at all rates of air movement. Rectal temperature was elevated on increasing the air velocity, which is the opposite of the relationship

between rectal temperature and air velocity noted by Wheeler et al. (1963) in long-term outdoor trials. The increased rectal temperatures associated with increased air velocity may be a reflection of the short term nature of these trials and represents a body storage of heat associated with increased metabolism, and this might have disappeared if the trials had lasted for longer periods.

Tissue insulation measured on sheep below their critical temperature was unaffected by fleece length, wind or rain. There did, however, appear to be a marked difference between different breeds in their tissue insulation, and results obtained in these trials agreed well with insulation values measured by other workers.

The external insulation of the sheep was dependent not only on fleece length but also on the wind velocity and body position with respect to the direction of the wind. The mean value of 4.63 insulation units/cm depth of fleece, excluding the air insulation, at a wind speed of 0.6 m.p.h. is lower than the values of 6.7 to 8.3 recorded by Blaxter et al. (1959a) but at least some parts of this difference must have been due to the lower wind speed (0.2 m.p.h.) operating in their respiration chambers.

Infrared radiation heat loads on a sheep below its critical temperature resulted in lower levels of metabolism both at high and low levels of air movement. Both fleece surface and skin temperatures were elevated when the sheep were radiated with infrared lamps. Without knowing the incoming level of infrared radiation it is impossible to compare these results with similar effects produced by solar radiation.

The heat production of sheep, subjected to artificial rain was greater than when they were under the same conditions with dry fleeces.

It was found also that the external insulation of sheep subjected to rain was lower than when the sheep were dry, but in contradiction to Alexander's (1962 a) results obtained with lambs the effects of rain and wind were non-additive. Indeed when the fleece was wet the effect of wind appeared to be lower than would have been expected if the effects of wind and rain had been additive.

D. Outdoor experiments under conditions comparable to those employed in the controlled environment studies

1. Introduction. These experiments were made for two reasons: firstly, to assess the extent to which the experimental results obtained from the indoor controlled climate experiments could be applied to natural outdoor conditions, and secondly, to measure the effect of solar radiation and natural rain on the energy metabolism of sheep. The results of studies on the effect of solar radiation are given later in section E.

Unfortunately the method of experimentation was bound to make the results obtained in some respects artificial in that the sheep were constrained for the collection of expired air and for the measurement of body temperatures and were not allowed to eat or move about as would occur in a free-grazing sheep. As already explained (p. 29) the sheep were also permanently orientated in one direction and could not adjust their body position with respect to the prevailing wind or the solar beam.

2. Environmental variation and stability. All the results for tests in which the sheep were below their critical temperature are shown in Appendix III. A relatively large range of environmental conditions

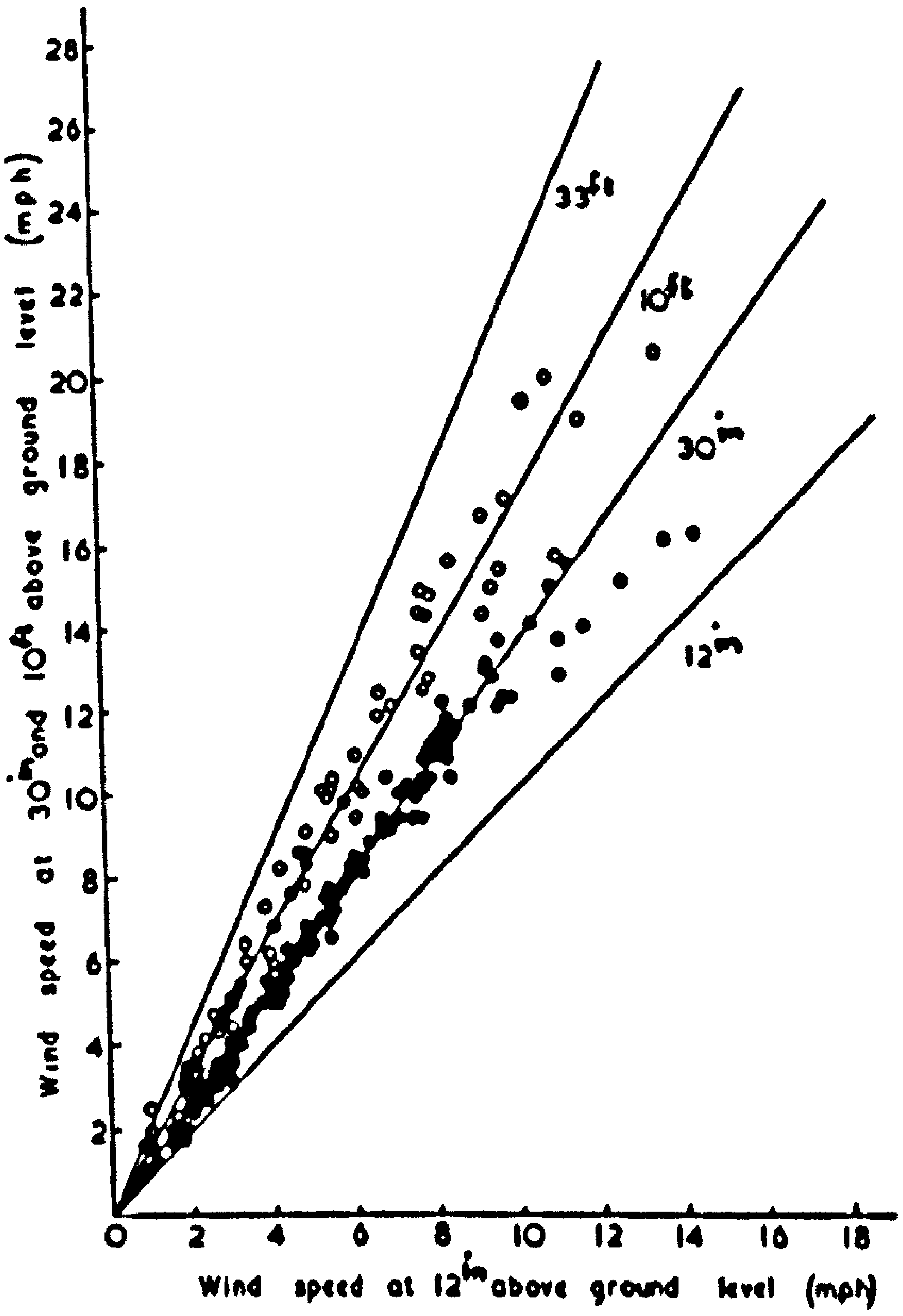


Fig. 19. The effect of height of anemometer above ground level on the wind speed recorded.

occurred, and the following ranges recorded; air temperature, -0.2 to 16.8°; wind velocity, 0.6 to 15.4 m.p.h.; solar radiation, 0.01 to 0.93 $cal/cm^2/min$. High wind speeds tended to be associated with higher than average air temperatures and higher solar radiation insolation. In any one day air temperature tended not to vary by more than ±2° and wind speed by not more than ±2 m.p.h. Solar radiation varied considerably over the experimental period each day especially under clear or partly cloudy sky conditions. Under heavy overcast conditions incoming solar radiation levels remained low and stable.

Very large variations were found to occur between the air velocity measured at the different heights of 12 in., 30 in. and 10 ft above ground level. These results are shown in Fig. 19, in which the predicted wind speed at the standard meteorological exposure height of 10 metres (35 ft) is included. This wind speed was calculated by adding 20% to the 10 ft exposure recordings, a correction factor which was obtained from the Handbook of Meteorological Instruments (1956). A standing sheep would normally be exposed to wind speeds at heights above ground level of 12 in. and 30 in., however, the wind speeds recorded at these heights are only 46 and 61% respectively of the wind speed computed for the 10-metre standard meteorological height, and this should be remembered when transposing any of the results presented in this section to areas of Great Britain for which wind speeds are available from Meteorological Office weather statistics.

3. Agreement of indoor and outdoor observations

(a) External insulation. For comparative purposes the external insulation of the sheep has been calculated in each of the 120 experiments. The results have been compared with the external insulation values

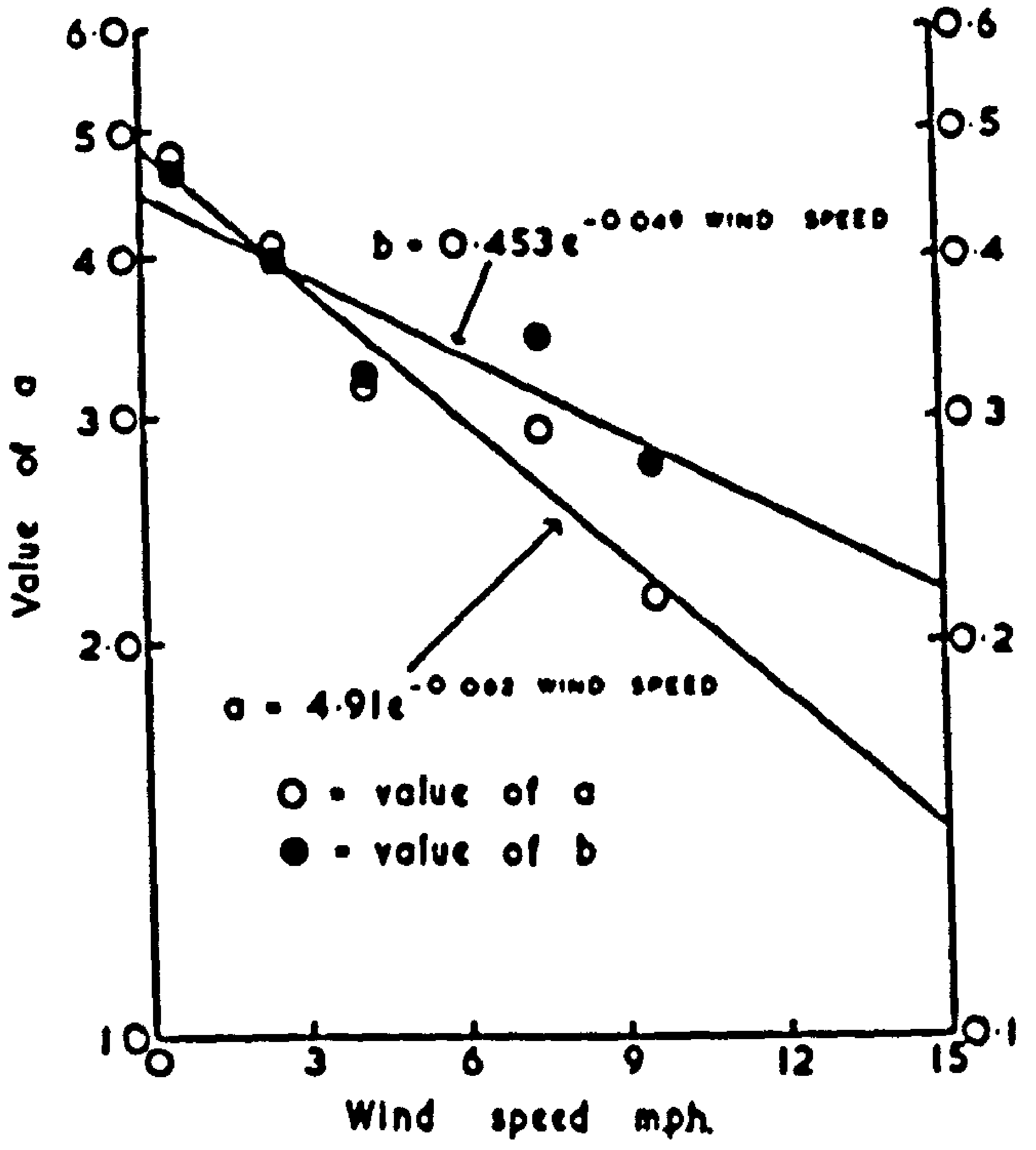


Fig. 20. The effect of wind speed on the factors "a" and "b" in the equation $I_E = a + bF$.

Table 18. Analysis of variance for factors "a" and "b" in the equation: $I_F = a + b^F$

Analysis of variance of log a

Source	d.f.	Sum of squares	Mean square	
Total	4	0.071103		
Regression	1	0.067396	0.067396	54.4^{**}
Error	3	0.003717	0.001239	

Analysis of variance of log b

Source	d.f.	Sum of squares	Mean square	
Total	4	0.028923		
Regression	1	0.024027	0.024027	14.7^{*}
Error	3	0.004896	0.001632	

** $P > 0.01$

* $0.01 > P > 0.05$

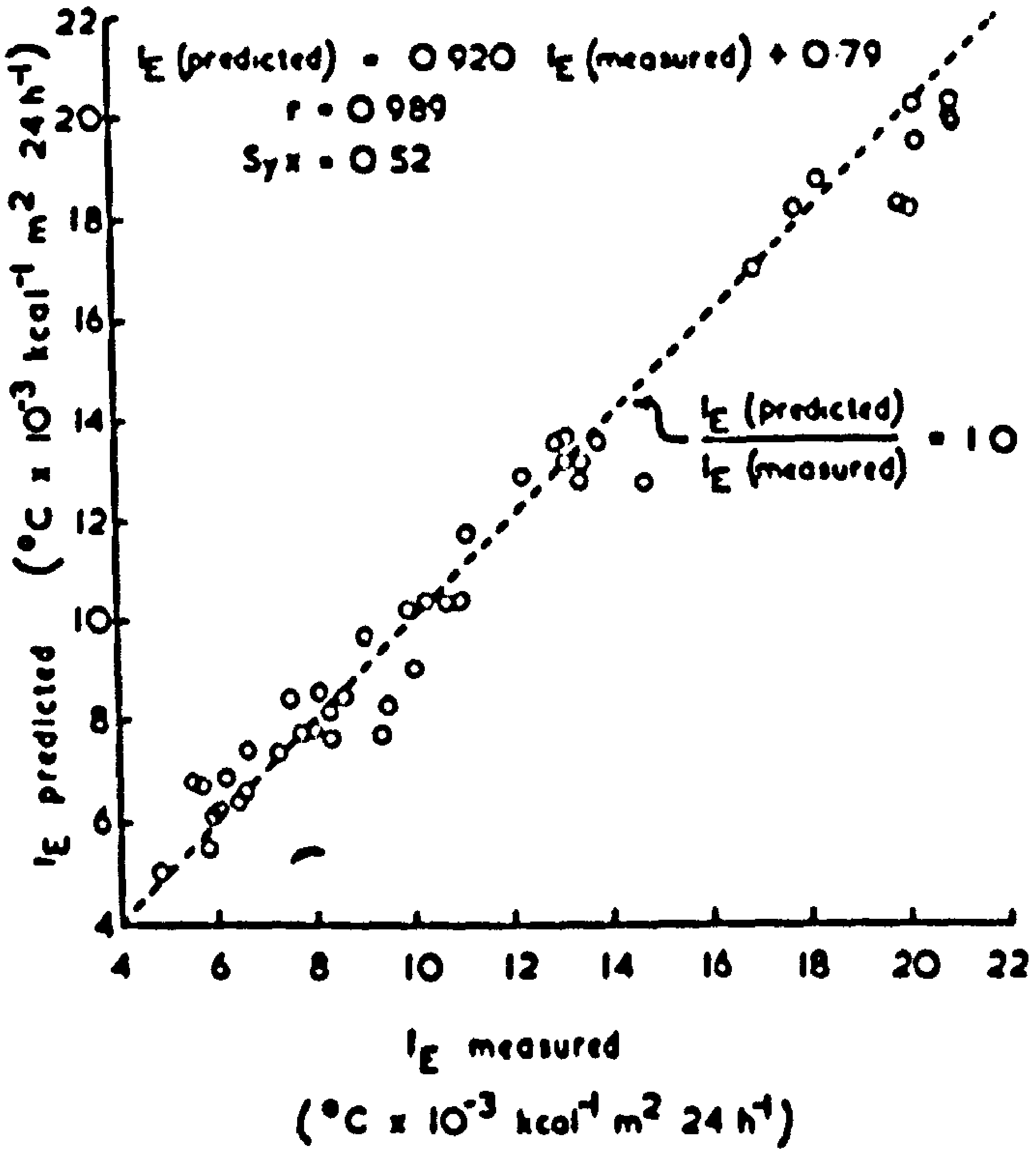


Fig. 21. Comparison of the external insulation predicted with the external insulation measured on sheep in the outdoor experiment when the incidence of solar radiation was less than 0.1 cal/cm^2/min.

predicted from the environmental conditions. Comparisons have been made only in the 45 experiments in which incident solar radiation was less than 0.1 cal/cm^2/min and the fleeces were dry. The external insulation was predicted from the regression equations calculated from the results for the tracheostomized sheep (see Table 12). The general form of these regression equations was $I_E = a + b\ F$, where I_E = external insulation, F = fleece depth in mm and a and b were constants. Exponentials have been calculated for the effect of wind velocity on the factors a and b. These were:-

$$a = 4.91\ e^{-0.082 \text{ wind speed } (\text{S.E.} = \pm 0.035)} \quad . \quad . \quad . \quad . \quad (10)$$

$$b = 0.453\ e^{-0.049 \text{ wind speed } (\text{S.E.} = \pm 0.040)} \quad . \quad . \quad . \quad . \quad (11)$$

and are shown in Fig. 20 and the analysis of variance in Table 18. At each wind speed experienced in the outdoor experiments, the external insulation was calculated and compared with that measured. These results are shown in Fig. 21 and it can be seen that predicted external insulations were very close to the measured values. The regression equation was:-

$$I_E \text{ (predicted)} = 0.920\ I_E \text{ (measured)} + 0.79$$

The correlation coefficient between predicted and observed values was 0.989 and the residual standard deviation 0.52 insulation units. From these results it would appear that results obtained from tracheostomized sheep under artificial climates can be transposed to outdoor conditions when solar radiation is minimal. It must be noted, however, that these results were obtained mostly under cloudy conditions and may possibly not be applicable to cloudless night environments when the long wave radiation heat loss from the sheep may be considerable.

Unfortunately, very few occasions were recorded when the wind speed exceeded the maximum air velocity of 9.6 m.p.h. used in the artificial climate trials and the solar radiation insolation over the same period was less than 0.1 cal/cm^2/min. The few recordings made at wind speeds greater than 9.6 m.p.h. showed no deviation from linearity of external insulation with increasing wind speed up to 15 m.p.h.

(b) Tissue insulation. The tissue insulations of the four sheep used in this experiment have been shown previously in Table 11. The value obtained for the Cheviot sheep Jr, fits within the range of tissue insulations for the Cheviot breed measured using other techniques. The other three sheep, Fr, By and Jr, were not purebred and therefore the results with them cannot be compared with the results obtained with the other sheep. Tissue insulations measured in this outdoor experiment tended to be more variable than those measured in the indoor experiments. This may be an indication that the environment on some occasions may have been close to the zone of thermoneutrality for the sheep.

(c) Rain. Unfortunately few days of rain were encountered during the experimental period, but the maximum decrease in external insulation caused by the small amount of rain that did fall, appeared to be -4.17 insulation units which was a decrease of 35% in the predicted dry external insulation value.

4. Discussion and conclusions. A relatively large range of environmental conditions was encountered in the course of the experiments. The results obtained from the wind speeds recorded at different anemometer heights emphasized the large frictional or drag effect of the ground on air movement. This effect prevents the sheep from being exposed to the full strength of the wind as measured at the standard meteorological height of 33 ft. The correlation coefficient of 0.989

between I_E predicted from the indoor experiments and I_E measured in the outdoor trial at low solar radiation intensities (with a standard deviation of 0.52 insulation units) emphasize the usefulness of indoor environmental studies to isolate the effects of air temperature and wind on the energy metabolism of sheep as would occur in natural outdoor conditions. Due to the small number of experimental periods in which rain fell the only general conclusion that can be drawn regarding the effect of rain is that when fleeces are wetted by it, the external insulation values tend to be lower than those predicted for dry environmental conditions.

E. The estimation of solar heat load and its effect on metabolism

1. Introduction. Solar radiation impinging on a sheep in a cold environment will help to relieve the effects of the cold. It will reach the sheep in three ways: (1) direct incoming solar radiation which arrives at the outside of the earth's atmosphere at a level of 1.99 cal/cm^2/min and is depleted by its passage through the atmosphere, (2) indirect sky radiation resulting from scattering of the direct solar beam in the atmosphere, and (3) solar radiation reflected from the ground. The ratio of direct to indirect levels of solar radiation will be largely dependent on the amount of cloud cover. The amount reflected from the ground will be controlled not only by the intensity of the solar insolation but also by the reflectivity of the ground for solar radiation (albedo). Similarly, of the incoming solar radiation impinging on the sheep the percentage that is absorbed will depend on the reflectivity of the fleece and hair of the sheep for solar radiation. The experiments described in this section were designed to measure, (1) the amount of solar radiation impinging on the sheep under various

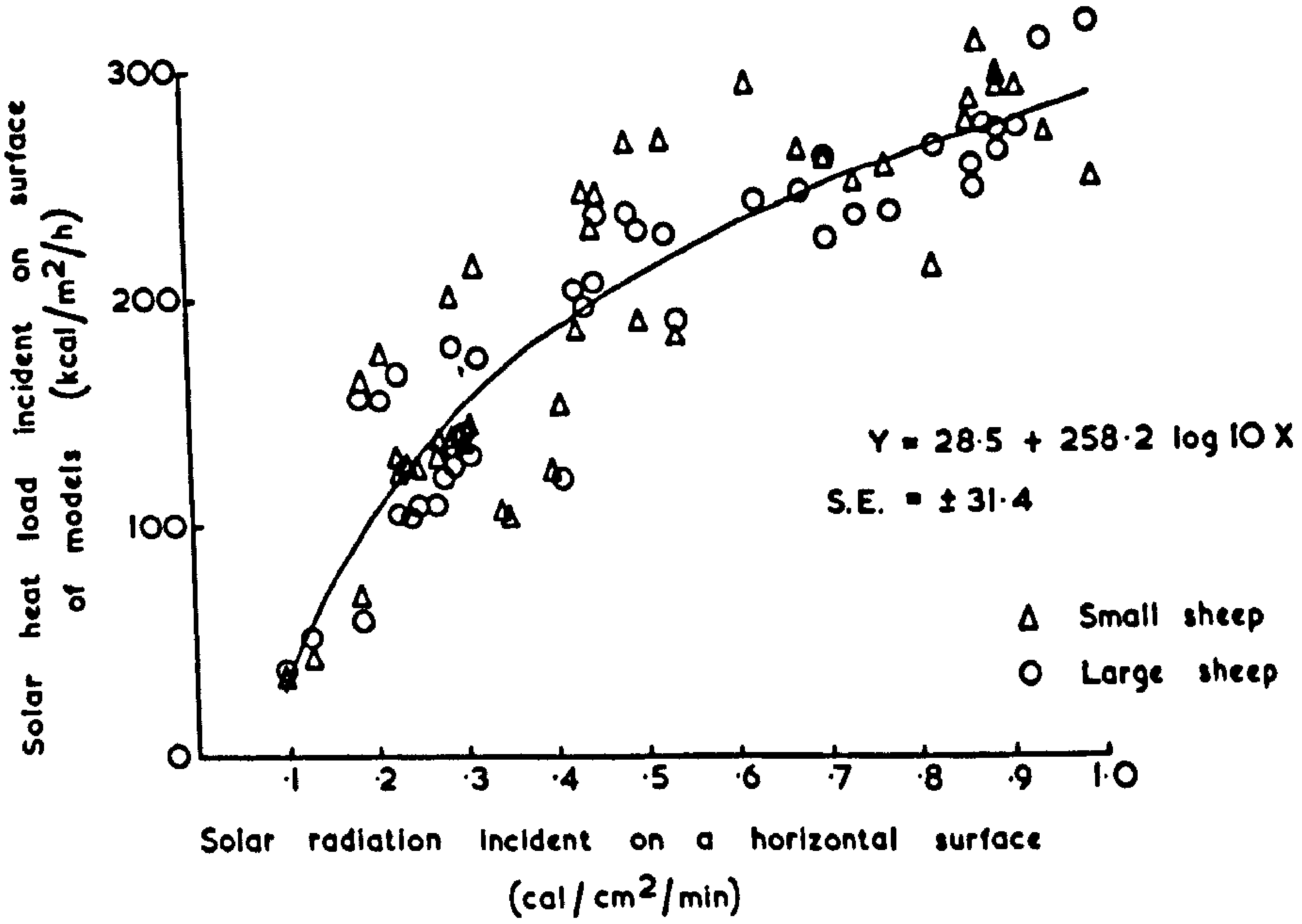


Fig. 22. The effect of level of solar radiation incident on a horizontal surface on the heat load incident on the exposed surface of sheep models.

conditions of solar elevation and cloud cover using models of sheep, (2) the amount of solar radiation reflected from grass swards and sheep fleeces, and (3) the effects of solar radiation on the external insulation of sheep in natural cold environments.

2. Solar heat load incident on models of sheep. Using the methods described previously, the solar radiation incident on models of sheep has been measured, one representing a fully fleeced sheep and the other a shorn sheep. The exposed surface areas of the two models used here have been compared with measurements on live sheep made by Clapperton & Blaxter (1963), and it has been found that the total exposed areas of 1.642 and 0.857 m^2 agree well with actual exposed area measurements on live sheep. The hypothesis that the sheep approximates to a right cylinder on four legs, an assumption necessary for this approach, has also been shown by Clapperton & Blaxter (1963) to be a reasonable approximation. In all, 45 measurements were made using the small sheep model and 42 using the large sheep model, and the results recorded in Appendix Table IV. The incoming radiation incident on a horizontal surface varied from 0.10 to 1.00 cal/cm^2/min, the solar elevation varied from 9° 55' to 53° 15' and the cloud cover from none (0/8) to full cover (8/8). Observations were made in the months of January, July and October. Total radiation loads on the sheep varied from 35 to 295 kcal/m^2/h. Very little difference was found between the small and large sheep models in the heat incident on them per unit area, and the total amount of heat received by each model was proportional to its surface area. In Fig. 22 the solar radiation incident per unit surface area of the sheep model has been plotted against the solar radiation incident on a horizontal surface. The calculated regression equation was:-

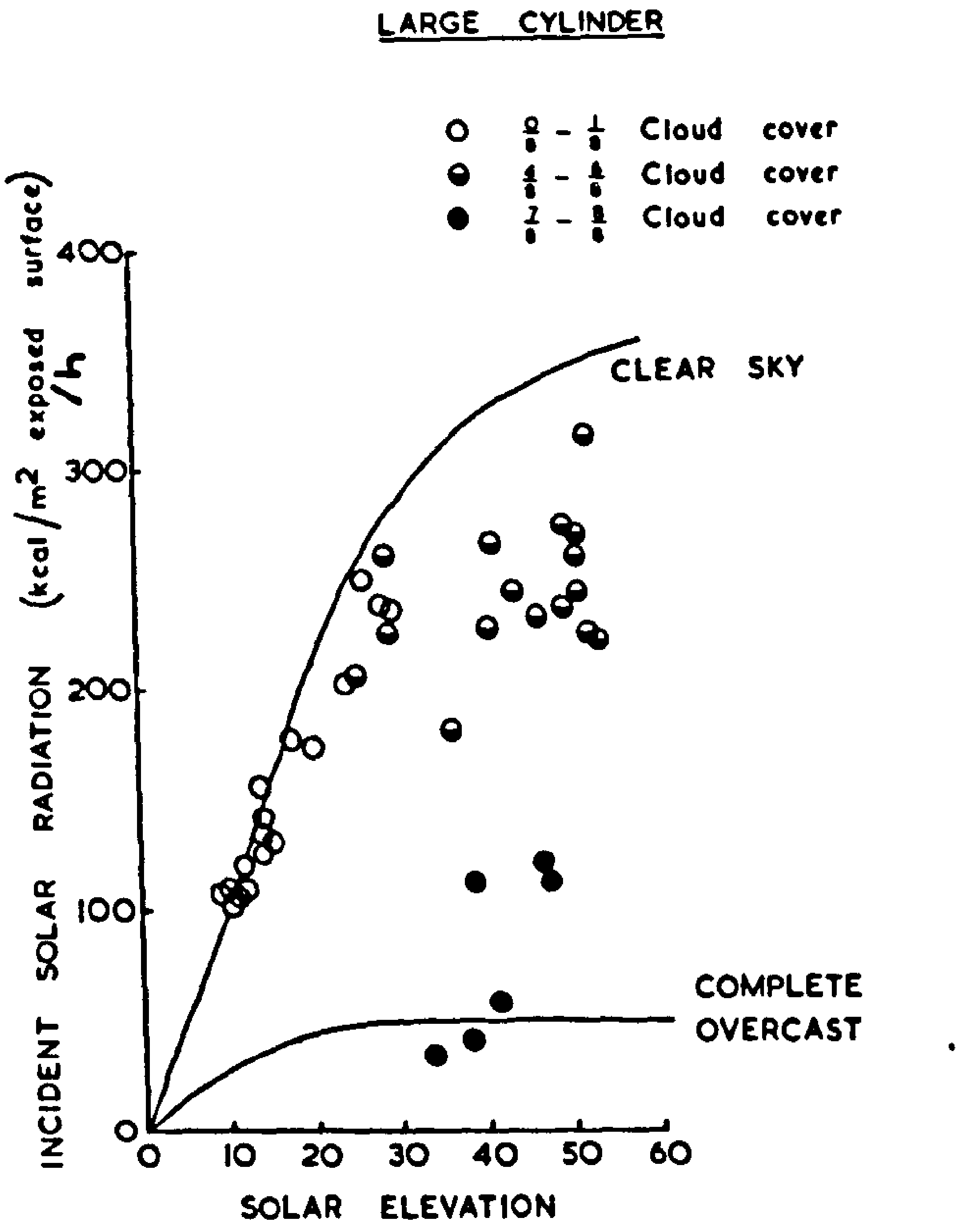


Fig. 23 A

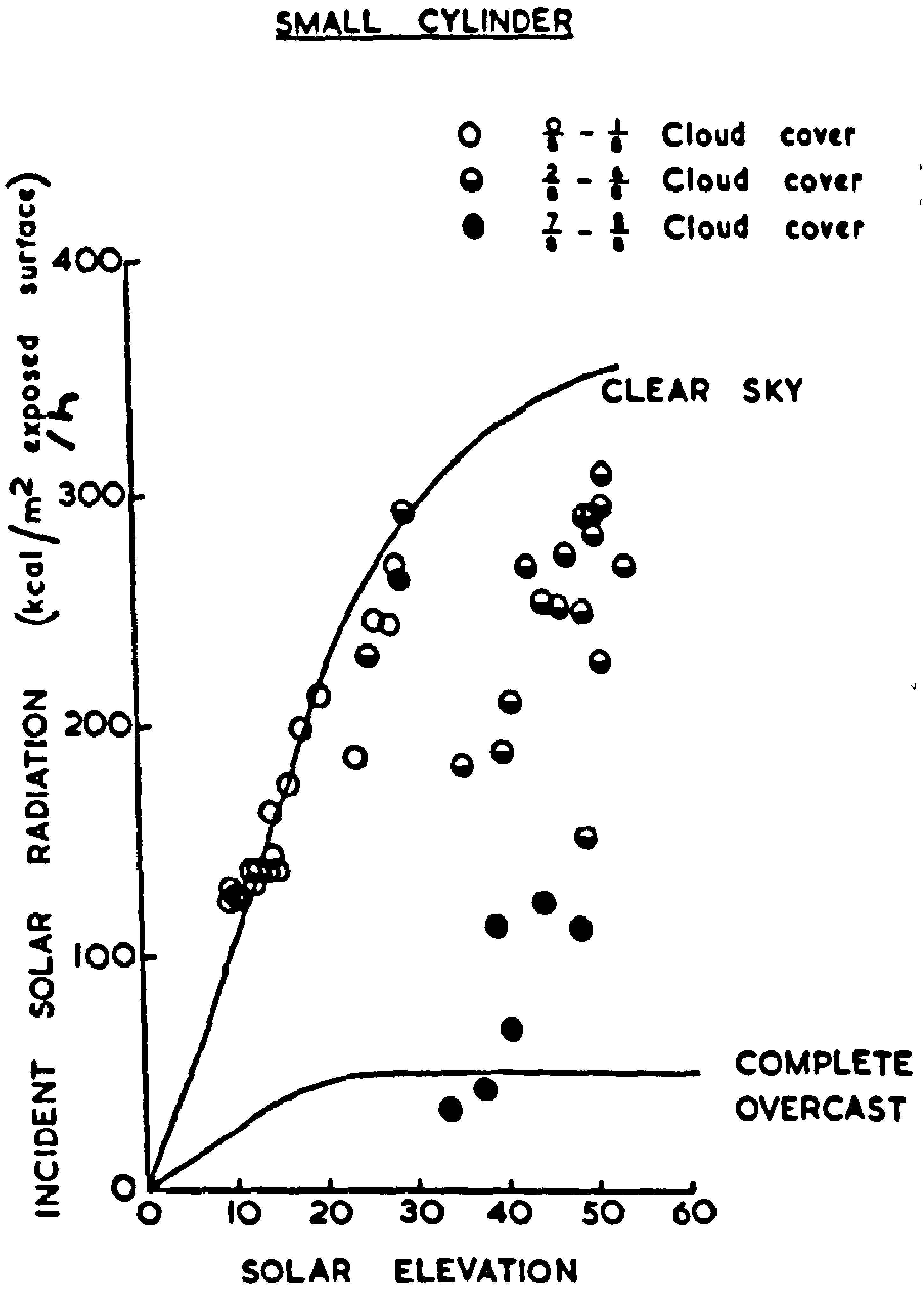


Fig. 23 B

Fig. 23. The effect of solar elevation on the solar heat load incident per m^2 exposed surface of the large (A) and small (B) sheep models.

$$Y = 28.5 + 258 \log_{10} 10 X$$

where Y is the incident solar heat load on the surface of the models ($kcal/m^2/h$) and X is the radiation incident on a horizontal surface ($cal/cm^2/min$).

The standard error of ± 31.4 $kcal/m^2/h$ was large, but the regression coefficient was significant at the 0.1% level. The maximal incident heat load appears to be about 300 $kcal/m^2/h$. In Figs. 23 a and 23 b the heat load incident per unit area on both sheep models has been plotted against the solar elevation as calculated from the Astronomical Ephemeris (H.M.S.O. 1962) and Sight Reduction Tables for Air Navigation (1953). Also plotted on the graphs (Fig. 23 a, b) are the theoretical solar heat load curves for clear sky conditions assuming a transmission coefficient of 0.7, and for completely overcast conditions. These theoretical curves have been computed by Clapperton & Blaxter (1963) from the atmospheric transmission of solar radiation and the exposed profiles of sheep. The results for the model sheep measured under 0/8 - 1/8th cloud conditions fitted closely the theoretical curve of Clapperton & Blaxter (1963) for clear sky conditions. The lower three overcast points in Fig. 23 a, b came close to the curve for completely overcast conditions. The other three overcast points are well above the theoretical curve but this is probably due to regarding all completely overcast conditions as falling into one category without being able to assess the thickness of the cloud layer and hence its percentage transmission of solar radiation. As would be expected the amounts of solar heat load as measured between 3/8 - 6/8ths cloud cover (Fig. 23 a, b) were intermediate between the results for clear skies and those for complete cloud cover. It is obvious that even when solar elevation is low or when the incoming radiation measured on a horizontal surface is

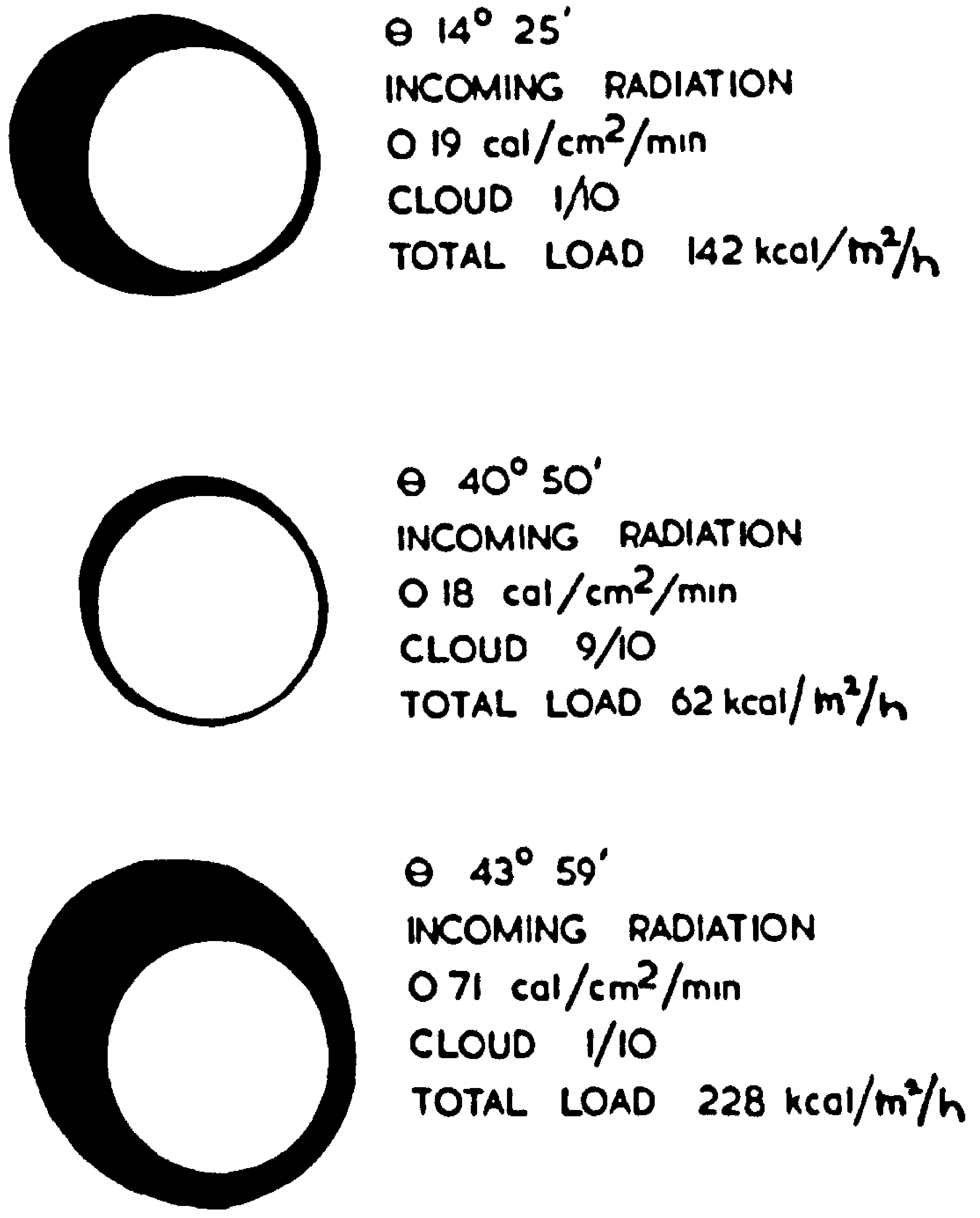


Fig. 24. The distribution of the incident solar radiation around the perimeter of sheep models at different solar angles (θ) and at different incoming levels of solar elevation. The distribution is indicated by the black areas.

small, the solar heat load incident on a sheep can be large. The incident load as measured at high solar elevations was found to be about 6 - 8 times the resting metabolism of the live sheep and was unevenly spread over the body. The greatest single factor in determining this heat load is the direct component of solar radiation which causes a unilateral heating of the side of the body. Parts of the body receive the indirect hemispherical sky radiation and radiation reflected from the terrain only, while other parts of the body have some of the incident reflected radiation affected by the shadow cast by the sheep. Some estimate of the uneveness of the solar heat load can be seen from the solar heat load diagrams shown in Fig. 24. The heat loads shown there were calculated from the angle measurements of solar radiation incident at 45° intervals around the perimeter of the cylinders. Only three different sets of results are shown. The first two diagrams in Fig. 24 show how, even though the total radiation incident on a horizontal surface was almost the same, 0.19 and 0.18 cal/cm^2/min respectively, the presence of cloud not only reduced the total heat load from 142 kcal/m^2/h incident on the sides of the sheep to 62 kcal/m^2/h, but also reduced the uneveness of the heat load pattern apparently by lowering the ratio of the direct to indirect solar radiation. In the third diagram (Fig. 24) an attempt has been made to indicate the range in the heat load incident around the perimeter of the body under conditions of high solar elevation and a moderate level of incoming radiation (0.71 cal/cm^2/min). From this type of experiment it is obvious that high fleece surface temperatures could be expected even under sunshine conditions that are typical of Scotland, and temperatures may even approach those recorded for the Merino by Priestly (1957) and MacFarlane et al. (1956) in Australia.

Table 19. The percentage of incident solar radiation reflected from fleeced and shorn sheep skins

	Fleece length (mm)	% of incident solar radiation reflected*
Blackface x Suffolk	70	28.6
Blackface x Suffolk	70	27.7
Suffolk x Cheviot	80	24.3
Suffolk x Cheviot	60	26.4
Suffolk x Cheviot	50	24.6
Greyface	80	22.8
Greyface	80	24.6
Greyface	80	23.1
Downcross	64	26.3
Downcross	85	29.7
South Suffolk	5	47.6
Cheviot	8	40.5
Cheviot	9	37.3
Aberdeen Angus	Summer coat 3 mm	10.1

Mean of fleece lengths 64 - 85 mm	25.8
Mean of fleece lengths 4 - 9 mm	41.8

* Mean of four measurements

3. Reflectance of solar radiation from skins, hides and terrain. Not all the solar radiation impinging on the surface of sheep is absorbed and dissipated in raising the surface temperature. A proportion of it is reflected without absorption and liberation as heat. No published information has been found on the reflectance of solar radiation by fleeces although a number of measurements have been made on cattle skins (Rhoad, 1940; Reimerschmidt, 1943; Reimerschmidt & Elder, 1945).

Measurements were made of the reflectance of solar radiation of the skins of thirteen sheep slaughtered within 2 h of the measurements being made. Ten of these skins carried a fleece more than 50 mm in length and the other three had been recently shorn. Four measurements were made on each skin, and the mean results are shown in Table 19. The mean reflectance of the fleeced skins was 25.8% and of the recently shorn skins 41.8%. The range of reflectance of the fleeced skins was only 22.8 - 29.7% whereas the range of the recently shorn skins was 37.3 - 47.6. This large range of reflectance for the shorn skins was probably due to the fact that the fleeces had visibly darkened to varying degrees since shearing. The skin classified in the shorn group which had the lowest reflectance value was also the longest in fleece length. From these results it is apparent that the solar heat load results given in the preceding section for the model sheep must be reduced by approximately 26% for fully fleeced sheep and by up to almost 50% for recently shorn sheep. Unfortunately it was not possible to obtain enough skins from purebred sheep and no breed comparison of reflectance values was possible. One Aberdeen Angus summer coat hide was available, and the reflectance value as measured with it may give some indication of the reflectance value of the black hair-covered areas of Scottish Blackface sheep and other breeds, e.g. Suffolks. The reflectance value of 10.1%

Table 20. The percentage of incident solar radiation reflected from various terrains

Terrain		% incident solar radiation reflected
Ryegrass sward, grass 1 in. in height		24.5
		23.9
		24.0
		23.5
		24.0
	mean	24.0
Ryegrass - cocksfoot sward, grass 10 in. in height		23.9
		25.0
	mean	24.5
Ryegrass - cocksfoot sward, grass 16 in. in height		24.0
		26.2
		25.4
		25.1
		25.4
		25.8
		25.6
	mean	25.4
Asphalt		11.5
		11.2
	mean	11.3
Tar macadam - stone ships		12.0
		13.1
		11.1
		11.6
	mean	12.0

obtained here agrees well with similar values for Aberdeen Angus hides obtained by Rhoad (1940).

As an adjunct to these fleece reflectance experiments, a number of albedo or solar reflectance values were obtained for various types of terrain. As has already been explained these values influence the level of diffuse solar radiation incident on the sheep. The results of this section of the work are shown in Table 20. The mean values of 24.0, 24.5 and 25.4% for 1 in., 10 in. and 16 in. ryegrass and ryegrass-cocksfoot swards are comparable to values of 25 - 27% measured by Monteith (1959 b) and values of 15 - 37% quoted in the Smithsonian Meteorological tables (1951).

4. Effects of solar radiation on the external insulation of sheep in the outdoor experiments. The external insulation of the fleece of each sheep was predicted, assuming conditions of no incoming solar radiation or rain, using equations (10) and (11) as described on page 66. These predicted insulations were subtracted from the measured insulation values to estimate the increase or decrease in external insulation due to solar radiation or rain for those sheep which appeared to be below their critical temperature (Appendix III).

Changes in insulation, ascribed to solar radiation, ranged from -2.15 insulation units at an incoming solar radiation incidence of 0.07 $cal/cm^2/min$ on a horizontal surface to +3.67 insulation units at a solar radiation level of 0.40 $cal/cm^2/min$. Greater increases in insulation than this were recorded, but the sheep were obviously no longer in a state of cold stress, and the approach used in this study to measure I_E is untenable in these circumstances.

An attempt was made to obtain a simple linear regression equation connecting the increase in the external insulation with the level of incoming solar radiation. However, it was found that it was necessary to compute two separate regression equations, one for fleece lengths of the range 5 - 18 mm and the other for fleece lengths of 30 - 42 mm. These were:-

$Y = 3.905\,X - 0.222$ (Fleece length range 5 - 18 mm)

$r = 0.885$ $Sy.x = 1.16$ insulation units

$Y = 10.641\,X + 0.092$ (Fleece length range 30 - 42 mm)

$r = 0.882$ $Sy.x = 1.46$ insulation units,

where Y = measured minus predicted external insulation, and

X = solar radiation incident on a horizontal surface ($\text{cal/cm}^2\text{/min}$).

From these regression equations it appears that the increase in external insulation was related to fleece length, the same level of incident radiation resulting in over twice the increase in insulation at the longer fleece lengths than it did at the shorter fleece lengths. In an attempt to overcome the necessity of having two regression equations, the ratio of the increase of external insulation to the predicted insulation $\left(\frac{\Delta I_E}{I_E \text{ predicted}}\right)$, the latter being largely dependent on fleece length, was compared with the incoming solar radiation flux level. The regression equation was:-

$Y = 0.529\,X + 0.004$

$r = 0.81$ $Sy.x = 0.093$

where $Y = \frac{\Delta I_E}{I_E}$, and X = solar radiation incident on a horizontal surface ($\text{cal/cm}^2\text{/min}$).

An alternative solution was to compute the relationship between the increase in external insulation and the level of incoming solar radiation weighted for fleece length or for total fleece surface area (one being dependent on the other) and the wind velocity. It appeared that part of the spread of points might be due to depletion of solar heat gain by the fleece due to wind. The multiple regression equation calculated was:-

$$Y = 0.45 + 2.17\,X_1 - 0.04\,X_2$$

where Y = increase in external insulation

X_1 = (solar radiation flux incident on a horizontal surface) x (exposed fleece surface area)

X_2 = wind velocity in m.p.h.

$\beta y_{1.2}$: t = 25.80^{***}

$\beta y_{2.1}$: t = $0.463^{N.S.}$

S.E. = ± 0.95 insulation units

*** Significant at the 0.01% level

N.S. Not significant

Since the regression coefficient $\beta y_{2.1}$ of 0.04 was not significant, the effect of wind velocity was deleted and a linear regression equation calculated:-

$$Y = 2.03\,X_1 + 0.24$$

S.E. = ± 0.96 insulation units

With a standard error of ± 0.96 insulation units this appears to be the simplest form of regression equation for this relationship but it appears that experimentation on a larger scale is necessary before any complete picture of the effect of solar radiation on the energy metabolism of sheep can be drawn. It was not possible to make solar radiation reflectance measurements on live sheep and only the visual observation that the surface of short fleeces tended to be whiter and cleaner than those of longer fleeces could be made. Hence, the effect of the sheep in these experiments having fleeces of different solar reflectance values has not been included in the calculated regression equations and this may account for a large proportion of the variation measured.

5. Discussion and conclusions. The solar heat load incident on a sheep as measured on models is extremely large especially under conditions of high solar elevation and clear skies, and it was concluded that the maximal heat load on a sheep resulting from solar radiation in clear sky conditions at mid-day in south-west Scotland is about 300 kcal/m^2/h. This amount is three to four times the heat produced from the metabolism of food when food of high quality is available *ad libitum*. This maximum heat load applies for only a small part of the day and to compute the total heat received throughout the 24-h period it would be necessary to integrate the heat load at various solar altitudes over the whole of the period of daylight. The effects of cloud in diminishing the solar heat load are apparent from Fig. 23. Completely overcast conditions can deplete the heat load to such an extent that only 10 - 15% of that measured under clear sky conditions falls on the sheep. There was little difference between the heat load (kcal/m^2/h) for the shorn model and that for the fleeced model, but consequently, because of the larger exposed surface of the fleeced model, the heat load per m^2 of skin surface would be greater. The reflectance of grass swards ranged between 23 and 26% (Table 20) and this agrees with similar values published by Monteith (1959 b). Solar reflectance values for fleeces indicated that approximately 26% of the solar radiation incident on fleeced sheep is reflected, whereas the corresponding value for shorn sheep is only 40 - 50%. Hence when applying the results of solar heat loads measured on models to live sheep the values must be reduced by 26% and 40 - 50% for fleeced and

shorn sheep respectively.

The results of the measurements on the effect of solar radiation on the external insulation of the live sheep in the outdoor trial are surprising in the smallness of the effect that solar radiation had on the external insulation. Larger increases would have been expected from the measurements made on the models, and possibly this discrepancy is due partly to improper comprehension of the complexity of the physics of the heat transfer involved in the dissipation of solar heat liberated at the surface of the fleece. A large proportion will presumably be lost as long wave radiation to the radiant sink of the sky and some by convection especially under windy conditions.

F. Measurement of environmental coldness

1. Introduction. It is often difficult to assess any natural environment in terms of degree of coldness. Before it can be done the relative importance of the various factors that make up the climate, viz, air temperature, wind, rain, solar radiation and long wave radiation must be assessed. One instrument that has occasionally been used in the past to integrate the coldness of an environment is the katathermometer. However, the results obtained from such an instrument may be inadequate in assessing coldness in relation to a living animal. From this study there appear to be three indirect approaches of assessing environmental coldness,

(i) the application of the calculated regression equations relating external insulation to wind velocity, solar radiation and rain,

(ii) the use of the artificial homeostatic sheep to integrate the different components of the weather into a simple function of heat output, and

(iii) the use of skin and rectal temperatures as an index of heat loss.

All these methods involve the assumption that the rate of heat loss or heat production is directly proportional to the environmental demand or coldness of the climate. In this chapter the relative value of each of these three methods is discussed.

2. <u>The application of the calculated regression constants relating the external insulation to wind velocity and solar radiation in assessing environmental coldness</u>. In an artificial environment, where wind velocity, rain and solar radiation are non-existant, the best way of assessing environmental coldness is simply to determine the degree to which the ambient temperature is lower than the critical temperature of the sheep, and in an environment where wind, rain and solar radiation have to be considered, one way of dealing with the matter is to convert the wind velocity, rainfall and solar radiation into terms of equivalent air temperature, and determine how far this equivalent temperature is below the critical temperature. Another solution is to determine the effect of wind, rain and solar radiation on the critical temperature of the sheep and then compare this new critical temperature with the ambient temperature to assess environmental coldness. Both these approaches have been used.

In order to compare the relative effect of different wind speeds at various air temperatures it is possible to calculate their equivalent still air temperatures. The heat production of a sheep per unit area at different wind speeds and air temperatures can be predicted from the formula:

$$Hp = \left\{\left[\frac{T_R - T_A}{\left(\frac{Hp}{Hp - 300A}\right) I_T + I_E}\right] + 300\right\} A \quad . \; . \; . \; . \; . \; (12)$$

where Hp = total heat production,

A = skin surface area of the sheep,

and I_T is weighted by $\frac{Hp}{Hp - 300A}$ since only the sensible heat (Hp-300A) is considered as flowing through the external coat. The factor 300 is the mean basal evaporative heat loss of sheep when they are below their critical temperature (Blaxter <u>et al</u>. 1959 b).

$$\text{Then} \quad Hp = \left\{\frac{(T_R - T_A) + 300\, I_E}{I_T + I_E}\right\} A \quad . \; . \; . \; . \; . \; . \; . \; . \; (13)$$

$$\text{and} \quad Hp/A = \frac{(T_R - T_A) + 300\, I_E}{I_T + I_E} \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; (14)$$

The external insulation can be predicted for different wind speeds from equations (10) and (11), and using equation (14) the increase in heat production per unit area due to different winds can be calculated. From this the equivalent change in air temperature that would cause the same change in heat production can be calculated from equation (16), assuming a constant rectal temperature of 39.0°.

$$Hp/A(w) = \frac{(39.0 - T_{Ao}) + 300\, I_{Eo}}{I_T + I_{Eo}} \quad . \; . \; . \; . \; . \; . \; . \; . \; (15)$$

$$\therefore \; T_{Ao} = (39.0 + 300\, I_{Eo}) - \left\{Hp/A(w) \times (I_T + I_{Eo})\right\} \quad . \; . \; (16)$$

where Hp(w) = increased heat production in wind environment

T_{Ao} = equivalent still air temperature

I_{Eo} = predicted external insulation if no wind were blowing

Table 20b. The effect of wind speed, fleece length and breed on the calculated equivalent still air temperatures at different ambient temperatures

(a) Cheviot sheep ($I_T = 6.95$) with 10 mm fleece depth

	Wind speed (m.p.h.)					
Air temperature (°)	0	3	6	9	12	15
20	20.0	18.1	16.1	14.2	12.4	10.6
15	15.0	12.5	10.0	7.5	5.1	2.9
10	10.0	6.9	3.8	0.8	-2.1	-4.9
5	5.0	1.4	-2.3	-5.9	-9.4	-12.6
0	0.0	-4.2	-8.4	-12.6	-16.6	-20.4
-5	-5.0	-9.8	-14.6	-19.3	-23.9	-28.3

(b) Cheviot sheep ($I_T = 6.95$) with 10 mm and 50 mm fleece lengths

		Wind speed (m.p.h.)					
	Fleece length	0	3	6	9	12	15
$T_A = 10^\circ$	10 mm	10.0	6.9	3.8	0.8	-2.1	-4.9
	50 mm	10.0	6.3	2.0	-2.0	-6.5	-11.4
$T_A = -5^\circ$	10 mm	-5.0	-9.8	-14.6	-19.3	-23.9	-28.3
	50 mm	-5.0	-10.7	-17.0	-23.8	-30.8	-38.4

(c) Cheviot sheep ($I_T = 6.95$) and Downcross sheep ($I_T = 3.74$) at 10° air temperature and fleece lengths of 10 mm and 50 mm

		Wind speed (m.p.h.)					
	Breed	0	3	6	9	12	15
Fleece length 10 mm	Cheviot	10.0	6.9	3.8	0.8	-2.1	-4.9
	Downcross	10.0	6.0	1.6	-2.9	-7.5	-12.1
Fleece length 50 mm	Cheviot	10.0	6.3	2.0	-2.0	-6.5	-11.4
	Downcross	10.0	6.2	1.0	-4.4	-10.2	-15.6

In Table 20 b are presented the equivalent still air temperatures for wind speeds up to 15 m.p.h. for

(1) a Cheviot sheep with a fleece depth of 10 mm (I_T = 6.95 insulation units) at ambient temperatures ranging from 20° to -5°,

(2) a Cheviot sheep with fleece depths of 10 mm and 50 mm at air temperatures of 10° and 5°, and

(3) a Cheviot sheep and a Downcross sheep (I_T = 3.74 insulation units) at an ambient temperature of 10° with fleece lengths of 10 mm and 50 mm.

Table 20 b shows that the effect of wind is increased at lower air temperatures. At an ambient temperature of 20° an increase in the wind speed from 0 to 15 m.p.h. decreased the equivalent still air temperature from 20.0° to 10.6°, a decrease of 9.4°, whereas at an ambient temperature of -5° a wind of 15 m.p.h. decreased the equivalent still air temperature from -5.0° to -28.3°, a decrease of 23.3°. An increase of fleece length from 10 to 50 mm decreased the equivalent still air temperature and this difference increased with increasing wind speed. These lower equivalent still air temperatures for the longer fleece lengths, especially at higher wind speeds, were due to the fact that the ratio of external insulation to tissue insulation decreased with increasing wind speed at a greater rate than it did with the shorter fleece length. As would be expected from the difference in their tissue insulations the equivalent still air temperatures were lower for the Downcross sheep than for the Cheviot sheep. The difference was less at the longer fleece lengths since the effect of any difference in tissue insulation became progressively smaller as the insulation conferred by the fleece increased.

Blaxter <u>et al</u>. (1959 a) have shown that the critical temperature (T_c)

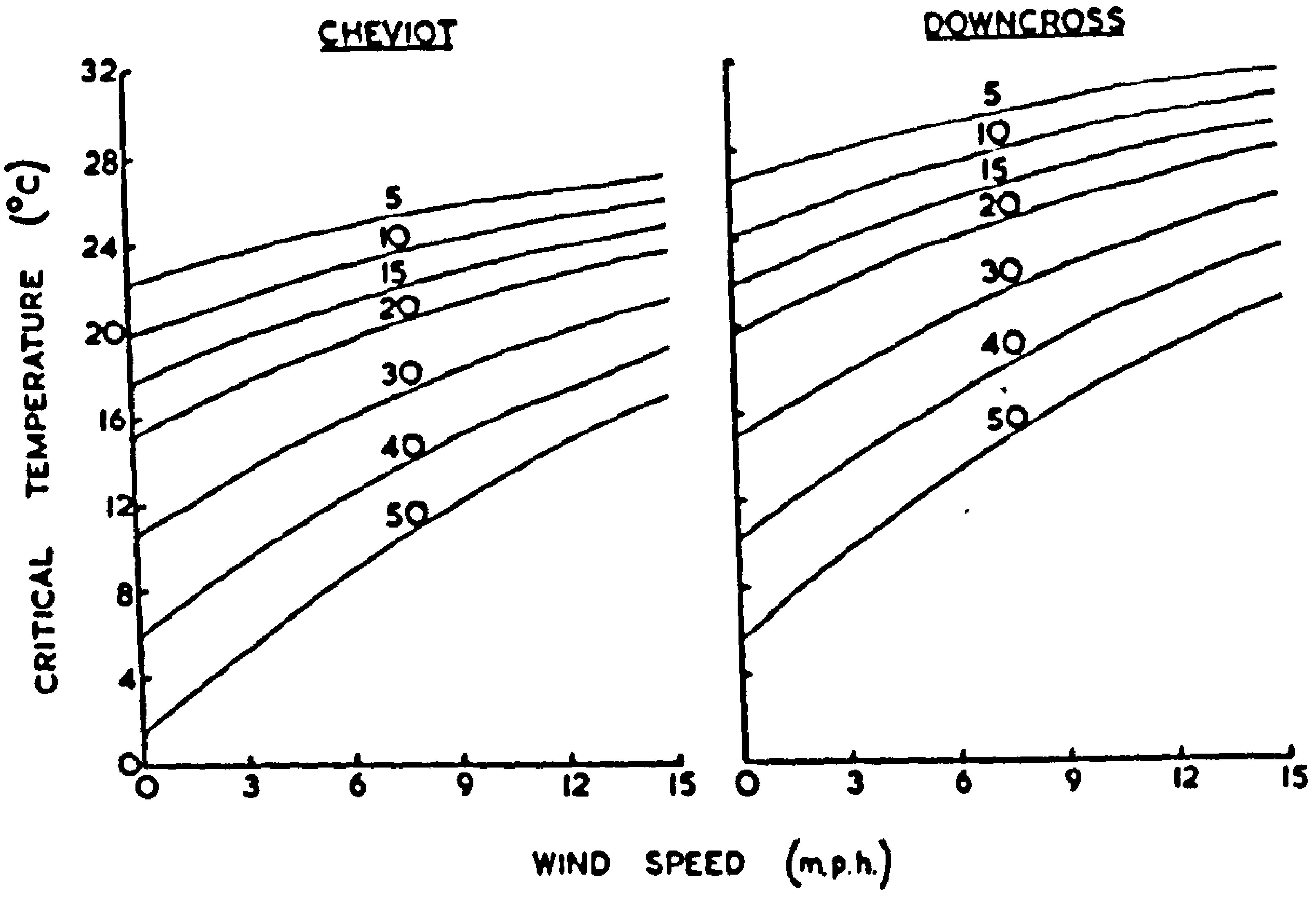


Fig. 25. The effect of wind speed on the calculated critical temperatures of Cheviot and Downcross sheep at different fleece lengths. The fleece lengths (indicated on each curve) ranged from 5 to 50 mm.

of a sheep is given by the equation:

$$T_c = 39.0 - \left[\frac{Hp - (H_E + H_W)}{CaA}\right] \quad . . . . (17)$$

where Hp = total heat production in a thermoneutral environment,

H_E = heat equivalent of the basal water loss,

H_W = heat expended in warming food and water from ambient to body temperature,

Ca = whole animal conductance, and

A = surface area.

In these experiments $H_W = 0$

$$\therefore \; T_c = 39.0 - \left[\frac{Hp - H_E}{CaA}\right] \quad . . . . (18)$$

and since $Ca = \frac{1}{I_\Sigma} = \dfrac{1}{I_E + \left[\left(\dfrac{Hp/A}{Hp/A - 300}\right) x \; I_T\right]}$

where I_Σ = whole animal insulation and the tissue insulation is weighted by $\dfrac{Hp/A}{Hp/A - 300}$ since 300 kcal/m^2/24 h is the minimum amount of heat lost as water vapour (H_E)

$$\text{Then } T_c = 39.0 - \left\{\left[Hp/A - 300\right]\left[I_E + \left(\frac{Hp/A}{Hp/A - 300}\right) x \; I_T\right]\right\} \quad . (19)$$

The mean heat loss of all the sheep used in this study was 1347 ± 73 kcal/m^2/24 h,[*] and none of the variation that occurred appeared to be associated with breed. Using this mean heat loss value the critical temperatures of sheep have been calculated for different fleece lengths at different wind speeds using values of I_E calculated from equations (10) and (11) and the mean Cheviot and Downcross breed tissue insulations of 6.95 and 3.74 units determined from Table 11. These critical temperatures are shown in Fig. 25 and they can be used to determine the extent to which wind

[*] measured in a thermoneutral environment.

and fleece length lower or raise the critical temperature of sheep being fed at a level approaching their maintenance requirement in a thermoneutral zone. As would be expected from the difference in tissue insulation, the critical temperatures of Cheviot sheep are lower than those of Downcross sheep, the difference being smaller at longer fleece lengths as the ratio of tissue insulation to external insulation value diminishes. This scale will only be applicable to sheep fed at the same level as that used in these experiments since Graham et al. (1959) have shown that the level of feeding will influence the critical temperature of sheep, the higher the feeding level, the lower the critical temperature.

A similar scale could be used to determine the effect of solar radiation on the critical temperature. This would involve an equation to determine the increase in external insulation and calculation of the new critical temperature in a manner similar to that which has just been used for the effect of wind. The equation would be

$$Y = 2.03 X_1 + 0.24$$

where Y = increase in external insulation, and

X_1 = solar radiation incident on a horizontal surface weighted for fleece exposed area.

Unfortunately this method could not be used with rain since insufficient data were available.

3. Use of the artificial homeostatic sheep as a weather integrator. As described previously (p. 35) the artificial sheep was positioned near the live sheep and oriented in the same direction. Hourly measurements made on the artificial sheep were compared with similar measurements on the live sheep. In all 37 comparisons were made. Comparisons of the sensible heat losses of the live sheep and heat production of the artificial sheep are

Table 21. Comparison of heat production of live and artificial sheep

Sheep	Fleece length (mm)	Range of sensible heat loss of live sheep (kcal/m^2/24 h)	Range of thermal demand from artificial sheep (kcal/m^2/24 h)	Mean sensible heat loss of live sheep (kcal/m^2/24 h)	Mean thermal demand of artificial sheep (kcal/m^2/24 h)	Factor for converting artificial sheep levels of heat production to levels in the live sheep
By	40	1351 - 1504	1272 - 1594	1417	1408	1.016 ± 0.016
Fr	37-38	1068 - 1576	1102 - 2234	1210	1527	0.810 ± 0.034
Fr	17	1893 - 2334	1430 - 2001	2079	1749	1.200 ± 0.046
Jr	15	1534 - 1755	1219 - 1430	1857	1313	1.265 ± 0.058
Fr	10-13	1922 - 2112	821 - 1360	1835	1108	1.664 ± 0.035
Jr	5	2170 - 2620	1172 - 1477	2508	1341	1.877 ± 0.062

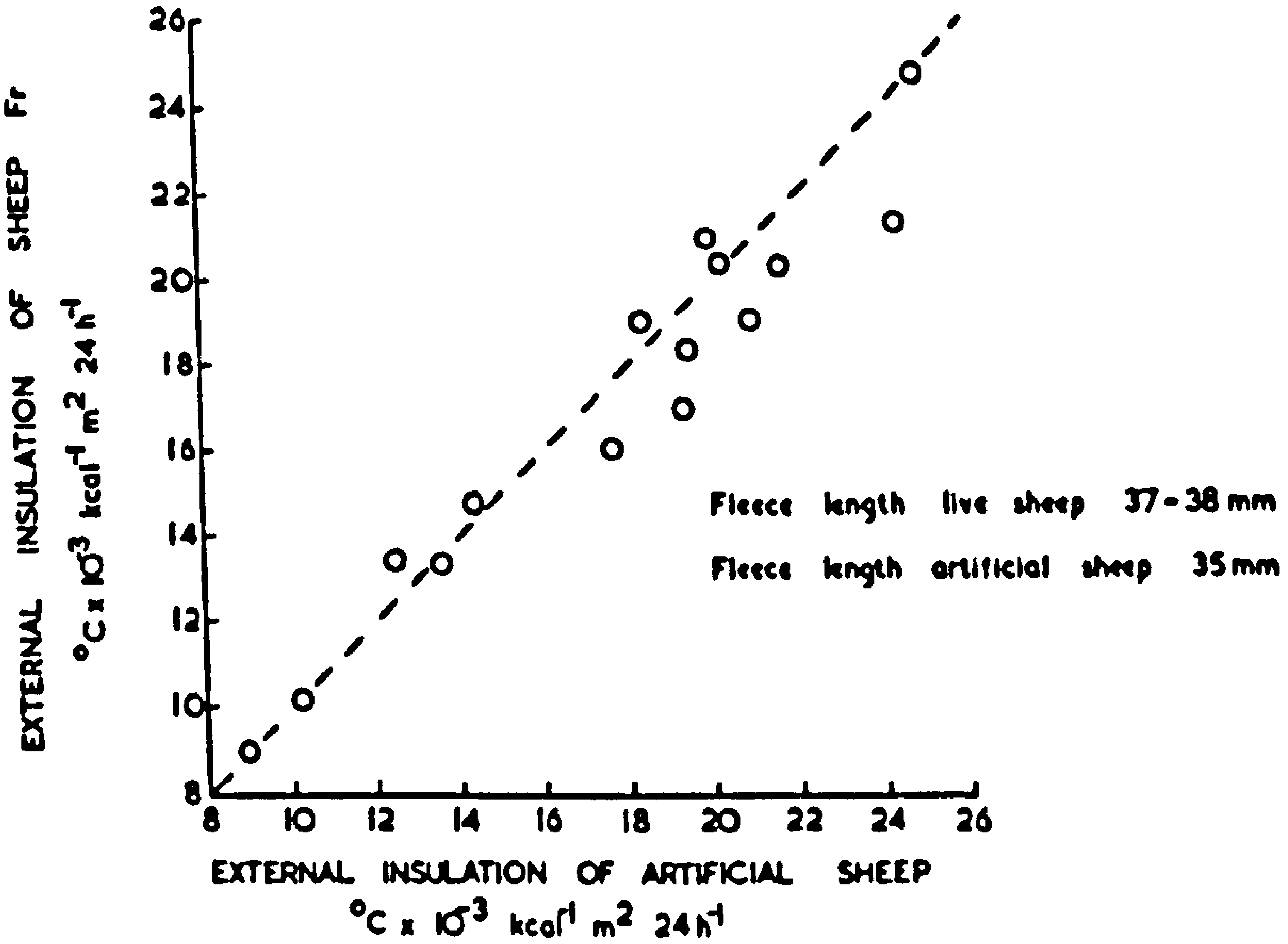


Fig. 26. Comparison of the external insulation values under different environmental conditions between the artificial homeostatic sheep with a fleece length of 35 mm and sheep Fr with a fleece length of 37 - 38 mm.

given in Table 21. Sensible heat losses of the live sheep ranged from 1068 to 2620 kcal/m^2/24 h, the greater heat losses being associated with the shorter fleece lengths. Electrical power consumption of the artificial sheep (k.w.h.) was converted into heat production values (kcal/m^2/24 h). To relate the heat production of the artificial sheep to that of live sheep, with different fleece lengths, conversion factors were calculated by dividing the heat production of the live sheep by the heat produced by the artificial sheep in the same environment. The conversion factors increased with decreasing fleece length on the live sheep. The factor of 0.810 for sheep Fr at the fleece length of 37 - 38 mm was lower than expected and possibly this sheep was not fully vasoconstricted. The external insulation of the artificial sheep was calculated by determining the total insulation using the equation

$$I_{\Sigma} = \frac{T_i - T_a}{Hp/A} \quad . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \ . \quad (20)$$

where I_{Σ} = total insulation (insulation units)

T_i = internal temperature ($^{\circ}$)

T_a = air temperature ($^{\circ}$)

Hp/A = heat production per unit area (kcal/m^2/24 h),

and then deducting the previously determined tissue insulation (2.9 insulation units) from this total insulation value, i.e. $I_E = I_{\Sigma} - I_T$. These calculated external insulation values are compared in Fig. 26 with those calculated from the results for the live sheep Fr with a fleece of 37 - 38 mm over the same period. It can be seen that agreement was reasonably good although the artificial sheep values tended to be slightly low at higher insulation values. From these results it would seem that artificial sheep of the type used in this experiment can be useful in integrating the different components of the weather for predicting the effect of the climate on the heat losses of sheep within the range of fleece length used in this trial.

4. Estimation of heat losses from skin temperature measurements. When attempting to measure heat losses from sheep, it may be preferable not to have to interfere with the sheep to the extent of subjecting it to tracheostomy or of using face masks to measure heat production by means of respiratory exchange. It may be possible to use methods such as those used by Doney (1963) in which a heat flow disc is attached to the animal between the skin and the fleece. However, such a method presents inherent difficulties in attaching the heat flow discs without altering the heat flow pattern and also in relating measurements at only a few sites to the total heat losses from the whole body. One alternative approach that presents itself from the experiments described in this thesis is to use skin temperature measurements. Tissue insulation (I_T) has been defined in equation (5) as:-

$$I_T = \frac{T_R - T_S}{Hp/A}$$

where T_R is rectal temperature, T_S skin temperature and Hp/A heat production per unit area. The constancy of tissue insulation under cold conditions has been shown previously, and it follows from equation (5) that the heat production per unit area of an animal kept in an environment below its critical temperature can be calculated from

$$Hp/A = (T_R - T_S)\frac{1}{I_T} \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; . \; (21)$$

In other words the heat production is obtained from the temperature gradient between rectum and skin multiplied by the reciprocal of the tissue insulation. If the rectal temperature is constant then:

$$Hp/A = \frac{T_R}{I_T} - \frac{T_S}{I_T} = k + T_S I_C \quad . \; . \; . \; . \; . \; . \; . \; . \; . \; . \quad (22)$$

where k = constant $\left(\frac{T_R}{I_T}\right)$ and I_C = tissue conductance = $\frac{1}{I_T}$

Equation (22) suggests that heat production per unit area could be estimated if the tissue insulation were known and if rectal temperature were constant. If rectal temperature were not constant then the gradient $T_R - T_S$ would have to be measured and equation (21) used to calculate heat production. These equations would apply only to sheep below their critical temperature since above the critical temperature the tissue insulation term would not be constant.

Using such methods heat production could be estimated and hence the thermal demand of environments could be assessed. This type of technique would be particularly useful in free-grazing sheep in natural environments so long as skin and possibly rectal temperature could be continuously recorded. In this respect, methods such as those of Bligh & Robinson (1963) in which skin temperature measurements are transmitted to a distant receiving set from a light-weight radio transmitting set carried on the back of the sheep are available. Besides continuous measurement and recording of skin temperature, it would be necessary to ensure that at each particular time the sheep was below its critical temperature as that the tissue insulation was constant. The problem of determining whether or not the sheep were in environments effectively below their critical temperature could possibly be answered by investigating whether or not the initial increase in heat production, which begins to occur at the critical temperature, is associated with a particular skin temperature, i.e. some "set-point" in skin temperature.

The results of the experiments previously described in this thesis

Table 22. Regression of heat production on skin temperature and the estimated skin temperature when heat production is that determined in a thermoneutral environment

Sheep	Breed	No. of experiments	Linear regression equation	Standard error of regression coefficient	Minimal heat production (kcal/m^2/24 h)	Set point (°)
Jr	Cheviot	15M	$Hp = 4463 - 99.7\ T_S$	±5.1	1160	33.1
Cs	Cheviot	31T	$Hp = 4584 - 99.8\ T_S$	±9.3	1305	32.9
Re	Mixed	9M	$Hp = 5143 - 109.8\ T_S$	±7.4	1235	35.6
By	Mixed	45M	$Hp = 10915 - 314.2\ T_S$	±22.9	1063	31.4
Yl	Downcross	21T	$Hp = 12675 - 331.8\ T_S$	±47.1	1422	33.9
Fr	Mixed	51M	$Hp = 5840 - 150.9\ T_S$	±12.8	1048	31.8
Z*	Blackface	5C	$Hp = 6047 - 146.3\ T_S$	-	1228	32.3
D*	Blackface	4C	$Hp = 5891 - 146.8\ T_S$	-	1143	32.9
C*	Cheviot	5C	$Hp = 4256 - 94.7\ T_S$	-	1172	32.6
J*	Cheviot	6C	$Hp = 4148 - 86.5\ T_S$	-	1225	33.8
3‡	Downcross	12C	$Hp = 8425 - 210.0\ T_S$	±14.3	1411	33.4
23‡	Downcross	12C	$Hp = 8614 - 209.0\ T_S$	±29.8	1529	33.9

Hp = Total heat production (kcal/m^2/24 h)

T_S = Mean skin temperature (°)

Set point = Skin temperature below which metabolism increases with a fall in skin temperature

M = Face mask experiments. T = Tracheostomy experiments. C = Chamber experiments.

* = Calculated from unpublished results of Armstrong *et al.* (1960).

‡ = Calculated from unpublished results of Blaxter *et al.* (1959 b) and Graham *et al.* (1959).

Table 23. Regression of heat production on the rectal-skin temperature gradient under cold conditions

Sheep	Linear regression equation	Error of intercept	Range of heat production (kcal/m^2/24 h)
Jr	$Hp = 337 + 119\ (T_R - T_S)$	±356	1570 - 2770
Cs	$Hp = 747 + 87\ (T_R - T_S)$	±229	1177 - 2816
Re	$Hp = 949 + 106\ (T_R - T_S)$	±213	1654 - 2581
By	$Hp = 635 + 126\ (T_R - T_S)$	±195	1219 - 2725
Yl	$Hp = 62 + 286\ (T_R - T_S)$	±480	2002 - 4864
Fr	$Hp = -170 + 170\ (T_R - T_S)$	±329	1210 - 3772

Hp = Total heat production (kcal/m^2/24 h)

T_R = Rectal temperature (°)

T_S = Mean skin temperature (°)

and also of a number of other environmental studies on sheep made by other workers have been used in an attempt to test the value of this approach. One hundred and seventy-two short-term tracheostomy and face mask short-term experiments and records of 44 respiration chamber experiments were available. Table 22 shows the results of regression analysis using equation (22). The range of the coefficient of T_S was from 86.5 to 331.8, and differences were statistically highly significant. In general, and in agreement with the tissue insulations of different breeds of sheep previously shown in Table 11, Cheviot sheep had values below 100 kcal/°C T_S; Blackface sheep had values of about 150 kcal/°C T_S, and values for Downcross sheep were over 200 kcal/°C T_S. The set-point of these sheep, i.e. the skin temperature at which heat production begins to increase, varied about a mean of 33.1° with a standard deviation of ±1.1°. Clearly there is a range of values both in the skin temperature coefficient and in the calculated constant, and it would be necessary to determine the precise relationship for each individual. There is also the possibility that the feeding level of the sheep may influence the skin temperature set-point but unpublished calorimetric data of Blaxter (1963)a) suggest that the feeding level has little if any effect on the set-point.

In Table 23 for the six sheep used in the short-term experiments, the corresponding regressions of heat production on the temperature gradient between the rectum and skin are given. The intercepts, with one exception (sheep Fr), were all positive, and the mean value was +427 kcal/m^2/24 h. These positive values are to be expected since not all the heat flows from the interior of the sheep to the skin. Some is lost in respiration as sensible heat and as water vapour.

5. <u>Discussions and conclusions</u>. The first method of assessing

environmental coldness, involving the conversion of the different climatic components into terms of their effect on the critical temperature of sheep, requires further experimentation to determine more precisely the effects of solar radiation, especially under windy conditions, and rain on the external insulation. No estimates are yet available for the effect of long-wave radiation or humidity effects on energy metabolism, and until the importance of these is assessed, this method cannot provide a complete solution to the problem. It certainly involves measurement of all the climatic variables, but it allows a complete assessment to be made of the weather area when measurements of the different attributes of the weather are available, i.e. it could possibly be used in conjunction with the weather statistics published by the Meteorological Office.

The artificial homeostatic sheep appears to be useful as a "weather probe" in that the heat output of the instrument can be related to the heat production of sheep of different fleece lengths. It should also be possible by the simultaneous use of white, black, silvered and fleeced artificial sheep to separate the relative importance of solar radiation, wind, air temperature, long-wave radiation and rain on the heat losses of sheep.

The use of skin temperature measurements to assess levels of heat loss would be most valuable in attempts to measure the metabolic response to cold of free-grazing sheep. A major criticism of the previous two methods is that all the measurements have to be made on static sheep whereas this method would allow measurements to be made, using suitable apparatus, with free-grazing animals. It would, however, involve prior determination of the correlations in individual sheep between heat production and mean values of T_S or $T_R - T_S$ and determination of the set point.

CHAPTER IV

GENERAL DISCUSSION AND CONCLUSIONS

1. Methods of measuring metabolism. It was found that tracheostomized sheep and sheep wearing face masks could be used equally satisfactorily for determining the sheep's rate of O_2 consumption. It was shown, however, that total CO_2 and CH_4 production could not be estimated with the tracheostomized sheep without applying a correction factor for the amounts lost by belching. Any such correction factor would, however, be affected by the level of feeding of the sheep. Unless it should be necessary to measure O_2 consumption during the act of eating, there appeared to be little advantage to be gained from using this method instead of a face-mask technique, especially since the useful life of a tracheostomy preparation is very limited.

In contrast to Pullar's (1962) observations made on sheep in a gradient layer calorimeter, the increase in heat production of a sheep on standing compared with the same sheep lying was only of the order of 1.7 kcal/kg body weight/24 h.

The O_2 incremental method of measuring heat production was very satisfactory, and on comparing it with the normal method of computing heat production using the total gaseous exchange, the calculated standard error of estimate was ± 52 kcal for total heat productions ranging from 1600 - 5200 kcal/24 h.

2. Equilibrium and steady state experiments. From the equilibrium experiments it can be concluded that the responses in O_2 consumption to change in environment were virtually complete within 50 min. However, the exception was the equilibration time of O_2 consumption of the sheep to the onset of rain which varied, and on most occasions during periods of rain no definite O_2 consumption equilibrium was observed. For the steady state experiments

with rain in which the sheep were subjected to 0.4 in. of rain/h at varying wind speeds, a constant pre-experimental wetting period of 2 h was used before the initiation of any measurements. The choice of this pre-measurement exposure period of 2 h is somewhat arbitrary especially when it is remembered that fleece lengths varied from 2 to 14 mm but after 2 h it always appeared on visual examination that the fleece was saturated before any measurements were made. This failure to establish true equilibrium times of O_2 consumption when the sheep were subjected to rain may possibly be due to the complex physico-chemical reactions concerned in wetting unscoured wool and the difficulty of saturating the fleece with water. In the outdoor trial the automatic rain guage recordings showed that during the experimental periods rainfall was intermittent and that during relatively short periods it could vary from intense to mild showers, whereas in the artificial environment the rate of 'rain' and the droplet size were constant. The degree of penetration of rain into a fleece will, to some extent, depend on droplet size and in these trials the droplet size was extremely small. Clearly it is difficult to simulate in an artificial environment the rain conditions that occur in a natural outdoor climate.

Most experiments were made with sheep carrying fleeces less than 60 mm long whereas the maximum fleece length for the breeds used is 100 - 130 mm. It was not possible to measure the heat production and insulation values of sheep carrying fleece lengths in the 60 - 130 mm range because of the difficulty in ensuring that they were below their critical temperature. A linear relationship was found to exist between the external insulation and fleece length up to 50 mm but it is doubtful if it would be correct to extrapolate results obtained from sheep with these fleeces to sheep with fleeces ranging from 50 - 130 mm.

The usefulness of artificial environmental studies as an indication of the effects of natural outdoor weather on metabolism has been emphasized by the comparisons that have been made between the results from the steady state climatic room experiments and those obtained under natural outdoor conditions. In the artificial climate room the only environmental factors altered were air temperature and air velocity, the radiant wall temperature always being close to the air temperature. Similar environmental conditions occur outdoors at night when incident solar radiation is zero and when, if there is a complete cover of low cloud, the radiant sky temperature approximates to air temperature. Although this type of environment is limited in its occurrence, the results indicated that these studies could be extended to daytime measurements when the incoming solar radiation was low. When the incoming solar radiation level, as measured on a horizontal surface, was less than 0.1 cal/cm^2/min, the correlation coefficient between the external insulation of the sheep is measured and that predicted from the climate room studies was 0.99 with a standard error of ±0.52 insulation units. When the incoming solar radiation level was higher than 0.1 cal/cm^2/min then the measured external insulation values were higher than those predicted from the indoor results and the difference between the two represented the increase due to solar radiation.

3. Importance of air temperature, wind, rain and solar radiation on the heat losses of sheep. The results of this section of the work confirm the fact that low environmental temperatures increase the heat losses of sheep as previously shown by Blaxter et al. (1959 a,b) and Graham et al. (1959). Measurements made at -3° and +5° showed that in sheep with short fleeces heat production was almost 50% greater at the lower air temperature than it was at the higher temperature. The effect of wind, especially at low environmental temperatures, was such that it increased heat production

Table 24. Comparison of calculated air insulation values in wind with other published estimates

Wind speed (m.p.h.)	Insulation of air ($^{\circ}C \times 10^{-3}/kcal/m^2/24$ h)		
	Calculated from these experiments[‡]	Calculated from results of Burton & Edholm (1955)[*]	Calculated from results of Winslow, Gagge & Herrington (1939)[*]
0.5	4.65	5.25	5.00
1.0	4.45	4.35	4.03
2.0	4.10	3.65	3.15
3.0	3.77	2.82	2.70
4.0	3.47	2.51	2.40
5.0	3.20	2.25	2.15
6.0	2.95	2.11	2.00
7.0	2.71	1.97	1.89
8.0	2.50	1.85	1.76
9.0	2.30	1.75	1.68
10.0	2.11	1.62	1.57

[‡] Based on experiments with sheep

[*] Based on experiments with man

to levels much greater than those measured in a thermoneutral environment. On occasions it was almost four times greater than the heat production as measured in the respiration chambers. The results showing the decreases in external insulation when winds impinged on the sides or hind-quarters of the sheep are in general agreement with the results of various studies made by other workers. Similar findings on isolated Merino sheep skins, in which a hot plate technique was used, have been reported by Hutchinson et al. (1960) where the total insulation of the fleece (1/2 in. and 3/16 in. in length) plus air interface fell markedly in winds of 4 - 10 m.p.h. From calculations by Doney (1963) based on the work of Hutchinson et al. (1960) it appears that the insulation of the air was 5.3 insulation units for still air conditions and approximately 2.0 insulation units at wind speeds of 10 m.p.h. These latter figures compare well with the results of 5.0 and 2.2 insulation units for wind speeds of 0.4 and 10.0 m.p.h. respecitvely calculated from the experiments reported here. The experimental results for the reduction in air insulation caused by wind are compared with the standard human values given by Burton & Edholm (1955) and Winslow, Gagge & Herrington (1939) in Table 24. Air insulation values determined on sheep were larger at higher air velocities than those calculated for man, but at lower wind speeds the differences between values based on experiments with sheep and man were small. As shown in the regression equations in Table 12 the fall in air insulation per unit reduction in air velocity was greatest at the lowest wind speeds and the rate of reduction of insulation decreased with increasing wind speed. Using heat-flow discs attached within the fleece Doney (1963) found large differences in heat flow between the windward and leeward sites on the body. Similar differences in heat flow at different sites on the body could not be shown in the experiments described in this study because of the approach used which depended on the determination of the total heat production and mean external insulation rather than on the insulation at isolated sites. However, the results of Doney showing these large differences in regional heat flow, while difficult to translate into terms of whole body or mean insulation, are confirmed indirectly by the large leeward-windward skin temperature gradients measured in the experiments described here when one side of the sheep was exposed to the wind source, the windward sites on the skin of the trunk always being lower in temperature than the corresponding sites on the leeward side. The fetlock skin temperature under cold conditions was always substantially lower than the temperature on any part of the trunk, and this has since been confirmed by Webster & Johnson (1964). The insulation of the fleece in winds varied from 4.63 to 2.75 insulation units/cm fleece length, the lower insulations being associated with the higher wind speeds. Comparable figures were obtained by Armstrong et al. (1960) in an experiment in which Scottish Blackface and Cheviot sheep were compared. These authors found that the insulation value, averaged over the whole coat, was 4 insulation units/cm depth of fleece for a fleece 10-cm long, and nearly 5 units/cm for a 5-cm fleece. The external insulation of fleece and hair was measured by Blaxter et al. (1959 a) and ranged between 6.7 and 8.2 insulation units/cm fleece. Both these sets of results, if the insulation of the air is added, are higher than those measured under the 0.6 m.p.h. air velocity conditions in the present experiments. However the air velocity inside the respiration chambers used in the experiments of Armstrong et al. (1960) and Blaxter et al. (1959 a) was only 0.2 m.p.h., which probably accounted for a large proportion of the differences in measured insulation. Hutchinson et al. (1960) recorded values of

12.7 - 13.0 insulation units/cm fleece for very short Merino fleeces, and these values compare well with the range of 10.0 - 17.4 insulation units/cm of coat depth obtained by Moote (1955) from measurements on dried pelts of fur-bearing animals. Similarly from thermal insulation measurements on fresh, dried and tanned furs of fifteen species of northern mammals, Hammel (1955) found an average insulation value of 12.4 insulation units/cm depth of fur. These last three sets of experiments, in which the insulation values/cm coat depth was over 10 insulation units were all measured using a hotplate technique. In some of the experiments the pelts were fresh, and it is possible that evaporation of moisture from the skin, when on the hotplate, gave results which tended to overestimate the level of insulation. However, as has been pointed out by Hutchinson & Wodzicka-Tomaszewska (1961), the large discrepancy between the low insulation values from measurements on the live sheep and the high values obtained from the hotplate method is probably due to disturbance of the fleece by movements of the sheep, a phenomenon which has been shown by Deighton & Hutchinson (1940) to occur in the feathers of poultry. Thus the values of insulation obtained with the living animal are likely to be less than those measured on a hotplate apparatus because of the convection that occurs under natural conditions. Furthermore, skins, when removed from the animal, tend to shrink causing the distance between separate coat fibres to be less, making the coat on the skin more compact than it was on the live animal and thus making it more difficult for the winds used in the experiments to penetrate the fleece. This may well be another factor accounting for the higher coat insulations measured by the hotplate technique.

The effect of rain on the heat losses of the sheep varied with air velocity. This was demonstrated in the steady state trials in which the external insulation of the sheep was measured at wind speeds of 0.6 and 9.9 m.p.h. both when the sheep were dry and when they were wet. If the effect of rain on the external insulation was independent of wind speed then the joint effect of wind and rain should have been simply additive as was found for lambs by Alexander (1962 a). In the present experiments however, the combined effect of wind and rain in reducing the external insulation was smaller than that predicted from the effects of rain and wind measured separately. This could possibly be due to the water in the fleece binding the wool fibres together and preventing the free penetration of the wind into the fleece. The effect of any exothermic reaction of the water with the fleece can probably be ignored in these experiments since the fleece was saturated and had been subjected to rain for 2 h, and any heat evolved from an exothermic reaction of water with wool would most likely have been dissipated at this stage of the experiment. The results of Bligh (1963) suggest that any exothermic effect due to a change in humidity in the fleece disappears within 50 - 60 min of the change and certainly within 2 h. However, on a large number of occasions the sheep outdoors would normally be subject to rain periods of short duration which would not saturate the fleece. On these occasions it would be expected that the sheep would benefit from any exothermic reaction involved in wetting wool and the decrease in external insulation would be lower than that predicted from these trials. Hedges (1926), King & Cassie (1940) and Speakman (1944) have demonstrated this exothermic effect of the complete wetting of wool. It is maximal at 24.1 cal/g wool when the initial moisture content of the wool is zero and disappears at a wool moisture content of 30%. Normally this heat would be dissipated slowly within the fleece at a rate controlled by the rate of wetting of the fleece. It is unlikely in Great Britain that the maximum heat production of

24.1 cal/g wool would ever be liberated since under the environmental conditions occurring out of doors, the initial relative humidity of the air before the fleece is wetted by rain would be high.

The use of sheep models has demonstrated the large solar heat load that can impinge on the surface of a sheep even under winter conditions and which is obviously a major source of relief from cold for animals out of doors.

4. Climate. In view of the large effects of the different components of weather on the energy metabolism of sheep it is of interest to attempt to categorize the climate of the United Kingdom to which farm animals are subjected. Any consideration of climate must involve mention of the complexity of the association of the different components of the environment that act together on the sheep. Large parts of Britain are composed of moorland and hill grazing areas with little shelter other than geomorphic. As pointed out by Taylor (1960) it is difficult to classify the country into regions where cold environments are likely to predominate. Any generalization based on altitude alone is difficult because of "ecological aberrations caused by land aspect, angle of slope, distance from sea and human interference" (Taylor, 1960). The general weather pattern associated with increasing altitude is one of increasing rainfall, cloud cover and humidity associated with decreasing intensity of solar radiation. In contrase to rainfall, air temperatures normally decrease with increasing altitude except in areas of local temperature inversion, and are associated with a greater incidence of frost and snow. With few exceptions wind speed usually increases with increasing altitude. Gloyne (1960) in discussing the wind on hills points out that not only is there an increase in wind speed with increasing altitude but there also

appears to be a summer "low" in air velocity and a winter "high". Studies of weather statistics by Blaxter (1961), however, show that the lowest wind speeds at Eskdalemuir Observatory in southern Scotland are associated with the lowest temperatures whereas high velocities normally occur at higher air temperatures. As pointed out by Gloyne (1960), however, this general pattern may be locally disrupted by topographically induced or constrained air mass circulation. A general annual mean wind speed pattern has been drawn up by Golding (1961) for Great Britain in which the mean annual wind speed appears to vary from 17.5 m.p.h. in the Outer Hebrides to less than 5 m.p.h. in certain central areas of England. Rainfall statistics for Great Britain (British Rainfall, 1958) are available and show the range of mean annual rainfall and the number of days on which rain falls. Published solar radiation statistics are not generally available except for tables which list the number of hours of sunshine and are of little use for the classification of climates for the purposes of this study. No statistics are available from which the long-wave radiation environment in the British Isles at different times can be assessed.

Even for those climatic variables, for which a statistical survey is published by the Meteorological Office or by others, the material is presented in such a form that it is impossible to determine the environmental conditions that a sheep would encounter. Most weather statistics are published in the form of a monthly mean in conjunction with the maximum and minimum for the month. Wind speeds are usually stated in terms of miles of wind run as measured on an anemometer, whereas rainfall is given as a total for the monthly period. This type of statistical presentation of weather data is useful for comparative purposes but is difficult to transpose into terms which will be related to the effect of the environment on the animal. There are two main reasons for this difficulty. Firstly, wind speeds are measured at a standard height of 33 ft and air temperatures at a screen height of 4 ft. The sheep, however, lives in an environment when encompasses the height from 3 ft to ground level and the environments at these lower levels probably differ greatly from those at the higher standard meteorological heights. This is particularly true for wind speeds, and as shown previously in Fig. 23 under the topographical and climatic conditions prevailing during the outdoor trial the air velocity at sheep height was calculated to be only 50% of that predicted for the standard meteorological height of 10 metres, and even this reduction can probably not be applied to areas other than that used in the trial due to differences in topography. Secondly, the sheep responds metabolically in terms of heat loss to the coldness of the environment as a whole which is determined by the joint combination of several components of weather. Consequently it is the particular combination of environmental factors at any one time period that determines the environmental demand on the metabolism of the animal. Mean monthly weather statistics may indicate that the air temperature duly weighted for the effect of wind is above the animal's critical temperature from which it might mistakenly be concluded that the sheep was never in a state of cold stress. However, if it were possible to integrate the weather statistics for the climatic variables, hour by hour, it might well be found that the sheep could have been in a state of cold stress for a considerable part of each 24-h period, especially at night when the level of incident solar radiation is zero. In this regard for biometeorological purposes in relating weather conditions to the environmental physiology of animals, the use of a weather probe such as the "artificial sheep" might be valuable. As shown in the present work, this type of instrument appears to integrate successfully the different components of the weather and can be applied to sheep bearing different levels of fleece growth. A simple single channel recorder such as is used with the artificial sheep would give a single variable which could be analysed in regard to weather records of the individual components made over the same period. Such an instrument would also be useful in determining the effectiveness of shelter for live stock.

The amount of metabolic response to cold ranges from that measured in a state of thermoneutrality to that of summit metabolism. The summit metabolism of the one sheep (5762 kcal/m^2/24 h) which successfully reached that limit of metabolic activity agreed with the level of 4800 - 6000 kcal/m^2/24 h calculated from the data of Alexander (1962 b) on Merino lambs. The occasions, however, on which adult sheep ever attain this level of heat production are likely to be few. It is probably encountered most commonly when sudden cold weather changes occur immediately after shearing. In the trials conducted in this study it was encountered only when a closely clipped sheep was exposed to continuous rain at a rate of 0.4 in./h with a wind speed of 9.9 m.p.h. and an air temperature of 7^o with no solar radiation, but under normal farm management practices a fleece length of 2 - 3 mm would never occur. The number of occasions on which a sheep will be above its thermoneutral heat production, however, must be quite numerous under natural conditions. As was shown in the work described here, even low levels of air movement at moderate air temperatures in the absence of sunshine could increase the level of heat production. However, in all the environmental metabolism trials carried out in this study the animals were fed only at a level which corresponded to their theoretical maintenance requirement under thermoneutral conditions. At times, however, the grazing sheep will be consuming herbage at levels in excess of its thermoneutral maintenance requirement, and consequently, according to the results of Graham et al. (1959), the critical temperature of these particular sheep will be much lower than if they were being fed at thermoneutral maintenance levels, although once below their critical temperature, the level of heat production will be the same irrespective of feeding level. Conversely during winter months, when pasture growth is retarded by cold weather, the level of feeding of free-grazing sheep may be below the thermoneutral maintenance level.

5. Effects on animal economy. All these experiments have been based on experiments in which only one animal has been exposed to any environment at any one time. Furthermore, each sheep was restrained in such a way that it was forced to stand during the entire pre-measurement and measurement periods (except in the respiration chamber experiments), and it was not possible for the sheep to orientate itself in any way to the prevailing wind. In its natural free-grazing state a sheep often lies down and in that way the body surface area exposed to the environment is diminished. At the same time under these circumstances the conduction of heat from the body to the ground becomes of increasing importance, especially in shorn sheep. The sheep may also seek shelter and then it is exposed to a microclimate which may be markedly different from the general climate. Sheep are gregarious by nature and as such tend to congregate and huddle together in inclement weather. Under these conditions the sheep tend to act as a mutual shelter for one another and

can possibly alter the pattern of long-wave radiation heat losses since their surface temperatures exposed to one another will possibly be higher than the mean environmental radiant temperature.

Any anomalies in heat production that may occur due to non-acclimatization were possibly partially overcome in these trials by maintaining the sheep in metabolism crates kept in an environment which was not artificially heated. However, there is the possibility that in sheep, which are continuously exposed to an outdoor climate, some greater degree of acclimatization may occur with a consequent diminution of heat production from that which would be predicted from the results of this study. The importance of this in its effect on the results obtained in the present work are impossible to assess.

6. Estimation of heat production in free-grazing sheep. Obviously the techniques used in this study to measure heat production cannot be applied to free-grazing sheep, and yet it is important to determine the extent to which the heat production of free-grazing animals differs from that of the static experimental animals. One approach that is possibly worthy of further study is the technique of estimating heat losses from skin temperature measurements. As already described (p. 87) the mean skin temperature of a sheep is a reasonably good index of its heat production and could be used with free-grazing sheep provided that it was possible, (a) to measure and record skin temperature continuously in relation to time, and (b) to know that at each particular time of measurement that the animal was below its critical temperature, i.e. the tissue insulation was maximal. These conditions would be met by an instrument that would either, (a) integrate the product of time x degrees departure of the rectal - skin gradient from a set value which is that

value of the temperature gradient which occurs when vasoconstriction has first taken place, or (b) integrate the product of time x degrees departure of the skin temperature from a set-point which is the value of the skin temperature when vasoconstriction occurs and hence the first metabolic adjustment to cold has taken place.

There are a number of instruments available which would meet these requirements and could be satisfactorily borne by the sheep without inconveniencing it in any way. An alternative solution would be to transmit the temperature directly from the sheep by radio to a receiver using equipment such as that developed by Bligh & Robinson (1963). No matter which method was used it would necessitate the determination of the minimum number of skin sites on the body of the sheep needed to give a satisfactory mean skin temperature of the whole body irrespective of the large gradients of temperature that can develop over the body under certain conditions. It would be necessary also to carry out individual metabolic experiments on each sheep in artificial climates to determine the set-point of skin temperature at which vasoconstriction first takes place and to determine the tissue insulation (I_T) and coefficient of T_S, i.e. I_C (p.85). In such a method it is inherent that the set-point is not altered by changes in feeding level and this is substantiated by unpublished calorimetric data of Blaxter (personal communication) which suggest that the feeding level has little if any effect on the set point.

Such a technique as that described above would allow hour by hour measurements of heat losses to be made from a number of individuals in a flock, and from such data it should be possible to assess any differences in levels of heat production compared with that of single isolated sheep.

Table 25. <u>Published estimates of the maintenance requirements of sheep when penned and when free-grazing</u>

Source	Crop	Food measured as	Live weight for which maintenance requirement was calculated	Maintenance requirement		
				Penned (a)	Free-grazing (b)	$\frac{(b) - (a)}{a}$ %
Greenall (1959)	Rape	g S.E./day	45 kg	549"	695	26.4
Coop & Hill (1962)	Pasture	g D.O.M./day	45 kg	418	676	62.0
Lambourne & Reardon (1963)	Pasture	g D.O.M./day	26 kg	200	420R 750Fg.	275.0
			32 kg	300	480R 780Fg.	160.0
			46 kg	420	490R 560Fg.	33.3
Coop & Drew (1963)	Pasture	g D.O.M./day	45 kg	459	663Fl. 767S	44.6Fl. 67.3S
Langlands *et al.* (1963 a, b)	Pasture	g D.O.M./day	45 kg	372	463	24.4
					Mean	86.6

" Estimated from Wood & Woodman (1930) feeding tables by Greenall (1959)
R Restricted in grazing time
Fg. Free-grazing
Fl. Fleeced
S Shorn

7. <u>Maintenance requirements of free-grazing sheep</u>. It is probable that metabolic responses to cold climates play some role in explaining the apparent anomalies that occur in the maintenance energy requirement of sheep when they are penned and when they are free-grazing. In Table 25 are shown the published comparisons of the maintenance requirements of penned and free-grazing sheep. The range of increase in the maintenance requirement of the free-grazing animals is from 275% to 24% with a mean increase of 86.6%. Part of this increase will be due to the energy cost of locomotion and part to the increased energy cost of having to graze the herbage as opposed to being given cut herbage. The work of Clapperton (1964) indicates that for sheep the cost of locomotion, for the distances normally walked in a day while grazing, increases the energy requirement of the sheep by approximately 10% if it is walking on a horizontal surface, and this increases to 15 - 20% when it is walking on an upward gradient. Only one estimate of the cost of grazing as opposed to that of eating cut herbage is available, namely that of Graham (1962). Graham found that when sheep grazed a turf floor in a respiration chamber, heat production increased over resting values by 0.6 - 0.8 kcal/h/kg body weight and that there was no significant increase over resting values when pre-cut grass was given. This latter finding is not in agreement with the results presented in this study where the respiratory exchange was measured in tracheostomized sheep while they were being fed cut dried grass. In this experiment the O_2 consumption and CO_2 production were increased almost twofold during the eating period, which suggests that the energy cost of grazing is nowhere near as energetically expensive as Graham supposed, since it is suggested that part of the increase in heat production due to grazing should be allocated, on the basis of the experimental results obtained in

this study, not to the cost of grazing per se but to the act of eating. Even so, his estimate indicates that the increment in maintenance cost due to grazing was only 12 - 18% which is not large. These estimates of the energy cost of locomotion and grazing can account for only a small proportion of the increase in the maintenance requirement of free-grazing animals and it is possible from the results presented in this study to suggest that a proportion of this increase in maintenance requirement might be due to the effect of climate on the energy metabolism of the sheep. It is of interest to note that the maintenance requirement of the restricted groups in the results of Lambourne & Reardon (1963) were lower than those of the free-grazing group. Lambourne & Reardon considered that this decrease might be due to the fact that the sheep of the restricted group walked for shorter distances, but it is also possible that due to the microclimate caused by the shelter of the pens themselves and of the crowding of the sheep into them, that the sheep in the pens were never subject to the extremes of climate experienced by the free-grazing groups.

8. Shearing. The results of the work done here emphasized the large increases in heat production than can be expected to occur in normal free-grazing sheep when they are shorn and which are likely to occur for a long time after shearing, especially if the weather is inclement. The fact that the maintenance requirement of sheep increases after shearing has been demonstrated in experiments by Coop & Drew (1963) in which the maintenance requirement of shorn sheep was 767 and for fleeced sheep 663 g D.O.M./day per 45 kg live weight (D.O.M. = digestible organic matter). Wheeler et al. (1963) showed also that D.O.M. intakes of grazing sheep rose by 42 - 62% after shearing and hay intakes of pen-fed sheep by

20 - 51%. Similar results are given also by Wodzicka-Tomaszewska (1963) in two trials in which penned sheep, fed <u>ad libitum</u>, increased their dry matter intake by 40 - 50% after shearing. Not only does this emphasize the importance of good feeding immediately after shearing especially under cold weather conditions but also it raises doubts about the economic practicability of twice-a-year shearing - a practice which is prevalent in some countries, notably in areas of Australia and New Zealand. In these areas the normal practice of summer shearing is repeated again in winter, and claims are made that this results in increased wool growth, in improved wool quality and in greater 'thriftiness' in the shorn animals. According to the results of the present work the advisability and economic value of this practice should be questioned. Not only does winter shearing increase the likelihood of a greater mortality due to cold stress, but also it must increase the maintenance requirements of the shorn sheep compared with those of similar sheep left to carry their normal fleece through the cold winter months. Any economic advantages of twice yearly shearing might well be outweighed by the increased feed requirement of the sheep, especially since this increased requirement would occur at a time of year when feed reserves are at their lowest.

9. <u>Breeding for resistance to cold</u>. As already described (p. 58), although the number of sheep used was necessarily small, there did appear to be a breed difference in tissue insulation, the breeds normally considered to be suitable for hill climates having a higher insulation than the lowland breeds. Highest in tissue insulation were the Cheviots and Scottish Blackface breeds, and lowest was the lowland Downcross breed. The effect of any differences in tissue insulation would be greatest

immediately following shearing and would decrease as the fleece grew. Not only is there the possibility of using breeds of known higher tissue insulations but there may be sufficient variation of tissue insulation within any one breed to warrant selection for tissue insulation within that breed. Due to the small numbers of each breed and the use of only three known breeds in these trials, experiments on larger groups of animals would be needed before any definite policy on this issue could be advocated.

10. Amelioration of cold. In the yearly cycle of animal husbandry practices on a farm, normally only three periods are likely to occur when the sheep are so obviously in a state of cold stress that there might be large economic advantages in taking precautions to ameliorate the cold stress. These are firstly when cold weather follows shearing, secondly during the winter months, and thirdly at lambing time in early spring. Cold stress is likely to occur at other times of the year but it could normally be minimized by assuring a sufficient level of feeding during the cold periods. Even in the three periods mentioned a higher level of nutrition will minimize the effects of cold stress. If low air temperatures, associated with high winds and rain, occur after shearing, it is essential that the sheep be well fed and have access to sufficient shelter. It is at this time that the possibility of adverse weather conditions acting on sheep bearing a minimum of wool cover, is so great that there is the possibility of heat production rising to that of summit metabolism. Under these conditions it is obvious that the housing of shorn sheep or the provision of good shelter to avoid deaths is necessary. It is probable that the provision of adequate shelter in combination with a good winter feeding policy would be sufficient.

Alexander (1961) has demonstrated that the critical temperature of newborn Merino lambs is 29°. This is obviously much higher than the critical temperature of the ewe bearing a fleece, and the advantages of shelter at lambing time to minimize lamb mortality rates is obvious. In some areas it might even be practical to shear the ewes before lambing since this practice has been shown by farmers to make the ewes seek shelter at partuition, but this would obviously be governed by the amount of shelter available. The work described here stresses the importance of providing good shelter for sheep in order to decrease wind speeds and to provide a screen from rain. Shelter in combination with good nutrition appear to be the main avenues of minimizing the effects of cold on the energy metabolism of sheep.

CHAPTER V

SUMMARY

1. Experiments have been made to determine the effect of the different components of the weather, singly and in combination, on the energy metabolism of sheep. For this purpose it was necessary to devise methods of measuring the heat production of the sheep without the need to keep them in a respiration chamber, and two methods were used. The first depended on tracheostomy, and the second on the use of a face mask. Both methods involved estimation of heat production from O_2 consumption only. The method of preparing permanent fistulas in the trachea of sheep is described, and seven sheep were satisfactorily tracheostomized using this technique. The design of a face mask, suitable for collecting expired air from sheep, is also described. The total expired gases were collected when the face-mask method was used, but only the pulmonary gases could be collected from the tracheostomy preparations and in this procedure belched gases, escaping through the mouth and nose, were lost. Details are given of the methods of collecting, measuring and analysing the expired air.

2. The results obtained for the O_2 consumption of the tracheostomized sheep, as measured by a Douglas bag technique, were the same as those obtained in experiments in which the same sheep were confined in a respiration chamber and given the same food. CH_4 production from the lungs as measured for these sheep, was only 17% of that determined for the same sheep when they were in the respiration chamber, and this amount did not vary with the amount of food given. Similarly CO_2 production from the lungs was also less than that determined by the respiration chamber method, the discrepancy being negligible at low feeding levels but increasing markedly at high levels of feeding.

These differences in the amount of CH_4 and CO_2 between the levels measured in the respiration chamber and those measured with the tracheostomy preparations were presumed to represent the amounts lost by belching. Indirect evidence is presented to show that during the act of eating large amounts of CO_2 are lost by belching. Direct determination of O_2 consumption and CO_2 production from the pulmonary exchange of tracheostomized sheep while they were eating shoed that considerable increases in O_2 consumption occurred between the 5th and 10th minute after the onset of feeding and that these increases were accompanied by the expiration of slightly greater volumes of CO_2 and lower volumes of air, associated with vasoconstriction of the extremities.

3. Methods of calculating the heat production of sheep from their pulmonary exchange of O_2, CO_2 and CH_4 are discussed, and a method has been evolved of calculating the heat production when sheep are in a state of cold stress, from the increase in O_2 consumption above that observed under thermoneutral conditions. Using the results obtained from the sheep with which the total gaseous exchange was measured using the face-mask technique, a comparison was made between the heat production calculated from the O_2 consumption only and that obtained from the more normal method which depends on conversion factors for O_2 consumption and for CO_2, CH_4 and urinary N production. The correlation coefficient between the two methods of calculating heat production was 0.99.

4. Experiments were made with four tracheostomized sheep and with two fitted with face masks to determine the effects of artificial rain and changes in air temperature, wind velocity and infrared radiation

on their heat production and body temperature. Responses of O_2 consumption to changes in wind velocity were virtually complete 50 min after the change. Responses to changes in air temperature and infrared radiation were practically complete 30 and 50 - 60 min after the changes were made. Responses of O_2 consumption to the initiation of wetting were not complete even when the wetting process had continued for 2 h 20 min. When either wind velocity or air temperature was altered changes in the skin temperature of the trunk occurred very rapidly but with changes in the intensity of infrared radiation the temperature of the skin of the trunk changed rapidly at first and then more slowly. Skin temperatures, in response to wetting, at first fell rapidly. This was followed by a transient rise occurring 10 - 15 min after wetting began, after which the skin temperatures became relatively stable. In all the experiments the response of the skin temperature of the fetlock to changes in the environment was much slower than that of the trunk.

5. Heat production was increased by wind, a value 3.3 times that noted in the thermoneutral zone being observed in a sheep with a short fleece kept at -3° in a wind of 4.2 m.p.h. Rectal temperature also increased when wind velocity was increased, and the validity of this increase is discussed in relation to the changes that have been found by other workers in longer term trials. When the sheep were wetted with artificial rain, heat production increased and a level of 5762 $kcal/m^2/24$ h was reached in one sheep bearing a short fleece, when it was subjected to wind and rain at the same time, compared with a typical value of 1350 $kcal/m^2/24$ h in the thermoneutral zone. Heat production was reduced in a given air velocity when the hind-quarters, rather than

the side of the sheep, were presented to the wind but only when the fleece was long. Wind resulted in the development of large windward-leeward gradients in skin temperature. The increase in heat production on subjecting the sheep to wind was greater when incoming radiation levels were small than when they were increased by infrared heaters.

6. Tissue insulation of sheep, defined as the rectal temperature - skin temperature gradient divided by the total heat production, once vasoconstriction has been established, was relatively unaffected by wind velocity, air temperature or wetting. Evidence is presented that the tissue insulation of Scottish Blackface and Cheviot sheep is greater than that of Downcross sheep.

7. External insulation, defined as the joint insulation of the air interface and the coat, increased linearly with increasing fleece length over the range 5 - 50 mm, but fell with increasing wind velocity, the fall being numerically greater when the fleece was long than when it was short. Partial destruction of the coat insulation by wind was detectable for the whole range of wind speeds studied (0.6 - 9.9 m.p.h.). Similarly decreases in coat insulation were found on wetting the sheep. The combined effect of wind and artificial rain appeared to be less than the sum of the two separate effects in decreasing coat insulation.

8. Direct measurements of the solar heat load impinging on sheep were made using a solarimeter at ten positions distributed around a cylindrical model of a sheep. Two such models, approximating in dimensions to those of fleeced and shorn sheep, were used and the results summated to give the total solar radiation impinging on the models. Results show that the total solar heat load on a sheep in the west of Scotland can be as

high as 300 kcal/m^2/h, i.e. some six to eight times the basal heat production of the animal. It was found that even under a completely overcast sky the solar heat load was seldom less than 10 - 15% of the basal heat production. Reflectance values of solar radiation were measured for sheep skins and for one black cattle hide. The mean reflectance of solar radiation was 25.8% for the fleeced sheep skins, 41.8% for the shorn sheep skins and 10.1% for the black summer-coated cattle hide. The albedo of grass swards ranged between 0.24 and 0.26, values that agree well with other published estimates.

9. Four sheep wearing face masks were used to measure the effect of the natural outdoor climate on their heat production. A correlation coefficient of 0.99 was found between the external insulation values, determined on these sheep when the incoming solar radiation level was less than 0.1 cal/cm^2/min, and the corresponding insulation values predicted from the results of the artificial climate experiments. Increasing levels of solar radiation increased the insulation of the coat and this increase in insulation appeared to depend on coat length as well as on the level of impinging solar radiation. However, the increases in coat insulation were not as large as would have been expected from the solar heat loads measured on models of sheep.

10. Methods of estimating heat production or external insulation from (1) measurement of climatic factors, (2) skin and rectal temperature measurements, and (3) heat losses from homeostatic artificial sheep, are discussed in relation to the measurement of the heat production of free-grazing sheep. The critical temperatures of sheep have been calculated for different fleece lengths, wind velocities and breeds. Similarly, equivalent still air temperatures have been calculated in

which the cooling power of wind has been combined with the ambient temperature by estimating the extent to which air temperature would have to decrease under still air conditions to result in an equivalent increase in heat production. It was shown that the effect of wind on the heat losses of sheep was greatest at low ambient temperatures.

11. The results obtained in this study are discussed with particular reference to present animal husbandry practices. The importance of effective shelter and good nutrition for sheep in cold environments is emphasized.

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APPENDIX I

Brit. J. Nutr. (1963), 17, 523

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The accuracy and ease with which measurements of respiratory metabolism can be made with tracheostomized sheep

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In developing methods to study the effect of the outdoor environment on the metabolism of sheep, we required a method for estimating heat production continuously over several hours. The fitting of a permanent tube in the trachea seemed ideal for this purpose, and this paper summarizes experiments carried out to test the validity of the technique. A second paper describes experiments on the effect of environmental factors using this method of measuring metabolism (Joyce & Blaxter, 1964). Tracheostomized sheep, cattle and horses have been used as experimental subjects since the 1880s as reviewed by Flatt, Waldo, Sykes & Moore (1958) and, more recently, Webster & Cresswell (1957), working with sheep, have used the method with success. Only one adequate test of the validity of the method has been traced. Klein (1915) compared estimates of the oxygen consumption and carbon dioxide and methane production of a tracheostomized bull made in respiration chambers of the open- and closed-circuit types with those made from the pulmonary exchange alone. He concluded that a large part of the CH_4 produced in the gut was not excreted by the lung. No experiments to find the extent of and variation in the pulmonary loss of gas formed in the gut with diet and other factors have been traced.

EXPERIMENTAL

Animals

Eight wether sheep were used as experimental animals. They were all over 4 years of age and the breeds included Scottish Blackfaces, Cheviots and Down crosses.

Establishment of tracheal fistulas

The technique of complete transection of the trachea developed with cattle by Colvin, Wheat, Rhode & Boda (1957) and used successfully by Flatt *et al.* (1958) was used unsuccessfully with one sheep. The trachea was transected, one cartilaginous ring removed and the distal and cranial ends were sutured to the skin. When the operation was complete a thin-walled Polythene tube was inserted to join the two severed ends which were then separated by a furrow in the skin about 3 cm long. It was found that the considerable dorsoventral movement of the neck by the sheep resulted in a movement of this Polythene tube, with consequent constant traction on the two sutured ends of the trachea. If softer-walled tubing was inserted, movement of the head resulted in its collapse, and if no tube was inserted, a contraction of the wound occurred which tended to obliterate the lumen of the trachea. The sheep was destroyed.

In the remaining seven sheep a tracheostomy was made. The sheep was anaesthetized with Nembutal (Abbott Laboratories Ltd) and placed on the operating table. To prevent possible drainage of blood into the lungs or of regurgitated rumen contents into the trachea, the rear of the animal was elevated. A mid-line incision 3 cm long was made, the omohyoideus muscle separated and the trachea exposed. The width of the cartilaginous rings and the internal diameter of the trachea varied considerably from sheep to sheep, and from either one ring where they were wide or two where they were narrow, a segment was removed to leave an opening approximately 1 cm × 1 cm. A circular plug of solid Perspex with two lips as shown in Fig. 1 was inserted and the skin sutured to the tracheal wall. Healing was complete in 10–14 days when the solid

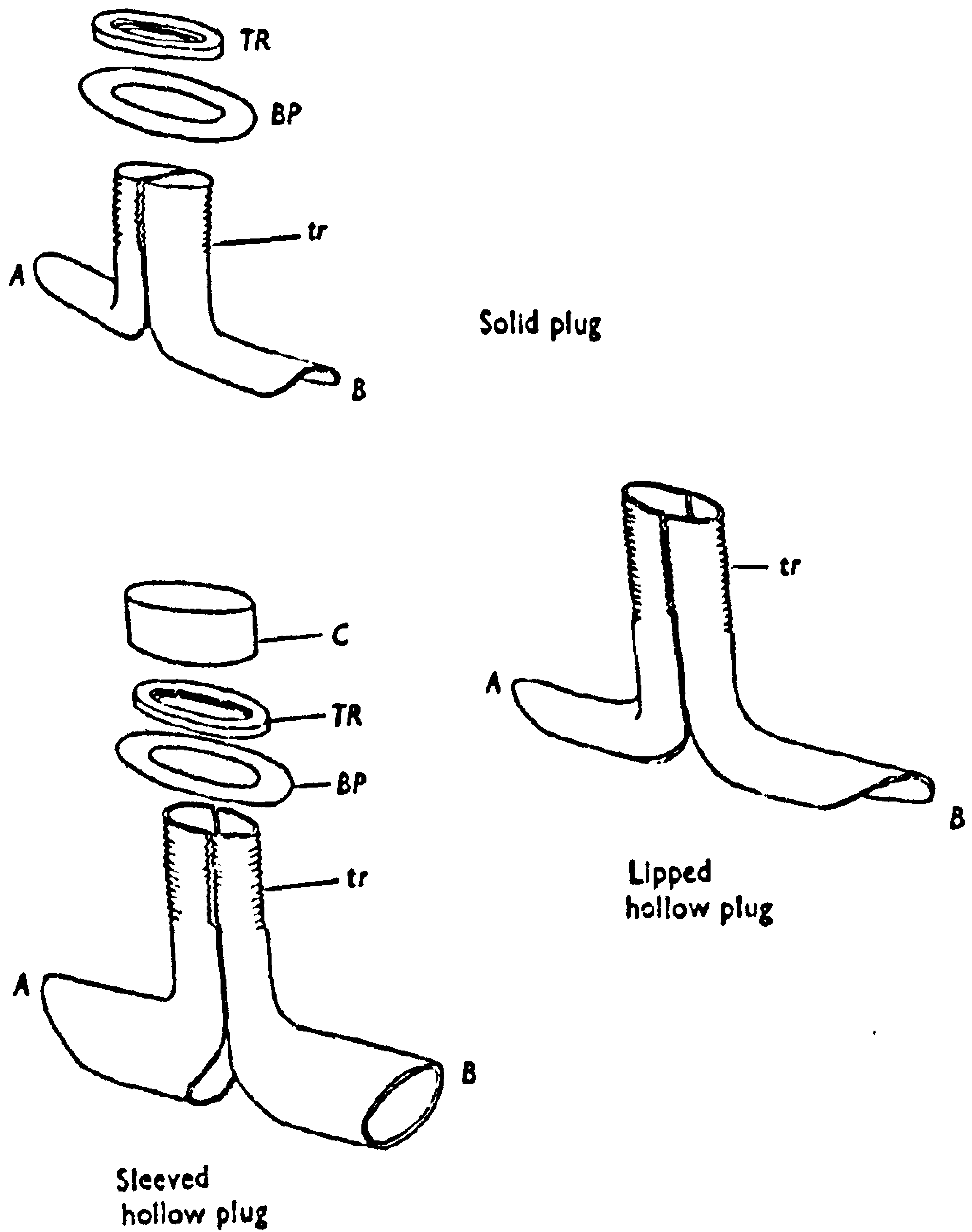

Fig. 1. Plugs used to close tracheostomies in sheep. The solid plug (upper), diameter 16 mm, length *A–B* 45 mm, was used immediately after the operation. The lipped hollow plug (lower right), external diameter 17 mm, internal diameter 14 mm, length *A–B* 55 mm, was inserted 10–14 days after the operation. The sleeved hollow plug (lower left) had the same dimensions as the lipped hollow plug, but the lips were replaced by a tube, 15 mm external diameter, 13 mm internal diameter. A sponge-rubber pad was inserted between the thin bearing plate and the neck of the sheep. *TR*, Threaded ring; *BP*, thin bearing plate; *C*, cap; *tr*, threaded.

plug was removed and a hollow plug of Perspex inserted. These hollow plugs were of two types, as shown in Fig. 1. One, the lipped type, consisted of a hollow threaded tube with two small lips and the other, the sleeved type, consisted of a hollow threaded tube to which was cemented a short tube of thin Perspex. The threaded tubes of both plugs were split into two to facilitate their insertion. With both types of plug a cap was screwed on to the threaded tube when the sheep was not on experiment so that breathing took place through the nose and mouth.

Maintenance of tracheostomized sheep. The sheep were anaesthetized at about 2-weekly intervals to remove the plug to clean or replace it. Considerable difficulties were encountered in ensuring that the trachea remained fully patent over several months. Evidently Cresswell & Harris (1961) encountered similar difficulties. Two types of closure of the trachea were encountered. In the first, the trachea tended to collapse laterally with oedematous swelling, particularly in those sheep in which the trachea had a small internal diameter. This danger was accentuated by the use of lipped plugs and obviated by the use of sleeved plugs. In the second, callus formation occurred at the point where the leading edge of the internal lip or internal sleeve was in contact with the tracheal wall. In addition, some sheep could not easily cough mucus past the internal sleeves. This mucus tended to harden on the internal wall of the sleeve, thus blocking its lumen. Except in those instances reported in the case histories below when distress was evident immediately after feeding necessitating the fitting of new types of plug, the behaviour of the sheep was perfectly normal in all respects.

Individual histories

Sheep Ax. A solid plug was fitted to this Cheviot sheep, collections of expired gas being made by insertion of a cuffed tracheal tube into the caudal trachea after removal of the plug. Lateral closure of the trachea with much swelling of the tracheal wall occurred after 50 days, when the sheep was destroyed.

Sheep Ct. A lipped hollow plug was fitted 17 days after the operation to this Blackface sheep. Partial closure through collapse occurred on the 84th day, when a sleeved plug was fitted into the cranial end of the trachea. A completely sleeved plug was fitted on the 131st day, but internal growth caused partial closure of the caudal part of the trachea and the sheep was destroyed on the 169th day after the operation.

Sheep Cs. A lipped hollow plug was fitted on the 17th day after operation in this Cheviot sheep. It was replaced by a sleeved plug on the 79th day since some signs of collapse of the trachea were noted. This plug was finally replaced by a complete sleeve (both caudal and cranial to the fistula) on the 318th postoperative day. Internal callus formation occurred in the cranial part of the trachea and the sheep was killed on the 361st postoperative day.

Sheep Zk. A lipped hollow plug was fitted to this Blackface sheep on the 14th postoperative day. A completely sleeved cannula was fitted on the 62nd day. Growth of an inoperable callus with partial closure of the trachea necessitated the sheep's destruction on the 118th postoperative day.

Sheep Yl. This Down cross was fitted with a lipped plug on the 14th postoperative day and the anterior part of the trachea with a sleeved plug on the 92nd day. On the 165th day both caudal and cranial parts of the trachea were sleeved. Callus formation on the wall of the cranial part of the trachea necessitated the sheep's slaughter on the 274th postoperative day.

Sheep Se. This Cheviot sheep was fitted on the 14th postoperative day with a lipped plug which in turn fitted into a short (2½ cm) segment of Polythene tube which was inserted into the trachea. This device, used to prevent the initial lateral collapse of the trachea, was not successful and a complete sleeved cannula was fitted on the 47th day. Growth of a callus in the cranial part of the trachea necessitated the sheep's slaughter on the 182nd postoperative day.

Sheep Dl. This Blackface sheep was initially treated in precisely the same way as sheep Se above. Respiratory distress due to oedematous swelling of the trachea developed on the 39th day. Cannulation with a sleeved plug was not successful and the sheep died under anaesthesia when a further attempt at repair was made.

Collection of expired air

The method used to obtain expired air from the tracheostomized sheep was similar to that described by Webster & Cresswell (1957) and by Cresswell (1961) in that an inflatable balloon was introduced into the upper trachea through the hollow plug so that all inspired and expired air was diverted through the hollow plug. The plug was connected by a short (8 in.) length of non-collapsible tubing (Siebe Gorman Co. Ltd) to a two-way mica valve assembly of the type used in studies with man (Zentral-Werkstatt Göttingen G.m.b.H., Göttingen, Germany). The expiratory side of this valve was then connected with large Douglas bags measuring 42 × 42 × 12 in., which were manufactured from butyl rubber (J. G. Franklin and Sons Ltd) to our specification. A two-way, 1 in. bore aluminium stop-cock (Siebe Gorman Co. Ltd) placed between the expiratory valve and the bag allowed the expired air to be directed to the Douglas bag when required. The volume of the bag allowed collections of expired air to be made for periods of up to 30 min. For the normal amount of gas collected the pressure exerted by the Douglas bags, that is the resistance they caused to breathing, was 2 mm water. This resistance was very constant throughout the collection period; indeed a pressure rise was only detected when the bags were obviously full and distended.

Measurement of expired air volume and respiratory metabolism

The Douglas bags were emptied by means of a vacuum pump (W. Edwards and Co. (London) Ltd). The outflow from the vacuum pump was led through 9 ft of rubber tubing to a precision wet-gas meter (Parkinson and Cowan Industrial Products). This length of tubing was found adequate for sufficient cooling of the air, which was heated slightly in its passage through the pump, to prevent a temperature rise in the wet-gas meter. The use of a vacuum pump ensured a standard and quantitative emptying of the bags in each experiment and a constant rate of air flow through the meter. The calibration of the meter was checked by passing through it weighed amounts of nitrogen and air in known volumes as measured in large spirometers. A sample of the air was taken from the outflow of the wet-gas meter, due precaution being taken to allow for wash-out time and for any equilibration of the CO_2 in the air stream with the water in the meter. This sample was dried by passing it over $CaCl_2$ and analysed for O_2 with a paramagnetic oxygen analyser and for CO_2 by an analyser that determined thermal conductivity. CH_4 was determined from the CO_2 formed after its combustion over palladium. The analyser (Cambridge Instrument Co. Ltd) was checked daily by analysis of outdoor air, pure N_2 and two standard mixtures of O_2, N_2, CO_2 and CH_4 and also by analysis of single samples of expired air by the Haldane method. Each complete analysis took 7 min and forty or more determinations could be made each day.

Calculations of inspired air volumes were made on the assumption that the volume of N_2 inspired was the same as that expired. O_2 consumption and CH_4 production were computed from the differences between inspired and expired amounts.

Testing the method. The whole assembly was tested for leaks by comparing the volume of N_2 inspired from one Douglas bag with that expired into another. A large volume of air of known N_2 content was measured into a Douglas bag with a wet-gas meter. The inspiratory valve of the assembly was connected with this bag and the sheep allowed to expire air into a second bag. When the inspiratory bag was almost empty, the residual volume of air was measured with the wet-gas meter to give the inspired volume of N_2. Measurement of the volume and N_2 content of the air expired by the sheep gave the volume of N_2 expired. In five such tests the recovery of N_2 was 99·0 ± 1·1%.

The introduction of a balloon into the upper trachea, and the diversion of expired air into a bag involved considerable interference with the sheep. To test the extent to which measurements of consumed O_2 made with Douglas bags agreed with the amounts consumed when the animal was not restrained, comparisons were made of the O_2 consumption of the tracheostomized sheep given constant rations and kept in a respiration chamber, and O_2 consumption determined from the Douglas bag measurements. Two series of such tests were made.

In the first series of tests, sheep *Ct* and sheep *Cs* were given 800 g dried grass (16·99% protein) and 200 g crushed oats in two meals at 5.30 am and 4.00 pm each day. On 5 consecutive days each sheep was confined in a respiration chamber and the consumption of O_2 and production of CO_2 and CH_4 were determined over 24 h. In addition, O_2 consumption and CH_4 production, but not CO_2 production, were determined hourly from 10 am to 6 pm, making eight determinations on each day. The times spent standing and lying were also measured in each hour. When these determinations were complete, measurements of O_2 consumption, CO_2 and CH_4 production were made by the Douglas bag method. Thirty-two determinations were made with each sheep between 10 am and 4 pm, measurements being spread over 6 days with sheep *Ct* and over 3 days with sheep *Cs*. In addition, with sheep *Ct* two series of measurements of metabolism were made with Douglas bags to cover the hour before feeding and the hour after feeding.

In the second series of tests, sheep *Cs*, *Se* and *Yl* were each given three different amounts of a diet of dried grass and oats in equal proportions. The amounts of the mixture given to sheep *Cs* were 900, 1350 and 1800 g/day, to sheep *Se* 450, 900 and 1350 g/day and to sheep *Yl* 450, 1350 and 1800 g/day. After a preliminary period of 14 days on each ration each sheep was confined in the respiration chamber for 3 days and on each day O_2 consumption, CO_2 and CH_4 production were measured for three consecutive periods of 3 h from 9 am to 6 pm and for the night period of 15 h each day. The sheep were given their rations in two meals at 6 am and 6 pm. When the experiments in the respiration chamber were complete, measurements of the respiratory exchange were made by the Douglas bag method between the hours of 9 am and 5 pm.

Respiration chamber experiments. The chamber described by Wainman & Blaxter (1958) was used.

RESULTS

Effect of standing on O_2 consumption

When in the respiration chamber the sheep, being unrestrained, could lie at will and usually did so for long periods. When the Douglas bag technique was used they could lie if they wished but they invariably stood. Pullar's (1962) observation that standing can increase heat emissions by up to 70% suggests that in any comparison between chamber and Douglas bag measurements account should be taken of any increase in rate of O_2 consumption during standing.

Analysis of covariance of the results of the two series of experiments in the respiration chamber was made and the regression of hourly O_2 consumption on standing time was computed from the residual sum of squares after components of variation attributable to ration, time of day, days of experiment and the interaction ration × time of day had been removed. The results are given in Table 1.

The results showed that standing resulted in an increase in O_2 consumption in both series of experiments but in neither was the effect significant statistically. The value of 1 l. O_2/h, corresponding to about 5·0 kcal/h or 1·7 kcal/kg body-weight 24 h is in agreement with observations of Hall & Brody (1933) that the increase in metabolism as measured from O_2 consumption in cattle is 2·1 kcal/kg body-weight 24 h. It is much smaller than the increased heat output noted by Pullar (1962) and, as it was not statistically significant, the effect of standing has been ignored in subsequent calculations.

Comparison of respiratory measurements and chamber measurements in the first series of experiments

In Table 2, a comparison is made between the measurements made over 24 h periods in the respiration chamber, those made over 1 h periods between meals in the respiration chamber and those made by the Douglas bag technique.

The results show that the Douglas bag method for determining O_2 consumption gave results that agreed with those determined by hourly measurements in the chamber, the means being 16·23 and 16·15 l./h respectively. The values were very close to those determined over 24 h in the respiration chamber. The CO_2 production determined by Douglas bag was 4·0 l. lower in sheep *Ct* and 4·2 l. lower in sheep *Cs* than the l./h values computed from the 24 h respiration chamber experiments.

CH_4 production measured by Douglas bag was very small and only about one-tenth of that obtained by hourly measurements in the chamber. Hourly measurements of CH_4 production made during the intervals between meals were lower than the mean values computed from the 24 h measurement of CH_4 production, which includes the effects of two meals.

Table 1. *Pooled regression of oxygen consumption of sheep (l./h on standing time (h))*

Series of experiments	df	Increase in O_2 consumption on standing	Mean O_2 consumption
1st* (1 h measurements)	53	0·79±0·85	15·26
2nd (3 h measurements)	36	1·07±1·34	17·31

* Results of an additional two experiments in which hourly collections were made have been included together with those of the two experiments included in series 1.

Table 2. *Comparison of the hourly oxygen consumption and carbon dioxide and methane production of two sheep measured in three ways*

		Method of measurement					
		Respiration chamber measurements				Douglas bag measurements	
		During 24 h		During 1 h			
Measurement	Sheep	No. of observations	Value (l./h)	No. of observations	Value (l./h)	No. of observations	Value (l./h)
O_2 consumption	*Ct*	10	16·08±0·18	30	16·33±0·22	27	16·09±0·29
	Cs	10	16·73±0·09	30	15·92±0·26	27	16·37±0·26
CO_2 production	*Ct*	10	16·89±0·19	—	—	27	12·89±0·26
	Cs	10	17·56±0·08	—	—	27	13·36±0·25
CH_4 production	*Ct*	10	1·47±0·03	30	1·29	27	0·11±0·01
	Cs	10	1·36±0·02	30	1·20	27	0·16±0·02

In sheep *Ct* probably about 4·0 l. of the CO_2 and 1·2 l. of the CH_4 produced were not collected when tracheal gas was collected for an hour. In sheep *Cs*, probably about 4·2 l. of the CO_2 and 1·0 l. of the CH_4 produced were not collected. The inference is that these volumes were lost by belching, but the possibility that small amounts were lost through the skin and anus is not discounted. Belching, however, was obviously the most important source of these large volumes of gas. When the caps of the hollow plugs were removed, belching could readily be detected by an amplification of its characteristic noise by the upper trachea. Dougherty (1961) has shown that when sheep belch the glottis remains open and belched gas enters the respiratory passages. When the cap is removed from the hollow plug, the belched gases emerge and can be smelled. There is rarely, if ever, a similar smell in the air expired normally from the nostrils of intact sheep or of sheep with closed tracheostomies.

The results show that the use of tracheostomized sheep gives results for O_2 consumption in agreement with those determined without restraint or interference but that CO_2 and CH_4 production are underestimated.

Comparison of respiratory measurements and chamber measurements in the second series of experiments

The second series of experiments was made to find whether belching was affected by the feeding level of the sheep, and whether an estimate of the respiratory quotient could be obtained by correcting the values found for CO_2 production and CH_4 production by the Douglas bag method for the amounts presumed to be lost in the belch.

Table 3. *Comparison of oxygen consumption and carbon dioxide and methane production of sheep given different rations determined in two ways*

Measurement	Ration (g/day)	Sheep	Respiration chamber measurements* (l./h)	Douglas bag measurements† (l./h)
O_2 consumption	450	*Yl*	14·34 ± 0·35	14·52 ± 0·15
		Se	14·96 ± 0·32	15·06 ± 0·17
	900	*Se*	15·17 ± 0·32	15·11 ± 0·26
		Cs	14·07 ± 0·24	13·59 ± 0·19
	1350	*Yl*	18·95 ± 0·35	19·10 ± 0·27
		Cs	17·90 ± 0·24	18·05 ± 0·13
		Se	17·38 ± 0·32	17·99 ± 0·26
	1800	*Yl*	22·19 ± 0·35	22·42 ± 0·30
		Cs	20·79 ± 0·24	21·08 ± 0·22
CO_2 production	450	*Yl*	12·06 ± 0·34	12·34 ± 0·17
		Se	13·20 ± 0·38	13·04 ± 0·16
	900	*Se*	14·94 ± 0·38	14·87 ± 0·22
		Cs	13·94 ± 0·29	13·55 ± 0·23
	1350	*Yl*	19·47 ± 0·34	18·02 ± 0·29
		Cs	18·56 ± 0·29	17·03 ± 0·28
		Se	18·11 ± 0·38	17·59 ± 0·27
	1800	*Yl*	24·06 ± 0·34	21·87 ± 0·29
		Cs	21·59 ± 0·29	20·90 ± 0·33
CH_4 production	450	*Yl*	0·66 ± 0·095	0·21 ± 0·0081
		Se	0·80 ± 0·056	0·13 ± 0·0077
	900	*Se*	1·23 ± 0·056	0·21 ± 0·011
		Cs	1·15 ± 0·104	0·35 ± 0·03
	1350	*Yl*	1·64 ± 0·095	0·16 ± 0·013
		Cs	1·43 ± 0·104	0·11 ± 0·02
		Se	1·58 ± 0·056	0·40 ± 0·0098
	1800	*Yl*	2·04 ± 0·095	0·44 ± 0·11
		Cs	1·57 ± 0·104	0·36 ± 0·04

* Mean values with their standard errors for nine observations.
† Mean values with their standard errors for sixteen observations.

The results of the nine experiments are given in Table 3. The mean O_2 consumption measured in the chamber was 0·02 l./h lower than that measured by Douglas bag. This systematic difference was not significant statistically and, in any event, it is numerically negligible compared with the mean consumption of 17·3 l./h. As in the first series of experiments, less CO_2 and less CH_4 were collected in the Douglas bags than were produced in the chamber.

The amount of CH_4 produced when a sheep was in the chamber can be taken as a convenient index of the amount of fermentation that occurred, and in Fig. 2 the amount of CH_4 belched (estimated as the difference between the amount produced in the chamber and that collected in the Douglas bag) has been plotted against CH_4 production. Fig. 2 includes also the results of two observations made in the first series of experiments.

The regression of CH_4 belched on CH_4 produced was:

$$\text{belched } CH_4 \text{ (l./h)} = 0{\cdot}833\ CH_4 \text{ (l./h) produced} - 0{\cdot}03. \qquad (1)$$

The regression was highly significant statistically ($P < 0{\cdot}001$) and the residual standard deviation was ±0·10 l./h. In Fig. 3 the CO_2 presumed to be belched has been plotted against the CH_4 production. No results for the first series of experiments are available in this instance. The regression of CO_2 belched on CH_4 produced was:

$$\text{belched } CO_2 \text{ (l./h)} = 1{\cdot}579\ CH_4 \text{ (l./h) produced} - 1{\cdot}38. \qquad (1)$$

This regression was significant ($0{\cdot}001 < P < 0{\cdot}01$) and the residual standard deviation was ±0·42 l./h.

Equation (1) shows that CH_4 loss on belching was proportional to CH_4 production since the intercept term (−0·03 l./h) was not significantly different from zero, and that about 83% of the CH_4 produced was lost by belching irrespective of the feeding

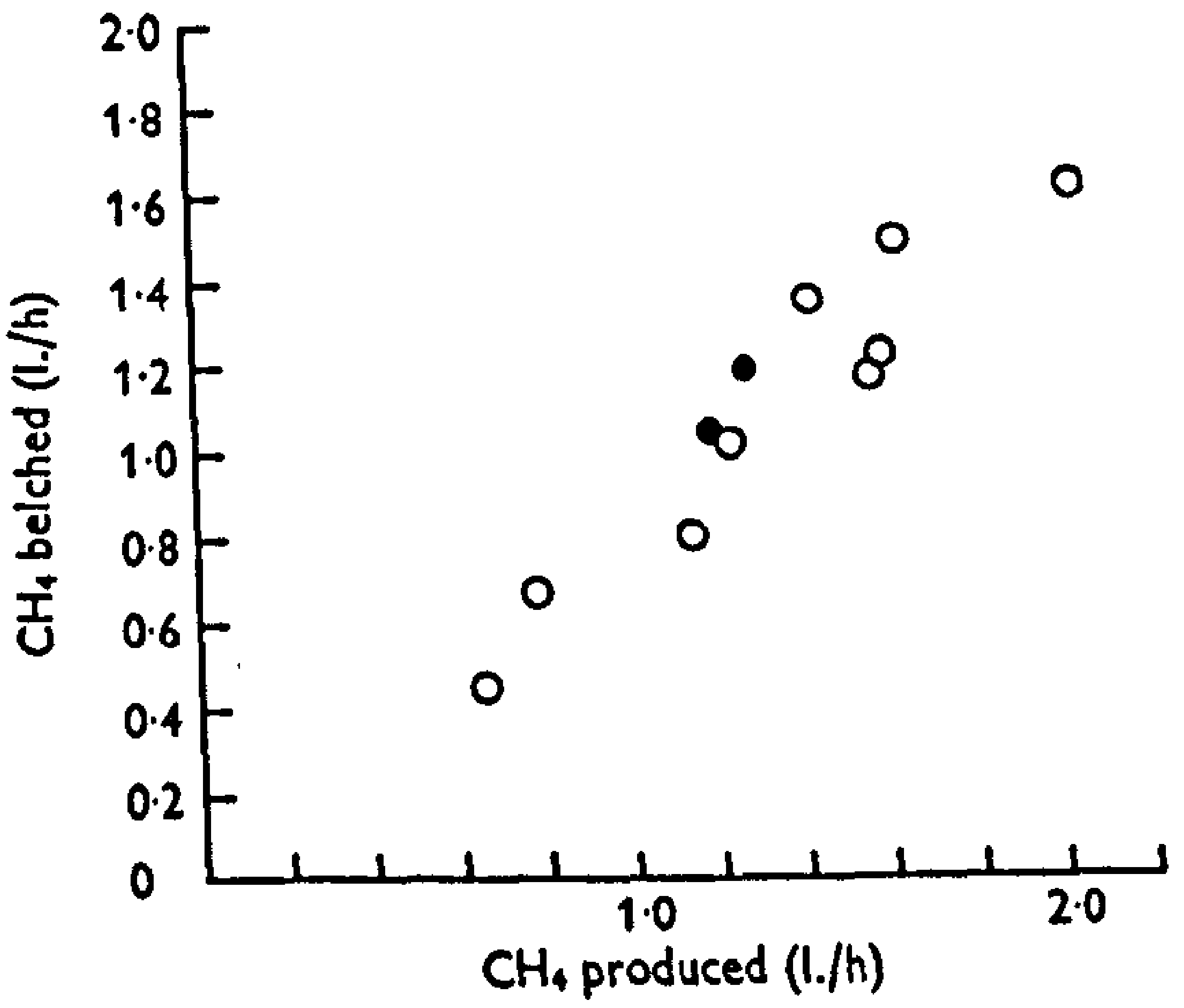

Fig. 2

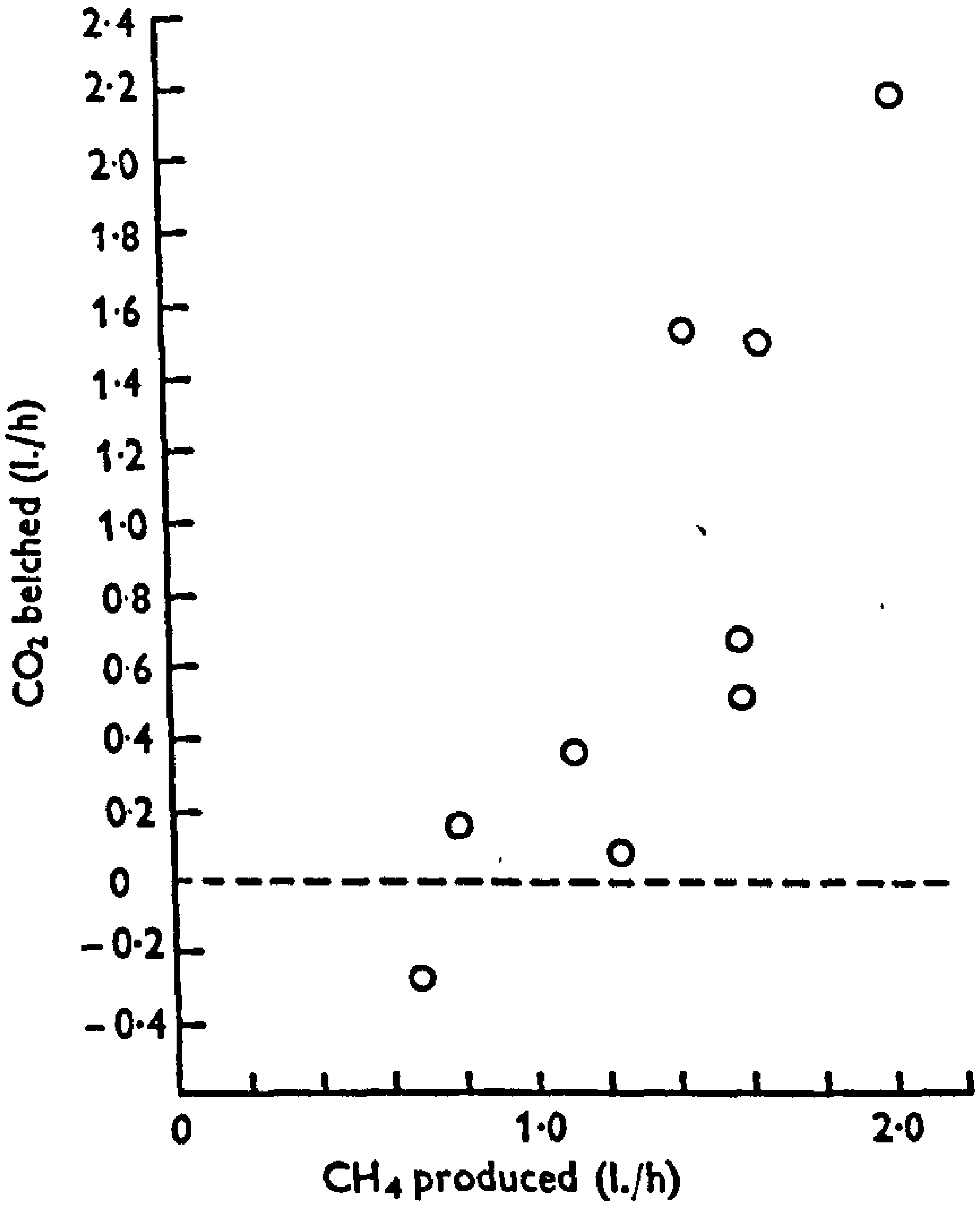

Fig. 3

Fig. 2. Volume of CH_4 not accounted for, and presumed to have been belched, when the pulmonary exchange of sheep was measured and volume of CH_4 produced, which is an index of the amount of fermentation. ●, values from the first; ○, values from the second series of experiments.

Fig. 3. Volume of CO_2 not accounted for, and presumed to have been belched, when the pulmonary exchange of sheep was measured and volume of CH_4 produced, which is an index of the amount of fermentation.

production, however, fell from one 3 h period to the next. The results for O_2 were in agreement with those obtained in the first series of experiments.

An estimate can be made of the O_2 consumption and CO_2 and CH_4 production associated with the two meals by making the assumption that the metabolism during the 9 h before the morning meal was the same as that for the 9 h before the evening meal. The mean hourly consumption of O_2 during the 3 h in which a meal occurred was thus

$$\frac{1}{2}\left(5\times\begin{array}{c}\text{hourly } O_2 \text{ consumption during}\\ \text{the 15 h night interval}\end{array} - \begin{array}{c}3\times\text{hourly } O_2 \text{ consumption during}\\ \text{the 9 h day interval}\end{array}\right).$$

The results of such calculations are given in Table 5. They indicate that, with the lowest amount of food, the increase in metabolism during the 3 h following food was apparently negative. This is undoubtedly an artifact since when this submaintenance ration was given the sheep were particularly active during the day and the negative value suggests that metabolism during the corresponding 9 h of the night interval was grossly overestimated. The results with the rations of 900, 1350 and 1800 g dried grass showed increases in O_2 consumption and, more particularly, of CO_2 production during the feeding period. The ratio of the increase in CO_2 production to the increase in O_2 consumption for these three rations exceeded 2·0 in all instances, suggesting very strongly that much of the CO_2 arose from incomplete degradation of the food, that is in the fermentation process. The excess CO_2 probably represents belched gas. The increase in CH_4 production during the 3 h period containing a meal was constant at 0·55 l./h.

Table 5. *Estimated rates of oxygen consumption and of carbon dioxide and methane production, before and during meals, by three sheep given four rations*

Measurement	Ration (g/day)	In 9 h preceding meal (l./h)	In 3 h including meal (l./h)	Estimated increment due to feeding (l./h)
O_2 consumption	450	14·0	11·5	−2·5
	900	14·6	15·3	+0·7
	1350	18·1	20·0	+1·9
	1800	21·5	25·9	+4·4
CO_2 production	450	12·6	10·7	−1·9
	900	14·4	17·7	+3·3
	1350	18·7	24·5	+5·8
	1800	22·8	32·1	+9·3
CH_4 production	450	0·73	0·64	−0·09
	900	1·19	1·74	+0·55
	1350	1·55	2·10	+0·55
	1800	1·80	2·36	+0·56

Experiments with sheep *Ct* were made to give further information on the effects of feeding. The Douglas bag method was used, and Fig. 4 shows the results obtained in one experiment. When food was brought into the room 10 min before feeding, both O_2 consumption and CO_2 production increased. O_2 consumption was maximal from production, however, fell from one 3 h period to the next. The results for O_2 were in agreement with those obtained in the first series of experiments.

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$$\frac{1}{2}\left(\begin{array}{c}5\times\text{hourly } O_2\text{ consumption during}\\ \text{the 15 h night interval}\end{array} - \begin{array}{c}3\times\text{hourly } O_2\text{ consumption during}\\ \text{the 9 h day interval}\end{array}\right).$$

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Experiments with sheep *Ct* were made to give further information on the effects of feeding. The Douglas bag method was used, and Fig. 4 shows the results obtained in one experiment. When food was brought into the room 10 min before feeding, both O_2 consumption and CO_2 production increased. O_2 consumption was maximal from the 5th to the 10th min after feeding when it was 67% higher than the values noted 20–30 min before feeding. CO_2 production from the lungs at this time was 84% higher than initial values and the ratio of the increase in CO_2 production to the increase in O_2 consumption was 0·88. After the 10th min, although the animal continued to eat, both O_2 consumption and CO_2 production fell. When eating stopped, CO_2 production and O_2 consumption fell to values slightly higher than those noted before the meal. One feature of the experiment was that during eating the volume per min of the respiration fell markedly and when the meal was consumed it rose to

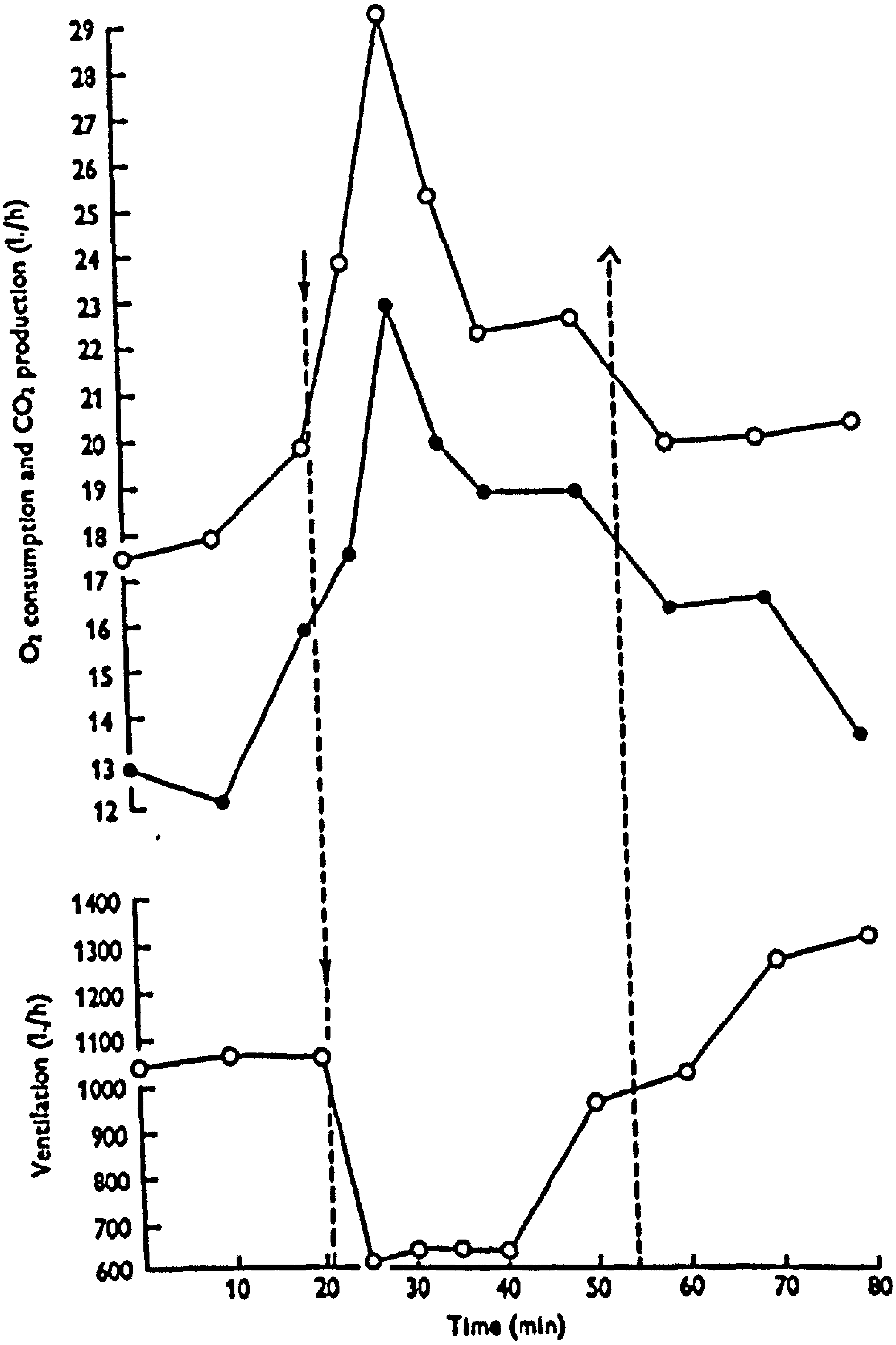

Fig. 4. Effect of a meal given at ↓ and finished at ↑ on O_2 consumption and CO_2 production (upper graph) and pulmonary ventilation/h (lower graph) in sheep *Ct*. Upper graph: ○—○, O_2 consumption; ●—●, CO_2 production.

values above those observed before feeding began. A second experiment with sheep *Ct* confirmed these findings. O_2 consumption rose 47% and CO_2 production 70% from the 5th to the 10th min during feeding, and after feeding they fell to values 9 and 13% respectively above prefeeding levels.

During the course of experiments on the effect of environmental temperature on sheep (Joyce & Blaxter, 1964), body surface temperatures were recorded continuously when the sheep were in the chambers. When the sheep were fed, an immediate vasoconstriction of the legs occurred which lasted for 10–15 min. This response was recorded on many occasions. Furthermore, it could be elicited by sham feeding, that is by operating the control mechanism of an empty manger, the animals being well accustomed to hearing this noise when they were fed.

These observations together with those for O_2 consumption suggest that the large increase in metabolism which occurs during the 1st h of feeding can be ascribed to the act of eating rather than to the specific dynamic effect of food in its classical sense. Neural or hormonal effects may be involved.

Pathological findings in tracheostomized sheep

The nature of the callus was investigated in the sheep that were killed and will be reported elsewhere by P. S. Blackburn.

DISCUSSION

Measurements of the gaseous exchange of tracheostomized sheep, though simple to make, are difficult to convert into estimates of heat production. As was recognized many years ago (Klein, 1915), the exchange of gas from the lung differs from that of the whole animal. A large amount of CH_4 and a still larger amount of CO_2 are not measured, for they are belched by the sheep. The O_2 consumption measured from the pulmonary exchange is, however, the same as that measured by confining the animal in a chamber. The experiments show that the discrepancy between the total amount of CH_4 produced and that collected from the lungs is not constant but varies with the amount of food given and the amount of fermentation elicited. About 83% of the CH_4 produced is not excreted by the lungs and is lost, presumably by belching. This value is higher than that of 70% found by Klein (1915). A correction could be made to the values obtained in measurements of pulmonary excretion to take belching into account by multiplying the measured CH_4 excretion by the lungs by 6, since about one-sixth of the total CH_4 is collected.

With CO_2 production, the discrepancy between total production and the pulmonary exchange is small when small amounts of food are given and increases markedly when the amount of food given is large. Moreover, indirect evidence suggests that during feeding the loss of CO_2 is proportionally greater than it is between meals. From equations 1 and 2, an expression could be derived for the prediction of total CO_2 production from the measured pulmonary loss of CH_4 and CO_2 which would apply to conditions operating in the 9 h before a meal. Such an expression would not apply to the pulmonary exchange measured during and immediately after feeding and might well not apply to diets other than those used in this experiment.

5. Indirect evidence is presented to show that during the act of eating even greater amounts of CO_2 are belched. Direct determination of O_2 consumption and CO_2 production from the pulmonary exchange during eating showed that considerable (50–60%) increases in O_2 consumption occurred between the 5th and 10th min after feeding and were accompanied by expiration of slightly greater volumes of CO_2, associated with vasoconstriction of the legs.

6. Methods of calculating heat production of sheep from measurements of their pulmonary exchange of O_2, CO_2 and CH_4 are discussed, and it is concluded that tracheostomized sheep are useful experimental animals in a limited type of experiment only.

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Appendix II. Mean heat production, body and surface temperatures and insulation of sheep exposed to different environments. Each of the results is the mean of duplicates made on consecutive days

Sheep	Surface area (m^2)	Fleece length (mm)	Air temperature (°)	Wind speed (m.p.h.)	Total heat production (kcal/24 h)	Rectal temperature (°)	Mean skin temperature (°)	Calculated insulation	
								Tissue	External
								(units*)	
Cs	1.38	19	5.2	0.2	2716	40.8	28.3	6.4	13.4
				5.2	3574	39.4	21.3	7.0	6.9
				7.1	3689	39.3	20.6	7.0	6.4
				7.9	3886	40.0	21.3	6.6	6.3
Cs	1.37	25	9.9	0.2	2209	40.6	32.0	5.3	16.2
				5.2	2450	39.2	26.9	6.9	11.0
				7.1	2524	40.1	24.5	8.5	9.2
				8.9	2659	40.5	24.1	8.4	8.4
Cs	1.37	39	5.0	0.6	1987	38.9	31.5	5.1	22.0
				2.5	2330	39.0	31.1	4.6	17.9
				4.2	1995	39.2	30.3	6.1	20.9
				7.5	2461	39.6	30.2	5.2	16.3
				9.6	2376	39.5	27.6	6.9	15.2

Appendix II (continued)

Cs	1.36	39	-3.0	0.6		2034	40.3	28.9	7.6	25.6
				2.5		2262	40.6	27.1	8.1	21.3
				4.2		2654	40.7	25.8	7.6	16.9
				7.5		2976	40.8	23.5	7.9	13.7
				9.6		3445	41.1	19.6	8.5	9.9
				9.6	(H.Q.)	3382	41.3	27.4	5.6	13.6
Cs	1.38	41	0.0	0.6		2114	39.5	32.1	4.8	25.0
				0.6	(R)	1625	39.5	36.3	2.7	39.1
				9.6	(R)	1675	39.9	33.9	4.9	35.1
				9.6		2500	40.0	32.8	4.0	21.0
Cs	1.31	50	5.0	0.6		1681	39.3	32.0	5.7	26.1
				2.5		1767	39.9	30.8	6.7	23.4
				4.2		1785	39.9	29.5	7.6	22.0
				7.5		1919	39.9	28.8	7.6	19.6
				9.6		2317	39.9	28.4	6.5	15.4
Cs	1.31	50	-3.0	0.6		1904	39.3	29.8	6.5	27.2
				2.5		1999	39.3	28.6	7.0	24.8
				4.2		2388	39.3	27.3	6.6	19.2
				7.5		2818	39.6	27.2	5.8	15.9
				9.6		3289	39.5	25.1	5.7	12.4
Y1	1.33	6	5.0	0.6		4462	39.1	29.0	3.0	7.8
				2.5		5072	39.4	27.8	3.0	6.6
				4.2		5588	39.5	27.4	2.9	5.7
				7.5		6073	40.2	26.2	3.3	5.0
				9.6		6470	40.3	27.3	2.7	4.9
				9.6	(H.Q.)	6130	40.7	24.4	3.5	4.5
Y1	1.33	10	-3.0	0.6		4528	39.8	27.0	3.8	9.6
				2.5		5259	39.8	25.6	3.6	7.8
				4.2		6271	40.0	23.9	3.4	6.1

Appendix II (continued)

Yl	1.33	12	0.0	0.6	4630	39.2	27.7	3.3	8.7
				0.6 (R)	3020	39.3	31.9	3.3	16.0
				9.6 (R)	3684	40.2	25.1	5.5	10.1
				9.6	6200	40.7	22.7	3.9	5.2
Yl	1.28	20	-3.0	0.6	3875	39.3	29.0	3.4	11.7
				2.5	4318	39.5	28.2	3.3	10.1
				4.2	4699	39.6	27.6	3.3	9.0
				7.5	5024	39.9	26.2	3.5	8.0
				9.6	5328	40.4	25.0	3.7	7.2
Yl	1.28	20	5.0	0.6	2562	39.3	31.1	4.1	15.2
				2.5	2769	39.6	30.3	4.3	13.4
				4.2	3199	39.7	29.4	4.1	11.0
				7.5	3455	39.8	28.5	4.2	9.7
				9.6	3937	40.0	27.6	4.0	8.1
Ct	1.42	89	5.0	0.2	2054	39.4	33.4		
			6.2	5.2	2054	39.5	31.4		
			6.9	7.1	2255	39.6	30.6		
			5.9	7.9	2366	39.2	31.1		
Zk	1.49	98	9.1	0.2	1848	39.2	33.7		
			10.0	0.2	1847	40.1	34.3		
			9.6	8.9	1946	40.0	32.7		
			9.8	8.9	2103	39.9	31.4		

R = infrared radiation

H.Q. = hindquarters exposed to wind source

* Unit insulation = $^{o}C \times 10^{-3}/kcal/m^{2}/24\ h$

Appendix III. Heat production, body and surface temperatures and insulations of sheep exposed to different outdoor environments

Sheep	Surface area (m^2)	Fleece length (mm)	Wind speed (m.p.h.)	Solar radiation incident on a horizontal surface (cal/cm^2/min)	Air temperature (°)	Rectal temperature (°)	Mean skin temperature (°)	Total heat production (kcal/24 h)	Tissue insulation (units*)	External insulation (units*)		
										Measured	Predicted	Measured - predicted
Fr	1.38	13	7.3	0.03	4.7	38.2	21.1	4156	5.68	5.74	6.79	-1.05 W
			8.2	0.08	5.5	38.0	21.3	3592	6.42	6.45	6.42	+0.03
			7.5	0.28	6.5	38.1	23.1	3054	6.78	8.07	6.71	+1.36
			6.0	0.17	7.6	38.3	23.0	3024	6.98	7.56	7.36	+0.20
			5.7	0.24	8.2	38.1	24.4	2753	6.87	8.80	7.49	+1.31
By	1.56	17	9.8	0.55	8.5	37.9	25.5	3552	5.45	7.93	6.94	+0.99
			8.6	0.78	9.0	37.9	27.2	3240	5.15	9.36	7.46	+1.90
			9.7	0.80	9.6	38.1	27.1	3475	4.94	8.35	6.98	+1.37
			10.9	0.93	11.0	38.5	27.4	3223	6.34	8.48	6.52	+1.94
Fr	1.36	18	8.1	0.33	5.9	37.8	21.1	3418	6.65	6.45	7.98	-1.53 W
			9.3	0.37	8.8	37.8	23.2	3137	6.33	6.70	7.44	-0.74 W
			8.6	0.32	8.3	37.7	23.9	3157	5.95	7.21	7.76	-0.55 W
By	1.56	17	10.6	0.42	8.8	37.8	24.5	3650	5.68	7.11	6.64	+0.47 W
			10.5	0.52	9.6	37.9	26.2	3070	5.95	9.04	6.67	+2.37
			9.6	0.30	9.6	37.8	25.3	3427	5.69	7.60	7.03	+0.57
			8.1	0.17	9.4	37.7	25.1	2975	6.60	8.85	7.68	+1.17

Appendix III (continued)

By	1.56	18	11.2	0.47	7.9	37.7	25.7	3356	5.58	8.82	6.69	+2.13
			13.0	0.69	8.2	37.8	28.4	4350	3.37	7.61	6.03	+1.58
			11.8	0.86	8.8	38.0	31.2	3996	2.65	9.22	6.46	+2.76
			13.5	0.91	9.2	38.4	32.1	4179	2.35	8.90	5.85	+3.05
			13.6	0.85	9.1	38.6	32.9	4296	2.05	9.08	5.82	+3.26
By	1.56	16	10.1	0.68	11.0	38.0	37.8	3082	5.16	8.50	6.55	+1.95
			7.3	0.29	9.8	37.8	25.0	4062	4.92	5.84	7.74	-1.90 W
			8.0	0.22	9.8	38.2	24.8	3510	5.96	7.08	7.43	-0.35 W
By	1.56	16	3.8	0.15	10.2	38.2	27.1	2706	6.40	10.22	9.26	+0.96
			4.5	0.30	10.4	38.2	26.8	2785	6.39	9.92	9.15	+0.77
			5.0	0.50	11.7	38.1	27.5	2521	6.56	10.65	8.87	+1.78
Fr	1.38	17	6.2	0.31	11.2	38.1	27.9	2490	5.65	10.12	8.59	+1.53
			5.7	0.43	11.8	38.1	28.5	2225	5.96	11.46	8.85	+2.61
			4.7	0.10	12.2	37.6	28.9	2579	4.65	9.74	9.38	+0.36
			5.6	0.28	14.4	37.6	29.8	2522	4.81	9.21	8.90	+0.31
By	1.56	16	5.4	0.65	16.6	38.5	33.5	2446	3.14	11.77	8.67	+3.10
			4.7	0.38	16.8	39.0	32.8	2681	3.61	10.08	9.03	+1.05
Fr	1.37	15	4.4	0.04	7.5	38.2	23.1	3446	6.00	6.61	8.83	-2.21 W
			4.0	0.07	7.9	38.0	24.0	2771	6.92	8.59	9.04	-0.55 W
			6.8	0.08	8.9	37.9	24.6	2802	6.50	8.31	7.66	+0.65
			8.8	0.24	10.2	38.4	24.4	2319	6.27	9.24	6.79	+2.45
By	1.56	12	9.2	0.27	6.5	38.0	22.3	4251	5.76	6.09	5.76	+0.33
			9.0	0.38	6.9	38.4	24.5	4113	5.27	7.03	5.83	+1.20
			8.4	0.61	7.2	38.5	26.5	3338	5.61	9.61	6.06	+3.55
			7.5	0.67	9.3	38.6	26.9	3084	5.92	9.54	6.40	+3.14
			7.1	0.57	9.3	38.6	27.3	3205	5.50	9.37	6.57	+2.80

Appendix III (continued)

Fr	1.38	10	9.6	0.01	9.2	38.4	21.8	3805	6.02	4.83	5.06	-0.23
			12.5	0.17	9.8	38.3	21.4	3478	6.71	4.89	4.18	+0.71
			12.5	0.20	9.8	38.1	20.5	3247	7.48	4.85	4.18	+0.67
			7.4	0.03	7.2	37.7	19.5	5204	4.83	3.40	5.82	-2.42 W
			7.4	0.03	7.3	37.7	19.5	5037	5.00	3.48	5.82	-2.34 W
			5.4	0.02	7.5	37.8	21.3	4479	5.08	4.46	6.60	-2.14 W
			5.4	0.04	8.0	37.8	21.3	4517	5.04	4.26	6.60	-2.24 W
By	1.71	37	1.2	0.10	3.0	38.5	31.1	2289	5.53	23.07	20.59	+2.48
			1.9	0.02	4.0	38.6	31.4	2562	4.81	20.34	19.54	+0.80
			2.9	0.02	4.5	38.9	30.9	2784	4.91	17.87	18.21	-0.34
			4.1	0.02	6.2	38.8	29.7	2619	5.94	17.02	17.08	-0.06
Fr	1.42	13	2.6	0.05	4.9	38.4	24.0	2921	7.00	10.08	9.09	+0.99
			3.2	0.17	6.3	38.5	25.7	2961	6.14	10.09	8.74	+1.35
			2.8	0.46	7.8	38.4	27.7	2480	6.13	12.47	8.95	+3.52
			0.6	0.01	5.0	38.6	26.1	3022	5.87	10.74	10.38	+0.36
			0.8	0.01	3.8	38.8	24.6	3230	6.24	9.85	10.23	-0.42
By	1.69	40	2.4	0.01	-0.2	37.2	27.7	2764	4.95	18.83	20.01	-1.18 W
			2.2	0.01	0.5	37.1	29.2	2596	5.14	20.30	20.34	-0.04
By	1.69	40	2.4	0.23	0.1	38.3	31.9	2542	4.26	23.54	20.01	+3.53
			2.5	0.08	2.8	38.2	31.6	2568	4.34	21.08	19.87	+1.21
			2.4	0.08	2.9	38.5	31.8	2575	4.40	21.08	20.01	+0.07
			2.2	0.06	3.0	38.5	31.1	2463	5.08	21.03	20.34	+0.69
			1.3	0.04	2.3	38.6	30.6	2628	5.14	20.19	21.79	-1.60 W
Jr	1.33	15	6.6	0.05	9.1	38.4	23.4	2225	8.97	9.41	7.74	+1.67
			5.9	0.17	9.4	38.5	23.8	2094	9.34	10.13	8.09	+2.04
			4.7	0.02	8.2	38.3	22.9	2427	8.44	8.79	8.70	+0.09
			6.5	0.03	8.8	38.2	21.8	2440	8.94	7.73	7.79	-0.06
			5.1	0.01	8.5	38.3	21.6	2538	8.75	7.46	8.48	-1.01

Appendix III (continued)

Re	1.35	32	15.4	0.08	8.8	37.8	27.0	2825	5.16	9.50	8.29	+1.21	
			14.0	0.15	8.9	37.6	26.9	2760	5.23	9.64	8.90	+0.74	W
			11.0	0.13	9.2	37.7	28.7	2731	4.45	10.56	10.45	+0.11	W
			12.9	0.10	9.7	38.7	28.4	3062	4.54	8.94	9.46	-0.50	W
			11.2	0.08	9.7	38.5	29.0	2455	5.22	11.75	10.35	-1.40	W
By	1.71	42	9.1	0.09	8.6	37.7	28.5	2359	6.67	15.88	14.43	+1.41	
			9.5	0.04	8.9	37.6	28.7	2531	6.01	14.62	14.15	+0.47	
			10.1	0.01	8.9	37.5	28.3	2724	5.78	13.22	13.70	-0.48	
			9.5	0.02	8.7	37.2	29.7	3294	3.89	11.67	14.15	-2.48	W
Re	1.35	35	10.2	0.02	8.9	38.1	28.7	2645	4.80	11.10	11.76	-0.66	
			8.4	0.02	12.2	38.6	31.3	2342	4.21	12.25	12.90	-0.65	
			9.9	0.01	7.8	38.4	24.9	3219	5.79	7.74	11.91	-4.17	W
			12.6	0.01	7.0	38.3	24.9	3485	5.19	7.44	10.33	-2.89	W
Fr	1.43	17	3.0	0.04	2.4	38.3	22.3	3006	7.61	10.26	10.41	-0.15	
			3.0	0.06	3.1	38.3	24.0	2939	6.91	11.04	10.41	+0.63	
			6.4	0.03	3.1	38.5	21.6	3296	7.33	8.63	8.48	+0.15	
			5.7	0.01	2.7	38.4	21.6	3569	6.73	8.10	8.68	-0.58	
Jr	1.35	11	6.2	0.01	10.3	38.3	24.0	2994	6.45	6.62	6.60	+0.02	
			7.0	0.01	10.7	38.3	23.7	3121	6.31	6.01	6.28	-0.27	
			7.3	0.01	10.8	38.4	23.7	3141	6.32	5.93	6.16	-0.23	
			6.0	0.01	10.8	38.3	23.8	3504	5.59	5.48	6.85	-1.37	
			5.5	0.01	10.8	38.4	24.3	3154	6.04	6.17	6.90	-0.73	
Fr	1.43	10	2.0	0.03	9.2	37.5	23.4	2664	7.57	8.35	8.20	+0.15	
			2.7	0.08	10.9	37.7	24.8	2722	6.78	7.98	7.84	-0.14	
			3.2	0.14	12.0	37.7	25.3	2325	7.69	9.08	7.60	+1.48	
			3.6	0.07	10.8	38.1	23.8	2786	7.34	7.23	7.41	-0.18	
			4.0	0.03	9.9	38.3	23.3	3135	6.84	6.60	7.22	-0.62	

Appendix III (continued)

Jr	1.35	5	3.5	0.08	3.1	38.3	18.4	3740	7.18	5.84	5.56	+0.28	
			4.8	0.22	4.7	38.0	19.0	3685	6.96	5.54	5.08	+0.46	
			6.0	0.31	5.7	38.1	19.7	3144	7.90	6.45	4.75	+1.70	
			4.5	0.25	6.8	38.5	21.0	3734	6.30	5.43	5.19	+0.24	
			4.0	0.11	6.5	38.5	20.5	3655	6.65	5.48	5.38	+0.10	
Fr	1.72	30	5.2	0.01	10.3	37.9	28.2	2430	6.86	13.84	13.64	+0.20	
			5.8	0.06	11.3	37.9	28.3	2423	6.74	13.50	13.19	+0.31	
			6.9	0.10	12.1	38.1	28.7	3081	7.77	13.72	12.44	+1.28	
			5.8	0.02	11.9	38.1	28.0	2360	7.36	13.18	13.19	-0.01	
			5.3	0.01	12.1	38.0	28.8	2473	6.40	12.97	13.59	-0.62	
By	1.72	34	4.8	0.17	11.1	38.2	31.8	2329	4.73	17.19	15.37	+1.81	
			7.1	0.20	11.8	38.3	32.5	2543	3.92	15.58	13.56	+2.02	
			6.5	0.40	12.9	38.4	33.1	2225	4.10	17.66	13.99	+3.67	
			7.7	0.21	12.5	38.2	32.1	2296	4.57	16.54	13.12	+3.41	
Fr	1.52	38	15.0	0.04	12.0	37.1	26.2	2628	6.30	9.01	9.76	-0.75	
			10.6	0.03	12.1	37.9	26.8	2427	6.95	10.18	12.29	-2.11	W
			9.8	0.03	12.0	38.0	27.5	1987	8.03	13.43	12.80	+0.63	
			12.0	0.10	13.1	38.3	28.5	1987	7.50	13.34	11.42	+1.92	
			9.8	0.06	12.9	38.3	29.2	1914	7.23	14.74	12.80	+2.06	
Fr	1.52	38	3.2	0.13	10.4	38.4	32.7	1842	4.70	21.06	18.32	+2.74	
			3.3	0.07	10.7	38.4	32.6	1869	4.72	20.33	18.18	-2.15	
			3.2	0.07	10.9	38.4	32.5	1856	4.83	20.22	18.32	+1.90	
			2.7	0.03	11.1	38.7	32.3	1996	4.87	18.28	18.82	-0.54	

W = rain falling or fleece wet following rain

* units of insulation are $^{o}C \times 10^{-3}/kcal/m^{2}/24$ h

Appendix IV. Solar radiation measurements on models simulating fleeced and shorn sheep with the side at right angles to the solar beam

Date	Solar angle (°)	Cloud cover (8ths)	Incoming radiation (cal/cm²/min)	Model of shorn sheep			Model of fleeced sheep		
				Incident radiation (cal/cm²/min) End	Incident radiation (cal/cm²/min) Side	Heat load (kcal/m²/h)	Incident radiation (cal/cm²/min) End	Incident radiation (cal/cm²/min) Side	Heat load (kcal/m²/h)
10.7.62	48.47	8	0.35	-	-	-	0.18	0.19	113
10.7.62	38.54	8	0.35	-	-	-	0.14	0.20	114
10.7.62	44.50	8	0.40	-	-	-	0.18	0.21	123
12.7.62	37.40	8	0.13	0.07	0.09	51	0.07	0.07	42
12.7.62	33.79	8	0.10	0.05	0.06	35	0.05	0.06	35
12.7.62	40.50	7	0.18	0.09	0.10	62	0.09	0.12	69
12.7.62	49.47	7	0.41	0.17	0.21	121	0.17	0.27	152
12.7.62	54.51	1	0.95	0.14	0.37	310	0.14	0.51	269
27.7.62	52.37	3	0.85	0.22	0.41	223*	0.22	0.41	227*
27.7.62	53.15	0	1.00	0.53	0.53	317	0.44	0.45	269
27.7.62	36.22	3	0.54	0.17	0.36	189	0.17	0.33	182
27.7.62	40.26	3	0.71	0.50	0.35	228*	0.48	0.28	188*
27.7.62	45.56	2	0.87	0.47	0.41	253*	0.47	0.41	252*
27.7.62	41.48	3	0.83	0.21	0.50	264	0.21	0.38	211
5.10.62	26.57	1	0.44	0.15	0.37	195	0.15	0.46	245
5.10.62	16.43	1	0.21	0.09	0.30	154	0.09	0.33	174
5.10.62	20.43	0	0.32	0.13	0.33	173	0.13	0.40	213
5.10.62	18.34	0	0.29	0.09	0.35	178	0.09	0.38	199
5.10.62	24.00	0	0.43	0.10	0.40	203	0.10	0.35	185
5.10.62	29.44	3	0.63	0.18	0.50	261	0.18	0.55	293
5.10.62	29.02	1	0.49	0.18	0.45	236	0.18	0.50	268
5.10.62	28.02	1	0.46	0.13	0.37	237	0.13	0.46	243
5.10.62	14.25	1	0.19	0.07	0.31	142	0.07	0.31	162
5.10.62	29.50	4	0.53	0.17	0.43	227	0.17	0.50	267
5.10.62	25.53	1	0.45	0.15	0.39	205	0.15	0.43	230

Appendix IV (continued)

22.1.63	14.15	0	0.29	0.12	0.25	134	0.12	0.25	137
22.1.63	13.28	0	0.29	0.13	0.23	126	0.13	0.25	138
22.1.63	14.19	0	0.31	0.13	0.24	130	0.13	0.26	143
22.1.63	12.49	0	0.28	0.12	0.22	120	0.12	0.25	137
22.1.63	11.30	0	0.25	0.10	0.20	108	0.10	0.23	125
22.1.63	9.55	0	0.23	0.09	0.20	167	0.09	0.23	124
22.1.63	10.39	0	0.23	0.08	0.20	105	0.08	0.24	128
22.1.63	10.48	0	0.24	0.10	0.19	103	0.10	0.23	125
22.1.63	14.09	0	0.30	0.13	0.26	140	0.13	0.25	138
22.1.63	12.47	0	0.27	0.11	0.20	109	0.11	0.24	131
31.7.63	51.26	5	0.92	0.30	0.49	270	0.30	0.52	290
31.7.63	51.54	5	0.90	0.30	0.47	261	0.30	0.53	295
31.7.63	50.46	5	0.90	0.25	0.51	274	0.25	0.53	290
31.7.63	51.38	5	0.68	0.33	0.43	245	0.33	0.46	263
31.7.63	50.46	4	0.87	0.33	0.45	255	0.33	0.50	283
31.7.63	52.24	4	0.88	0.29	0.50	274	0.29	0.56	309
31.7.63	45.53	4	0.79	0.20	0.44	234	0.20	0.47	255
31.7.63	49.34	4	0.74	0.23	0.44	238	0.23	0.45	248
31.7.63	43.59	4	0.71	0.20	0.42	228	0.20	0.48	260
31.7.63	48.03	4	0.87	0.29	0.44	245	0.29	0.49	274

*

MODEL WITH SIDE PARALLEL TO SOLAR BEAM.