STUDIES   IN   THERMAL   TRANSPORT

AND   LOSS   IN   THE   BOVINE

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by

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C O N T E N T S

CHAPTER I

INTRODUCTION

A homoeotherm may be described as an animal that maintains
a nearly constant body temperature by means of physiological
mechanisms which act in such a way that the physical gradients
determining heat flow from the body to the environment are
being continuously adjusted to maintain heat loss equal to
heat production.

The physical pathways for heat loss are convection,
conduction, radiation and evaporation. For many practical
purposes the first three of these may be grouped together
as non-evaporative heat loss. There are therefore two
basic equations which determine heat loss from the body:

The evaporative heat loss, H_e, is given by

$$H_e = A(P_s - P_o)K_e$$

where P_s is the vapour pressure at the surface,

P_o is the vapour pressure of the surroundings,

K_e is the evaporative heat flow coefficient, and

A is the surface area.

The non-evaporative heat loss, H_n, is given by

$$H_n = A(T_s - T_o)K_n$$

where T_s is the temperature at the surface,

T_o is the temperature of the surroundings, and

K_n is the non-evaporative heat flow coefficient.

A third basic equation is contained in the description
of a homoeotherm given in the first paragraph

$$H_p = H_e + H_n + H_s$$

where H_p is the heat production and H_s is the heat storage.

H_s is defined as positive when body temperature is rising, and over long periods approximates to zero.

These three equations, though oversimplifications, embody the basic physical laws to which the homoeotherm is subject.

The physical properties of practical importance that describe the climatic environment are air temperature and humidity, radiant temperature, the temperatures of any objects (particularly the ground) in contact with the animal and the wind velocity. In the basic equations all these temperatures are expressed as a weighted mean temperature of the surroundings T_o. For any given wind velocity T_o is thus analagous to the 'operative temperature' proposed in relation to human environmental physiology by Winslow, Herrington & Gagge (1937). Air humidity is described by P_o, and wind velocity is one of the major factors that determine the values of the coefficients K_e and K_n. There are thus two variables (T_o and P_o) which are unique properties of the environment and two more (K_e and K_n) which are properties of the environment but subject to physiological influence.

In the experiments to be described it was necessary to limit the number of physical variables. To this end the effects of wind velocity and radiation were standardised and the studies were confined to conditions causing heat stress rather than cold stress. These limitations were achieved by exposing the animals to temperatures of not less than 15°C in a psychrometric chamber where wall temperatures were equal

to air temperature and air movement was constant.

The physiological mechanisms for controlling heat loss include alterations in the rate and distribution of peripheral blood flow, alterations in the rate at which moisture is made available for evaporation from the surface, alterations in pulmonary ventilation and pilomotor activity. Changes in the rate of heat production provide another means of body temperature regulation. Blood flow changes affect heat loss by altering tissue insulation thus influencing the surface temperature T_s and vapour pressure P_s. P_s is, however, more directly influenced by the rate at which moisture penetrates the skin, i.e. by the sweat rate and the rate of diffusion through the skin. Pilomotor activity can influence both the heat loss coefficients K_e and K_n. The physiological control of evaporation from the skin is primarily achieved by variation of the quantity P_s. The physiological control of evaporation from the respiratory tract, on the other hand, is primarily achieved by alteration of pulmonary ventilation, i.e. by variation of the quantity K_e. Respiratory and cutaneous evaporative heat losses are therefore better expressed separately from one another by two equations, each having the same form as the basic evaporative heat loss equation given on page 1.

A full understanding of the environmental physiology of cattle would require a description of how all the physiological processes, working together, bring about the quantitative inter-relationships that exist between the physical and physiological variables in any environment. These inter-

relationships have been described qualitatively by many authors
and there is general agreement as to which physiological
processes are involved and how they are adjusted to counteract
environmental changes. Quantitative descriptions of heat
losses have also been made but some disagreement exists between
different reports, particularly in regard to evaporative heat
losses. In the studies described here the approach used is
firstly to make a quantitative analysis of the heat losses
under different environmental conditions and to compare the
results with those obtained by others. Secondly a comparison
is made of the relative influences of the physical and
physiological barriers to heat flow at different environmental
conditions. By this means an attempt is made to assess the
limits of effectiveness of the various physiological
adjustments to heat stress.

Until recently the experimental work reported on problems
of heat tolerance of cattle was confined to occasional studies,
conducted in the field with limited equipment. Much of the
experimental evidence was obscured by uncontrollable factors
connected with the weather. In the last twelve years,
however, many studies have been reported on the reactions of
cattle exposed to controlled environments in the psychrometric
chambers at the Universities of Missouri and Queensland, at
the Agricultural Research Center, Beltsville, Maryland, and
at the Hannah Dairy Research Institute, Ayr. The background
to the subject of the environmental physiology of domestic
animals has been fully discussed by Brody (1945) and the
early work has been reviewed by Findlay (1950) and by Findlay &

Beakley (1954).

The body temperature* of cattle is subject to a considerable degree of variation with climate (Findlay, 1950; Beakley & Findlay, 1955a). The increasing level of body temperature with environmental warmth is a measure of the inability of the animal's thermoregulatory mechanisms to be fully effective, and it has been used as a basis for a quantitative assessment of heat tolerance (Rhoad, 1944). Diurnal fluctuations in body temperature resulting from temporary periods of first positive and then negative heat storage tend to level out the varying demand on the thermoregulatory processes caused by variations in air temperature and by specific dynamic action. The elevation of body temperature during prolonged exposure to heat has, however, no thermoregulatory value except in so far as it limits the decrease in the thermal gradient for the transport of heat from the body to the surroundings; it thus represents no more than the attainment of a new equilibrium temperature.

At very low air temperatures the heat production of most homoeothermic mammals is linearly related to the depression of the air temperature below 38°C, which approximately represents normal body temperature (Scholander, Hock, Walters, Johnson & Irving, 1950). At these low air temperatures the insulation of the body tissues and fur is maximal and heat production follows non-evaporative heat loss which is governed by Newton's law of cooling, evaporative heat loss being small. As air temperature increases from conditions of extreme cold, heat production declines to a minimal value. The air temperature

* Throughout this thesis the term 'body temperature' refers to the temperature of the rectum.

where this occurs is termed the critical temperature and its depression below normal body temperature, the critical gradient (Scholander et al. 1950), is determined by the product of the maximal insulation of the animal and the minimal heat production. The experiments described here do not extend to this region below the critical air temperature.

Above the critical temperature lies the range of physical regulation or the zone of thermoneutrality. In this air temperature range the heat production of cattle is minimal and is primarily determined by the level of food intake (Kriss, 1930b). The rate of decrease of non-evaporative heat loss with rising air temperature is limited by vasodilation, but as the skin tends to become fully vasodilated non-evaporative heat loss, as a result of the reduction in overall insulation, starts to decline more rapidly with rising air temperature than before. In this air temperature range evaporative heat loss increases to compensate for the reduced non-evaporative loss and body temperature rises slightly as air temperature increases. The rise in body temperature tends to cause increased heat production due to the Van't Hoff effect. With increasing thermal stress heat production may therefore rise (Blaxter & Wainman, 1961) but after prolonged exposure to high temperatures it is often reduced (Kibler, 1960).

Evaporation as a means of heat loss becomes increasingly important as air temperature rises, and when air temperature reaches body temperature evaporation is the only means of heat disposal available to the animal. The sources of evaporated moisture are the respiratory tract and the skin.

The fact that cattle pant vigorously at high environmental temperatures led to the belief that evaporation from the respiratory tract was their major method of heat loss under warm conditions. The quantity of pulmonary moisture loss is however small compared with the loss from the skin (Riek & Lee, 1948a; Kibler & Brody, 1952; Kibler & Yeck, 1959), and it is still doubtful whether panting always offsets the increased heat production which results from the extra muscular work involved.

The readily observed panting action and the fact that streams of sweat are not normally observed on cattle as on man and horses probably accounts for the use of the term 'non-sweating' that has frequently been applied to cattle. Nevertheless, as stated in the previous paragraph, the skin is the major source of evaporated moisture from cattle at high air temperatures. There is clear histological evidence that the skin of cattle is abundantly supplied with sweat glands (Findlay, 1950; Findlay & Yang, 1950) and the appearance of sweat droplets on the skin of cattle exposed to high air temperatures has been observed (Ferguson & Dowling, 1955).

Cutaneous evaporation, as well as being affected by the environmental temperature, appears also to differ between breeds, between individuals within a breed, between separate skin regions and with the age of the animal. Ferguson & Dowling (1955) have reported that evaporation from the skin of a Zebu-Jersey crossbred heifer was far greater than that from an Ayrshire heifer subjected to the same high temperatures.

Taneja (1959) found higher rates of evaporation from the shoulder of a Zebu-Australian Illawara Shorthorn calf than from the shoulder of a Shorthorn calf, but similar rates from the belly region of both animals. In both these instances the animal with tropical blood appears to have made the greater use of its capacity to vaporize water from the skin. Kibler & Yeck (1959), however, found rates of evaporation to be highest from Shorthorn cattle, intermediate from Santa Gertrudis and lowest from Brahman cattle all exposed to the same air temperature. They concluded that evaporative cooling per se is not the determining factor in the heat tolerance of different breeds of cattle.

Volcani & Schindler (1954) measured relative rates of cutaneous evaporation from different skin regions of Holstein-Syrian crossbred cows. They listed the regions in the following order of diminishing evaporation: face, shoulder, neck, dewlap, back, rump, thigh, abdomen. Berman (1957) using the same technique on similar animals gave the order as: neck and front flank, back (thoracic and sacral) and thigh, forehead and abdomen. McDowell, McMullan, Wodzika & Fohrman (1955) working with Jersey and Sindhi-Jersey crossbred cows listed the regions in the order: mid neck, remainder of the trunk, legs and mid belly line. Kibler & Yeck (1959) reported successively decreasing rates from the back and dewlap, the flank and chest, and the navel flap of Brahman and Santa Gertrudis heifers, and they recorded the highest rates of all from the hump in Brahmans. There is broad agreement between the rankings of the regions given by all these observers but the measurements of McDowell,

Table 1. Summary of previously reported estimates of the rate of cutaneous evaporation from cattle exposed to air temperatures between 38 and 42°C and relative humidities between 50 and 65%.

Ref.	Animals	Mean rate of cutaneous evaporation g/m².hr.	Total evaporative weight loss g/m².hr.	Method
a	Jerseys (lactating)	142	179	Insensible weight loss measurements corrected for metabolic weight loss
a	Holsteins (lactating)	161	203	
a	Brown Swiss (lactating)	162	228	
a	Brahmans (lactating)	148	176	
a	Brahmans (dry)	112	141	
a	Brown Swiss (heifers)	156	209	
a	Brahmans (heifers)	122	151	
b	A.I.S* (lactating)	-	179	Insensible weight loss measurements not corrected for metabolic weight loss
c	Jerseys (lactating)	170	196	
d	A.I.S* (1 year)	-	178	
d	Zebu-Hereford (1 year)	-	191	
e	Zebu-A.I.S* (1 year)	180	191	
e	Shorthorn (1 year)	271	294	
f	Brahmans (heifers)	170	186	Hygrometric tent.

		Rates of cutaneous evaporation from different regions (g/m².hr).		

Ref.	Animals	Withers	paunch	neck	loin	fore-chest	Method
g	Cow	646	402	363	296	-	Ventilated capsules.
g	Jersey (cow)	-	591	-	-	583	
g	Sindhi-Jersey (cow)	-	582	-	-	650	

Ref.	Animals	shoulder	belly	Method
h	Zebu-A.I.S* (7-8 months)	336	229	Ventilated capsules.
h	Shorthorn (7-8 months)	229	222	
h	Brahman (7-8 months)	381	-	
j	Zebu-Jersey (heifers)	320	-	desiccated capsules room R.H. 28%.
j	Ayrshire (heifer)	160	-	

Observers: a. Kibler & Brody (1952
          b. Robinson & Klemm (1953)
          c. Knapp & Robinson (1954)
          d. Klemm & Robinson (1955)
          e. Taneja (1958)
          f. Kibler & Yeck (1959)
          g. McDowell, Lee & Fohrman (1954)
          h. Taneja (1959)
          j. Ferguson & Dowling (1955)

* Australian Illawara Shorthorn.

Lee & Fohrman (1954) provide a contrasting result. They reported the skin regions in the following order of decreasing evaporation: withers, paunch, neck, loin.

A number of observers have reported increasing rates of cutaneous evaporation per unit area of the surface of cattle during the first year of life (Riek & Lee, 1948b; Klemm & Robinson, 1955; Taneja, 1958; Kibler & Yeck, 1959).

In view of the variety of factors just described, which in addition to the environmental conditions, can affect the rate of cutaneous evaporation, a quantitative comparison of results obtained by different methods is difficult. Table 1 summarises the results that have been previously reported for the rates of cutaneous evaporation from cattle aged from 7 to 8 months and upwards and exposed to air temperatures of 38 to 42°C and relative humidities of 50 to 65%. Estimates of the overall mean rate of cutaneous evaporation obtained by weighing methods are, with one exception, all within the range 112 to 180 g/m^2.hr. Even those which include respiratory evaporation (and in some instances metabolic weight loss as well) are, again with the one exception, all below 228 g/m^2.hr. Estimated rates of cutaneous evaporation obtained from capsules placed over individual skin areas are however, with one exception, all greater than 222 g/m^2.hr and extend to 650 g/m^2.hr. Even the measurements made on the paunch or belly area, which as discussed earlier is agreed by most observers to be a region of low evaporation, appear to be generally high compared with the overall mean rates obtained by weighing methods.

At the time when the present investigation was begun it

appeared that there was a discrepancy between estimates of cutaneous evaporation by weighing and by capsule methods. Subsequent publication of the more recent results quoted in Table 1 (Taneja, 1958, 1959; Kibler & Yeck, 1959) have not altered this view. The first object of the experiments to be described here took the form, therefore, of a critical investigation of the capsule technique. Capsule methods used previously with cattle had all been dependent on weighing absorbers; the weighings being made at intervals of 5 min or more. A further object of the experiments was therefore to evolve a satisfactory method of assessing the rate of evaporation instantaneously. The observations were later extended to include simultaneous measurements of cutaneous and respiratory evaporation and of metabolic weight loss as well as of total insensible weight loss so that all methods of measurement could be checked against one another quantitatively. In order to estimate total cutaneous evaporative loss from observations on certain selected regions of the body surface it was necessary to investigate the regional distribution of cutaneous evaporation and to determine to what extent this was affected by age and by the thermal severity of the environment. The investigation of some of these secondary problems was made simultaneously with the main investigation, in which the object was to analyse the heat losses under different environmental conditions of temperature and humidity.

Chapter II gives a description of the animals, equipment and methods used in the experiments. It contains a full account of the development of the capsule technique employed

and a description of the apparatus used for respiratory analysis.

Chapter III describes the procedures employed and the results obtained in three physiological experiments in which the rate of cutaneous evaporation was investigated in relation to the anatomical site of measurement, the environmental conditions and the age of the animal. In the second of these experiments a partition was made of the heat losses by the animals when exposed to each of eight environmental conditions employed.

The results are discussed in Chapter IV, firstly in relation to the information they provide on the accuracy and limitations of the methods employed, and secondly in relation to the physiological aspects.

It is stressed that the experiments on cutaneous evaporation were quantitative. They were not designed to provide information as to the anatomical origin of cutaneous evaporation or the neurological or biochemical control of thermoregulatory processes. The results, however, do have an obvious bearing on these subjects and a limited discussion, of a speculative nature, on their implications is included in Chapter IV. More detailed discussion on these lines would be premature at present and must await the outcome of further experiments currently being made at this laboratory with a view to providing qualitative information on cutaneous evaporative processes.

CHAPTER II

Table 2. Data on climatic chambers

	Small climatic chamber used for the early work	New general purpose climatic chamber used for the later work
Length (m)	3·8	5·9
Width (m)	2·2	3·9
Height (m)	2·5	3·3
Air movement (m/min)	6	15
Air temperature variation (°C)	±0·2	±0·6
Dewpoint temperature variation (°C)	±0·2	±0·2
Maximum difference between mean wall and air temperatures (°C)	±2·0	±1·0

Table 3. Summary of animals used for experiments

Calves	Experiments	Age at start (weeks)	Age at end (weeks)
84, 93, 95, 111, 112, 115, 122, 129	Preliminary trials	> 17	< 25
136	A	24	26
138	A	19	21
139	A	20	22
140	A	20	22
193	B	32	40
196	B & C	32	38
197	B & C	32	42
199	B & C	21	32
210	D	36	44
219	E	10	34
220	E	10	34
221	D	24	38
222	E	11	34
226	D	23	31

MATERIALS AND METHODS

Climatic Chambers

Studies of animals' reactions to different levels of environmental temperature and humidity were made in two climatic rooms at the Hannah Dairy Research Institute. The early trials for developing measuring techniques were conducted in a small climatic chamber (Beakley, 1952, Chapters 1 and 8) and the later experiments in the general purpose chamber of a new climatic laboratory (Findlay, McLean & Bennet, 1959). Details of these rooms are summarised briefly in Table 2.

Animals and Management

The animals used were Ayrshire bull calves. Their ages and the experiments for which they were used are shown in Table 3. Climatic chamber exposures lasted from 3 to 7 hr, during which time no food or water was given to the animals. When not in the climatic chambers the animals were housed in an unheated byre. They were fed twice daily at 7 a.m. and 4 p.m. on a diet of 1·4 kg concentrates per day and in addition were offered hay and water ad lib. On days when they were to be exposed in the climatic chamber, except for some of the preliminary trials, the morning feed and hay were withheld until after the exposure.

Thermometry

Copper constantan thermocouples were used for all temperature measurements. The thermocouple system in the small climatic chamber has been fully described (Beakley,

1952, Chapter 9) and that in the general purpose chamber is similar. Both systems have an accuracy of ±0·1°C. Any one of a large number of thermojunctions may be selected by means of switches and its temperature displayed as a direct reading on a galvanometer. In addition, the output from up to eight thermocouples may be connected to a Sunvic multichannel printing millivolt recorder. The thermojunctions were made from 40 S.W.G. wire. For skin temperature measurements a circular patch of thin rubber, approximately 1 cm. diameter, was stuck with latex cement over the thermojunction which had been placed on a small shaved area of skin. A different method was used for mounting thermojunctions inside skin capsules (see p. 26). For deep body temperature measurements the thermojunctions were cemented onto the end of a plastic rod measuring 15 cm long by approximately 5 mm in diameter. This was inserted its full length into the rectum. For air temperature measurements the junctions were threaded into fine-bore polythene cannulae, which could be covered by wicks if desired for wet bulb temperature measurements. Other thermocouple mountings used and their specialised applications are described later.

Cutaneous Evaporation

Possible techniques

Methods of measuring cutaneous evaporation fall broadly into two categories, direct and indirect.

Direct methods are those in which the moisture loss from a small area is measured by placing an inverted cup or capsule over that area. The capsules may be ventilated or unventilated.

In the ventilated capsule the rate of evaporation is usually determined by passing dry air into the capsule and measuring the weight gain of a moisture absorber through which the outlet air is passed for a period of 5 to 20 min. McDowell, Lee & Fohrman (1954) criticised the use of dry inlet air because the skin under test is exposed to abnormal atmospheric conditions. To overcome this, they recirculated air round a closed circuit incorporating a capsule and an absorption bottle, the latter containing a saturated salt solution. The factors influencing the choice of air flow rate through ventilated capsules do not appear to have received enough attention. Air flow rates appear to have been chosen more to suit the absorbers used than by consideration of the effect this variable may have on the rate of evaporation within the capsule.

In the unventilated capsule air flow rate is at least standardised, although at a level below that to which surrounding skin areas are exposed. Unventilated capsules normally contain a pad of desiccant material which is weighed at intervals. This method has been critically analysed by Randall, Peiss & Hertzman (1953) who showed that the quantity of desiccant used and the distance between the desiccant and the skin surface can considerably affect the observed rate of evaporation. Buettner (1953) has employed sets of four unventilated capsules, the air inside each being conditioned to different vapour pressures. This method has enabled him to throw much light on the relationships between diffusion, sweating and evaporation in man.

A disadvantage common to most capsule methods is that

the measurement of evaporation, since it depends on the weight gain of an absorber, can be made only over periods of several minutes. Albert & Palmes (1951) have used an infra-red gas analyser to monitor continuously the humidity of air leaving a ventilated capsule, but the method was not accurate. More recently Kibler & Yeck (1959) have made continuous comparisons of moisture collected under capsules by use of an electrolytic hygrometer, but they have not as yet reported quantitative results.

Indirect methods are those in which cutaneous evaporation is calculated by difference from simultaneous measurements of total evaporation and respiratory evaporation. The hygrometric tent (Yeck & Kibler, 1956) is effectively a ventilated capsule, but the entire animal is enclosed in a tent. Cutaneous evaporation from cattle has also been determined from insensible weight loss measurements combined with simultaneous determination of both respiratory evaporation and metabolic weight loss due to oxygen-carbon dioxide exchange (Kibler & Brody, 1950). There is some confusion in the literature regarding the definition of the term 'insensible weight loss'. In this thesis it refers to all gaseous exchange between the animal and the atmosphere, i.e. it includes any weight loss resulting from the evaporation of sweat but excludes the weight of faeces, urine and any saliva that may be lost.

In order to compare evaporation from different body regions, only capsule methods are suitable. The ideal method would therefore appear to be one which uses a capsule for collection of moisture combined with an instantaneous means of estimating

the moisture output. These considerations led to the choice of the ventilated capsule technique described in the next sections. Later, when it became necessary to obtain an independent check on the quantitative accuracy of the capsule method used, estimates of total cutaneous evaporation based on insensible weight loss measurements were also made.

Wet and dry bulb thermocouples

The classical instrument for measuring humidity is the wet and dry bulb hygrometer. Trials were made of a number of other methods including a dewpoint thermometer, an electrolytic hygrometer and a capacitance hygrometer. None of these was found to possess the combined advantages of a form of wet and dry bulb thermocouple apparatus that was designed with the special requirements of the capsule method in mind.

The recommended air velocity for ventilating a wet bulb is between 4 and 10 m/sec (List, 1951), but if the physical dimensions of the thermometer are kept small the air velocity as well as the speed of response may be greatly reduced (Gregory & Rourke, 1957 p. 19). Experiments with wet bulb thermocouples enclosed in metal tubes, down which a stream of air was passed, showed this method to be suitable for the intended application if the following conditions were observed: (1) The wet bulb thermocouple must be sited centrally in the tube, and even slight alterations in the position of the wick must be avoided in order to obtain consistent results. (2) Ambient temperature surrounding the apparatus must be close to the dry bulb temperature of the airstream in the
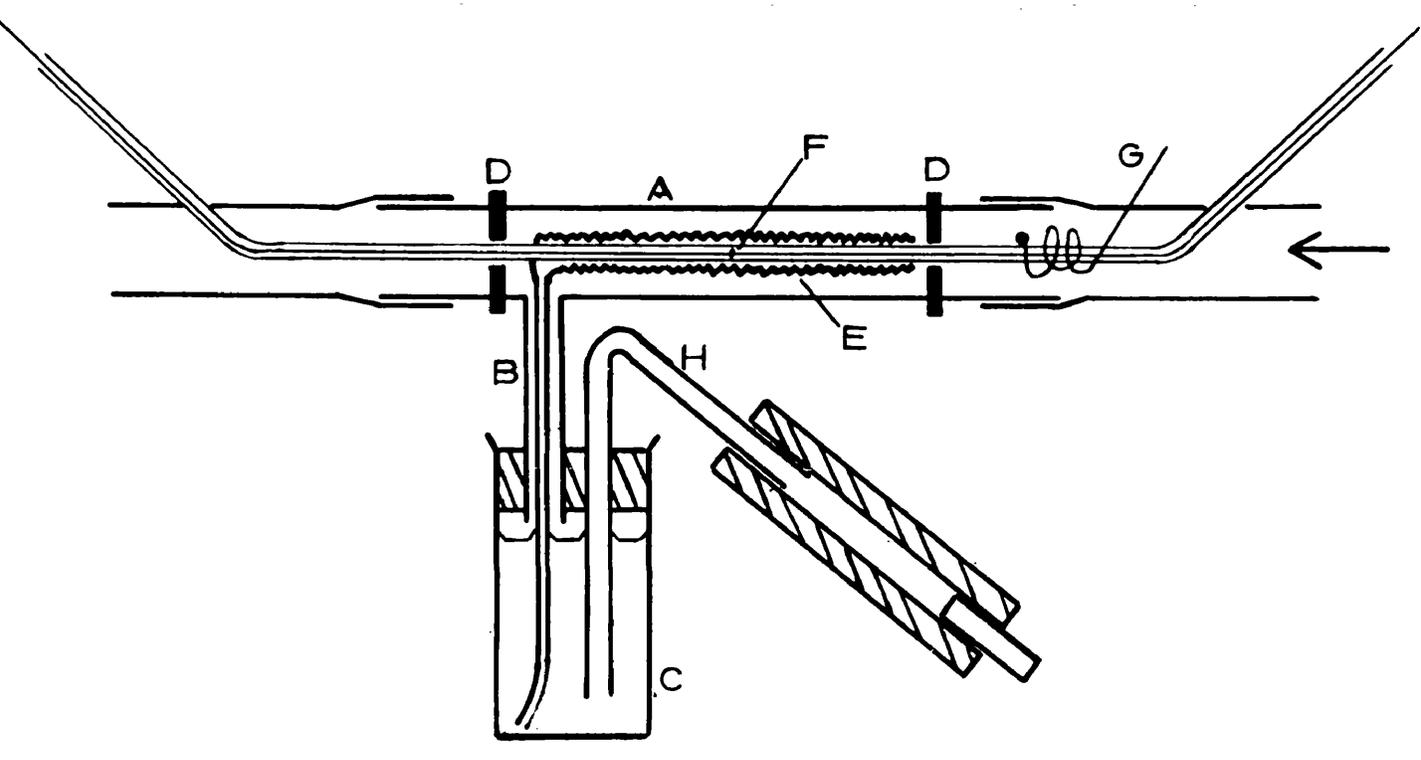
Fig. 1.   Wet and dry bulb thermocouple apparatus.   Scale -
     approximately actual size.   (A & B brass tubes, C
     reservoir, DD insulating supports, E wick, F & G
     thermojunctions, H glass tube.   The arrow
     indicates the direction of air flow).

tube.

(3) Air velocity must not fall below a minimum of approximately
10 cm/sec.

The form of wet and dry bulb apparatus finally adopted
is shown in Fig. 1.   Air passes from right to left along a
polished brass tube A.   This tube is connected to vinyl tubes,
which are slipped over the ends of it.   A smaller brass tube
B is soldered on to the lower side of A near one end to form
a T piece.   The lower end of the smaller tube is sealed into
a glass reservoir C by means of a rubber stopper.   A length
of polythene cannula of 1 mm external diameter, containing
40 S.W.G. copper constantan thermocouple lead wires, is
threaded through punctures in the vinyl tubing, through holes
in insulating supports DD and along the axis of tube A.   The
wick E is a hollow cotton sleeve of the type normally used in
petrol lighters.   The wick rises from the reservoir as far
as the axis of tube A where a hole in the side of the wick
allows the polythene cannula to enter its bore.   The wick
surrounds the cannula for a distance of 4 cm.   The wet bulb
thermojunction F is situated mid-way along the portion of
cannula surrounded by the wick.   Another thermojunction G
for dry bulb temperature measurements, made from varnished
40 S.W.G. wire, is fixed at the upstream end of tube A by
being lightly twisted a few times round the polythene cannula.
A glass tube H also enters the reservoir through the rubber
stopper, and onto the other end of this tube is fitted a
short length of pressure tubing whose bore is closed by a
piece of solid glass tube.   The reservoir is filled with

distilled water by piercing the pressure tubing with a
hypodermic needle; this procedure avoids disturbing the
position of the wick. Before being fitted, the wick is
boiled in distilled water for at least 10 min. After
assembly all joints are sealed with plastic vapour-proof
paint.

Measurements of wet bulb temperature between individual
apparatuses made to this pattern at flow rates of 1 l./min
or greater, differ from those given by a standard Assman
hygrometer by ±0·3°C. The error of a given apparatus is,
however, consistent and is probably related to the exact
positioning of the wick and thermojunction. For capsule
measurements the apparatuses were always used in pairs, one
for inlet and the other for outlet air, and the zero error
due to differences between the two apparatuses was determined
experimentally at least twice daily by passing room air
through both. The useful life of an apparatus is from one
to eight weeks, after which the wick loses its ability to
absorb water. The effect of this happening is usually
marked and readily recognised as an abnormally large apparent
change in the rate of cutaneous evaporation. On only a
very few occasions was it necessary to abandon capsule
readings due to wick failures that were not recognised until
the following zero check.

At flow rates below 1 l./min the performance of the wet
bulb apparatus falls off. In most instances the decline
starts at approximately 0·75 l./min and at 0·5 l./min the
depression of the wet bulb temperature below that of the

dry bulb is approximately 98% of the correct value. At still
lower flow rates the decline is greater and differs between
individual apparatuses. Some capsule measurements were made
at flow rates down to 0·5 l./min by applying a correction to
allow for the reduced depression of the wet bulb temperature.

All wet and dry bulb apparatuses were situated in the
climatic rooms and the air whose humidity was being measured
was thus cooled or heated, as it passed along the connecting
tube, to the same dry bulb temperature as the room air. This
was particularly important for the measurement of the humidity
of expired air.

Interpretation of wet and dry bulb temperatures

The relationships between the wet and dry bulb temperatures
and the aqueous vapour pressure of moist air that are used in
the computation of psychrometric tables are empirical and vary
slightly between different compilers. The results in this
thesis are all based on the formula given by Hellman (1955):

$$e \;=\; p_w \;-\; 0 \cdot 5 \,(t - w)\, P/755$$

in which e is aqueous vapour pressure (mm Hg), p_w is saturation
vapour pressure of water (mm Hg) at wet bulb temperature w (°C),
t is dry bulb temperature (°C) and P is barometric pressure
(mm Hg). The relationship between absolute humidity or
moisture content m' (mg/l.) and aqueous vapour pressure may be
derived by assuming that water vapour is a perfect gas of
which 18g at s.t.p. occupies 22·4 litres:

$$m' \;=\; \frac{1 \cdot 057 e}{1 + t/273} \;=\; \theta\, e$$

Proof that the assumptions regarding water vapour do not result

in errors of practical importance is given by the fact that
the equation exactly ~~relates~~ *fits* published tables of 'Vapour
pressure of water below 100°C' and 'Mass of water vapour in
saturated air' (Hodgman, 1939).

These two equations may be applied to evaluate the gain
in absolute humidity m(mg/l.) of a stream of air ventilating
a capsule; the air having dry bulb temperature t, and wet
bulb temperature initially w_1 and finally w_0. It may thus
be shown that

$$m = \theta \eta [(p_0 - p_1) + \frac{\beta}{2}(w_0 - w_1)]$$

where
$$\eta = \frac{P}{P - e_1}$$

$$\beta = P/755$$

p_0 and p_1 denote the saturation vapour pressures (mm Hg)
at wet bulb temperatures w_0 and w_1, and e_1 is the initial
vapour pressure of the air.

In practice θ, η and β, which are all properties of the
environmental conditions in the climatic room, all approximate
to unity and the equation reduces to:

$$m \approx (p_0 - p_1) + (w_0 - w_1)/2$$

The relationship between temperature and saturation
vapour pressure of water is not readily expressible as an
equation. As a rough approximation, however, it may be stated
that for small differences in wet bulb temperatures, $(w_0 - w_1)$
is proportional to $(p_0 - p_1)$. Consequently the gain in
absolute humidity of the air passing through a capsule is
approximately proportional to the difference between the wet
bulb temperatures of outlet and inlet air. By connecting

the two wet bulb thermojunctions together in opposition to form a thermocouple the quantity $(w_o - w_1)$ was made available for direct automatic recording. This method gave a continuous visual record of evaporation rate that proved useful in detecting sudden changes, and in displaying an overall record of evaporative patterns with time.

For quantitative determinations of moisture output from capsules it was necessary to revert to the fuller equation:

$$m = \theta \eta \left[(p_o - p_1) + \tfrac{1}{2}(w_o - w_1) \right]$$

The only approximation made in this equation is the assumption that barometric pressure is equal to 755 mm Hg. In practice the error in the estimate of m caused by this assumption never exceeded 1·2%. A further assumption implied in the derivation of the equation, is that the two dry bulb temperatures are equal. This was always found to be true experimentally within the limits ±0·3°C which corresponds to an error of ±0·15 mg/l. in m. In practice the error in m due to unequal dry bulb temperatures was less than this, as the routine zero checks of the wet bulb apparatuses tended to provide automatic compensation for this type of error. Making allowance also for the accuracy of the thermocouple system, it is thus estimated that the overall error of any experimental determination of m is ±0·2 mg/l. or ±1·2% whichever is the greater.

Capsules

The early experiments were mainly concerned with investigating methods of fixing capsules to the skin with adhesives. Although it was found possible to make an

airtight seal that would last for a few hours, this was not suitable for the types of experiments envisaged. The aim was a method of fixing capsules onto the same piece of skin on successive days. Hair growth, which destroyed any seal after not more than 24 hr, and the difficulty of removing the adhesive from the hair tips after an exposure without disturbing the test area, prevented a satisfactory method being found.

The capsules used in these early experiments were fitted with peripheral flanges to which the adhesion was made; the limits of the test area being assumed to be defined by the inside edge of the flange. Part of the moisture collected by the air passing through the capsule may, however, have originated from the area covered by the flange itself, if the adhesion was not complete. Since the area of the flange could not, especially for small capsules, be kept small compared with the area under test, this could result in falsely high estimates of evaporation rate per unit area. The observed increase in evaporation rate per unit area, as the area under test was reduced, was at the time assumed to be accounted for by collection of moisture from the area covered by the flange. Subsequent experiments have shown that another factor (see p. 27) was also involved, although the flange may have been partially responsible. Even if a vapour-proof seal could have been formed under the whole area of the flange, the very fact that moisture loss from that area was inhibited might have affected the moisture loss from the area within.
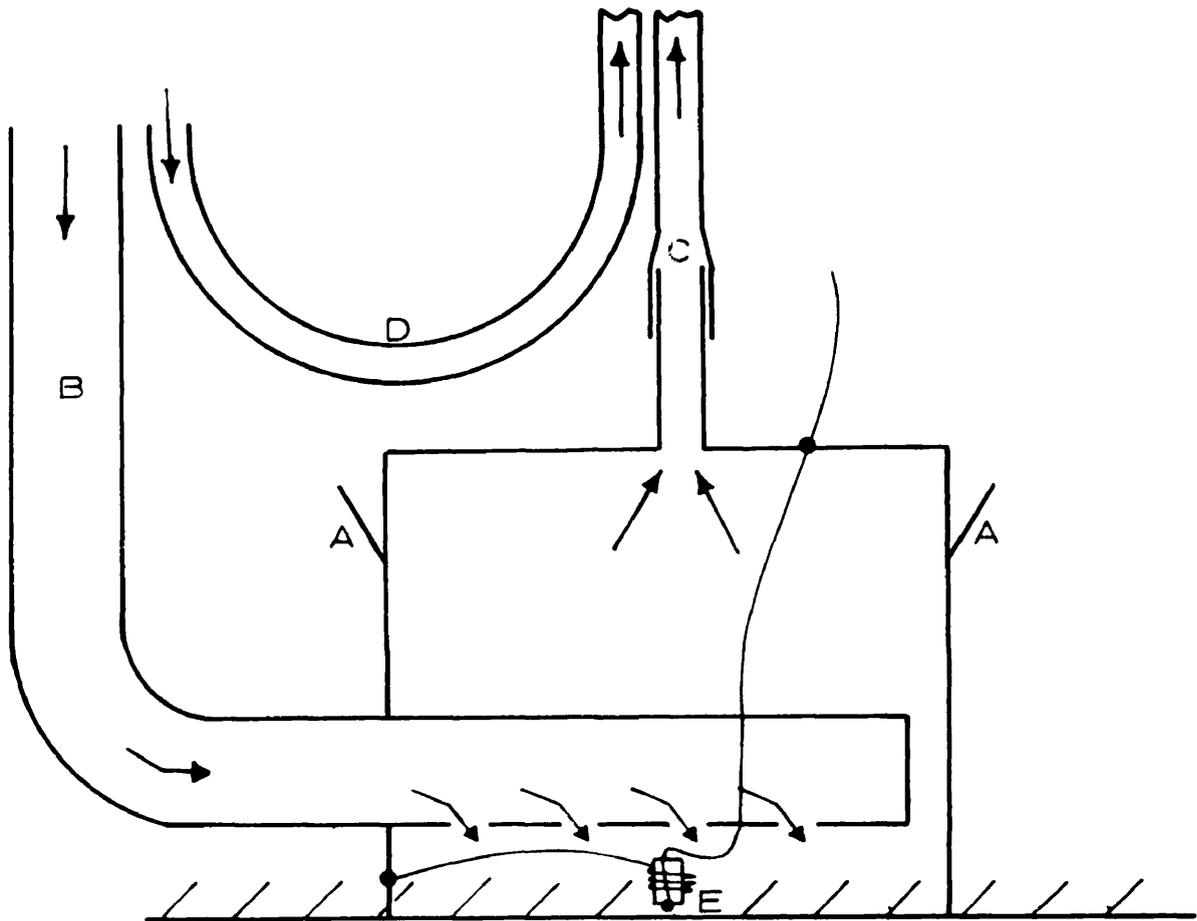
Fig. 2. The final form of ventilated capsule. Scale - approximately actual size. (AA fixing lugs, B inlet tube, C outlet tube, D inlet sampling tube, E thermojunction.)

The difficulties of sealing the capsule to the skin,
together with the accompanying uncertainty as to the
contribution to the moisture collected, made by the area under
the flange, led to a new approach. A capsule, in the form
of an inverted cylinder, was held onto the skin by means of
an elastic belt passing round the trunk of the animal. No
attempt was made to achieve a perfect seal, but the capsule
was fitted with a wide opening at the top, which served as
an easy inlet path for room air. The capsule was ventilated
by applying suction to an outlet tube also fitted in the top.
Capsules of this type were initially fitted with a band of
foam rubber round the rim to improve the seal, but this was
found to bend and bed down unevenly and form an irregular
flange, and was eventually abandoned in favour of straight
metal sides. In order to provide more even distribution of
air over the test area the inlet tube was later altered to a
form similar to that of the capsules described by Taneja
(1959). This resulted in the final form shown in Fig. 2
which has standardised dimensions of $41 \cdot 8$ cm^2 area and 6 cm
depth. The capsule is made from an ordinary sealed can of
the type commonly used as a food container. When opened,
using the type of can opener that cuts out one end round the
rim, the resulting edge is not sharp and perfectly satisfactory
for the present application. The capsule is normally held
in place by means of an elastic belt connected to the wire
lugs AA. Ambient air is drawn into the inlet tube B by
applying suction to tube C. The end of tube B that projects
inside the capsule has a number of holes drilled in its wall
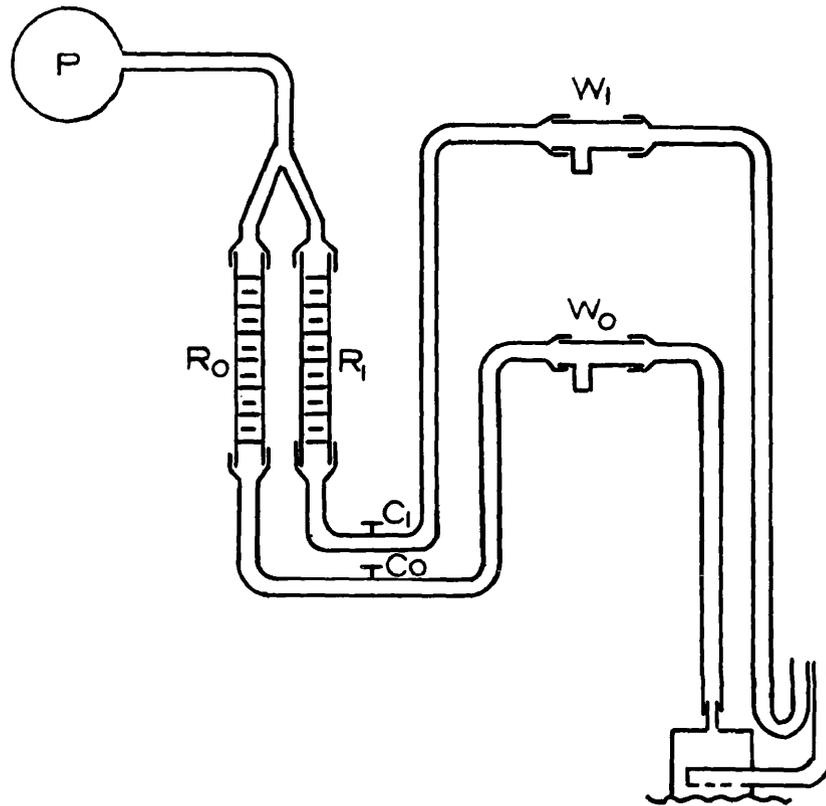
Fig. 3. The apparatus associated with a capsule. (W_1 & W_0 inlet and outlet wet and dry bulb apparatuses, R_1 & R_0 Rotameter flow meters, C_1 & C_0 air flow adjusting clips, P air pump.)

so as to distribute the air over the test area. A separate tube D mounted beside the inlet is used for sampling inlet air. Tubes C and D are each connected through wet and dry bulb apparatuses and Rotameter flowmeters to a common air pump. If skin temperature measurements are required a thermocouple E is mounted on a short length of plastic rod, which in turn is spring mounted onto the wall of the capsule by a length of piano wire, the thermocouple lead passing through a sealed hole in the top of the capsule.

The capsule requires no previous preparation of the skin area under investigation; it can be used on shaved or normal areas and can readily be reapplied to the same area any number of times. Its main disadvantage is that there is no means of telling directly whether there is any leakage under the rim, since the fitting of any air flow measuring device to the inlet tube defeats the main object of the design, i.e. to leave the air inlet side unimpeded. Only ambient air may be drawn into the capsule.

Fig. 3 shows the arrangement of the apparatus associated with each capsule. W_i and W_o are the inlet and outlet air wet and dry bulb apparatuses, C_i and C_o adjustable clips and R_i and R_o the flow meters. All suction tubes from all capsules are ventilated by a common pump P. The flow meters were calibrated by connecting them to a large bottle from which water was run out into a measuring cylinder at a rate timed by a stopwatch. It was found that the flow meters were accurate to within $\pm 2\%$ of the maker's calibration and that within this degree of accuracy they were unaffected by

changes in ambient temperature and humidity in the ranges 15 to 40°C and 6 to 36 mm Hg, nor by normal variations in atmospheric pressure.

The practical effects of ventilation rate and of capsule size and geometry (Experiment A)

It became clear during the early experiments that the rate of evaporation per unit area per unit time, as measured by the capsule technique, was dependent on the rate of air flow through the capsule and on the size and geometry of the capsule.

In order to investigate these effects more fully Experiment A was carried out. Capsules of four different cross-sectional areas (22, 42, 59 and 84 cm^2) and two different depths (2 and 6 cm) were employed. Four calves (Nos. 136, 138, 139 and 140) were used. Each was exposed in the small climatic room to air temperatures of 41°C for two periods at each of four humidity levels (12, 17, 24 and 32 mm Hg). The capsules were each placed in turn on finely clipped areas of skin on the left and right foreflanks and ventilated at a rate of 1 l./min. Afterwards the capsules of 42 cm^2 were ventilated successively at rates of $\frac{1}{2}$, 1, 2 and 4 l./min. The capsules used were similar to the type shown in Fig. 2 except that the inlet tube did not project inside; the dimensions were of course different. Skin temperature outside the capsules, but adjacent to them, were measured using the method described earlier (p. 15).

The results of this experiment are summarised in Tables 4 and 5. It is apparent that the geometry of the capsule and

Table 4.   Measured evaporation rates (g/m².hr) for capsules
of area 42 cm² at 41°C (Experiment A)

Capsule depth cm	Flow rate l./min	Absolute humidity mm Hg				Mean
		12	17	24	32	
2	½	112	117	109	100	109
	1	152	171	158	153	158
	2	171	199	198	197	191
	4	184	232	240	244	225
6	½	101	96	86	81	91
	1	137	140	135	130	135
	2	157	163	160	158	159
	4	178	175	175	210	184

Table 5.   Measured evaporation rates (g/m².hr) for a ventilation
rate of 1 litre/min at 41°C (Experiment A)

Capsule depth cm	Capsule area cm²	Absolute humidity mm Hg				Mean
		12	17	24	32	
2	22	145	152	154	158	152
	42	145	162	156	148	153
	59	170	160	156	141	157
	84	150	140	135	117	136
6	22	152	153	152	154	153
	42	141	141	135	124	135
	59	128	126	118	109	120
	84	140	128	117	103	122

the rate of ventilation affected the measured rate of evaporation profoundly. The rates of evaporation recorded at an absolute humidity of 32 mm Hg, by the capsule techniques that gave the highest and lowest results, differed by a factor of three. Moreover, had a single combination of depth, area and ventilation rate been chosen to carry out a physiological experiment to investigate the effect of ambient humidity on the rate of evaporation from the skin, the conclusions drawn would have depended on the particular combination chosen.

Theoretical consideration of the effect of the capsule on evaporation rate

The application of a capsule to the skin of an animal may alter the physical conditions at the site of measurement and so affect evaporation rate as follows:

(1) By changing the rate of air movement near the skin - this would be expected to result in alteration to the heat losses by evaporation and convection.

(2) By changing air temperature and humidity near the skin - this would also affect evaporation and convection.

(3) By changing the radiant temperature of the local surroundings - this would affect heat loss by radiation.

(4) By changing the local blood flow pattern if excessive pressure were used to hold the capsule in place - this might affect all forms of heat loss.

Of these the first two are obviously of great importance since they directly affect the quantity being measured, i.e. cutaneous evaporation. Since evaporation is a physical process it must of necessity be influenced by alteration of

the physical conditions, i.e. air movement, temperature and humidity. These effects may in theory be eliminated if ventilation of the capsule is provided by drawing ambient air into it at a rate equivalent to the rate of ventilation outside. The difference between skin temperature inside the capsule (T_{si}) and that outside (T_{so}) may be used to compare ventilation inside and outside if radiation (factor 3) is unaltered by the presence of the capsule. The condition of no alteration in radiation is also obtainable if the air temperature (T_a) and that of the walls (T_w) are maintained at the level of the animal's skin temperature (T_{so}). Under these conditions the capsule also attains the same temperature T_c, and so

$$T_{so} = T_a = T_w = T_c$$

If room air temperature is adjusted so that these conditions are satisfied, T_{si} in theory equals T_{so} only if the air flow rate is such that it gives equivalent ventilation to that experienced by the test area when the capsule is removed. This ventilation rate may be termed the 'critical flow rate' for the particular capsule used. At higher air flow rates $(T_{si}-T_{so})$ is negative due to increased evaporative cooling under the capsule and at lower air flow rates $(T_{si}-T_{so})$ is positive.

The measurement of $(T_{si}-T_{so})$ is difficult since it represents the difference between two nearly equal quantities. Moreover, the skin temperature within the capsule may not be uniform over the test area, although baffling the inlet port of the capsule may help to eliminate variations.

The effect of factor 3 (radiation) may be eliminated in this way only at the air temperature corresponding to $T_a = T_{so}$. The critical flow rate for equal ventilation inside and outside the capsule determined at this air temperature may be still valid at other temperatures; but the condition $T_{si} = T_{so}$ is no longer applicable, since radiative loss is now altered by the application of the capsule. It remains to be proved that alteration of the radiative loss within the capsule does not affect evaporation from this area. This may be shown at $T_a = T_{so}$ by heating or cooling the capsule. If no change in evaporation rate occurs, it may be assumed that the alteration to the radiative loss, when a capsule is applied under conditions when T_a is not equal to T_{so}, is also without influence on evaporation rate.

The results of the experiment, in which capsule depth and area and ventilation rate were varied (Experiment A) may not be strictly interpreted by this reasoning as the experiment failed to satisfy the required conditions in the following respects:

(1)   Different thermocouple mountings were employed for the measurement of T_{si} and of T_{so}, and the two measurements were not always made on the same flank.

(2)   Skin temperature measurements under the capsule for the first animal were measured by a different technique. This technique proved unsatisfactory due to the thermocouples becoming detached from the skin, and it had to be abandoned. The final method of fixing the skin thermocouples inside the capsules described earlier (p. 26) was therefore only used
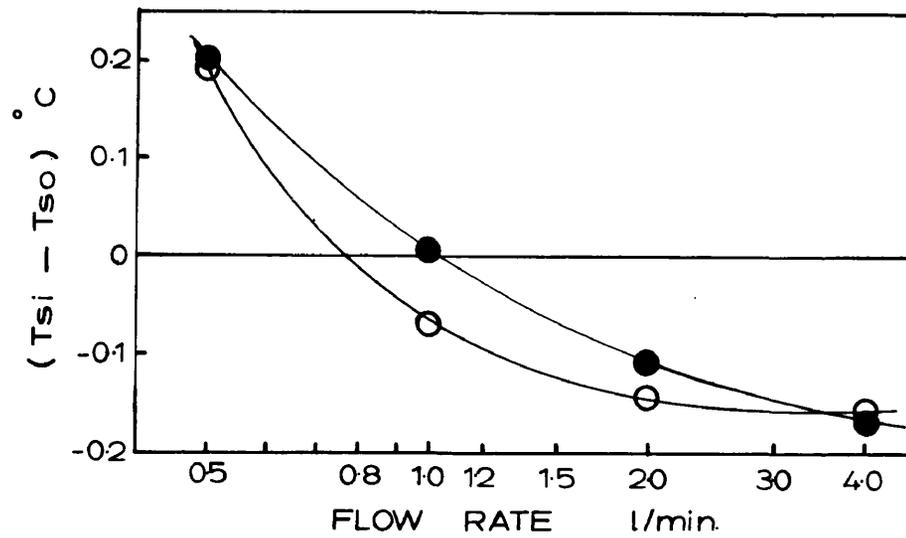
Fig. 4.   The effect of varying ventilation rate on the
          difference between skin temperatures measured
          inside and outside the capsule $(T_{si} - T_{so})$ for
          capsules 2 cm (o) and 6 cm (●) deep (Experiment A).
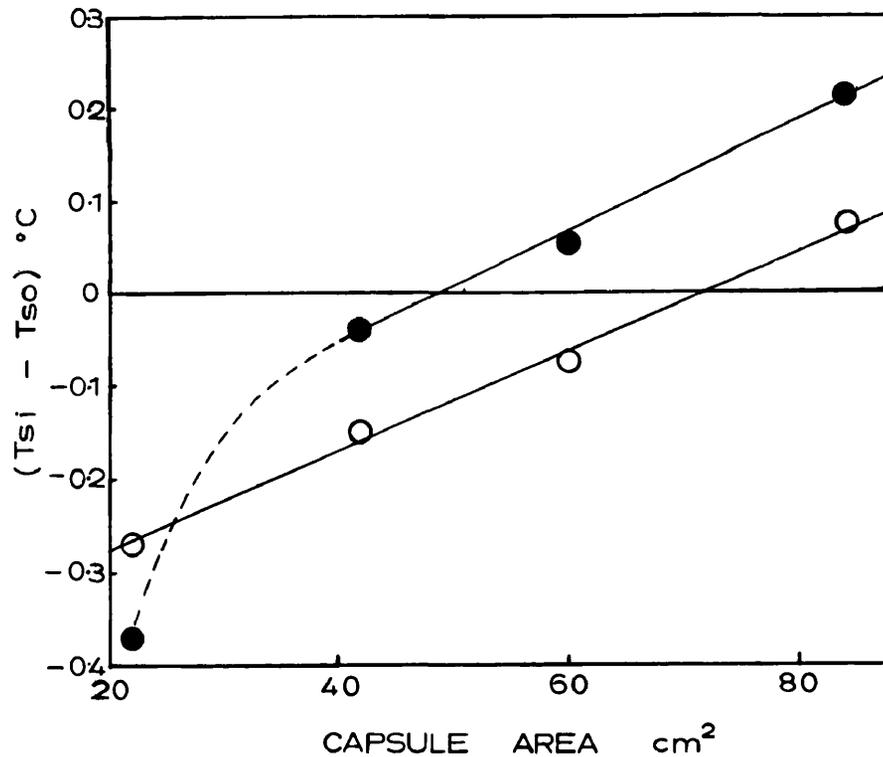
Fig. 5.   The effect of varying capsule area on the difference
          between skin temperatures measured inside and
          outside the capsule $(T_{si} - T_{so})$ for capsules 2 cm
          (o) and 6 cm (●) deep (Experiment A).

for the remaining three animals.   It is only for these animals
(Nos. 138, 139 and 140) that $(T_{si}-T_{so})$ measurements are
available.

(3)   The capsules used were not specifically designed with a
view to even distribution of inlet air over the test area and
T_{si} was measured only at the centre of this area.

(4)   Air temperature was in general some 2 to 3°C above skin
temperature.

It was nevertheless expected that the results would provide
some guide as to the validity of the theoretical approach.

The skin temperatures for each flow rate-capsule depth
and for each capsule area-depth combination were averaged
over all exposures and these are plotted in the form of $(T_{si}-T_{so})$
against flow rate and against capsule area in Figs. 4 and 5.
From these figures the four specific conditions of measurement,
at which $T_{si} = T_{so}$, were obtained as follows:

(a)   For capsules of standard area 42 cm² and 2 cm deep, at a
flow rate of 0·75 l./min.

(b)   For capsules of standard area 42 cm² and 6 cm deep, at a
flow rate of 1·02 l./min.

(c)   For a standard flow rate of 1 l./min using capsules 2 cm
deep and of area 71·7 cm².

(d)   For a standard flow rate of 1 l./min using capsules 6 cm
deep and of area 49·0 cm².

The evaporation rate corresponding to each of these four
conditions was found graphically from the data of Tables 4 and
5.   This gave for each humidity level four separate estimates
corresponding to the experimental conditions a, b, c and d, of

Table 6.   Estimated rates of evaporation from the

skin in the absence of capsules

$(g/m^2.hr)$ (Experiment A)

Method of estimation (see p. 32)	Absolute humidity (mm Hg)				Mean
	12	17	24	32	
a	133	144	134	125	134
b	138	141	136	132	137
c	160	152	149	130	148
d	135	133	126	116	128
Mean	142	142	136	126	137

the evaporation that would have taken place from the test areas had the capsules not been applied. These estimated evaporation rates are presented in Table 6. The evaporation rates in this table for any one humidity level are more consistent than in Tables 4 and 5 and the dependence of evaporation rate on humidity is similar for all four sets of estimates. The agreement between estimates a and b, derived from the data where flow rate was varied, is remarkably close. The agreement between estimates c and d, derived from the data where area was varied, is not so close. This is due to the fact that the variation of evaporation rate with area (Table 5) is not so clearly defined as that with flow rate (Table 4). Leakage of air under the rim of the capsule may be responsible for many of the inconsistencies in Table 5; this would be most likely to occur with the largest capsules and would be most serious in its influence on the measurements in the smallest.

The consistency of the results in Table 6 especially those in rows a and b appears to justify the reasoning leading to the concept of a critical flow rate. The quantitative values obtained for critical flow rates in Experiment A are however invalid since the necessary conditions for their determination were not satisfied.

Determination of critical flow rate (including Experiment B)

Further experiments to test the theories stated in the preceding section and to determine the value. of critical flow rate (F_o) were carried out using capsules of standard dimensions and design as described earlier (p. 25 and Fig. 2). These capsules had been modified from those used previously with a

view to securing more uniform ventilation of the test area.
In these experiments and in all succeeding physiological
experiments the general purpose chamber of the new climatic
laboratory was used and the capsules were placed over unshorn
skin areas. The experiments were as follows:

(1) <u>Examination of skin temperature variation over the
area covered by a capsule</u>

A capsule was fitted with seven thermojunctions mounted
as described on p. 26 for measuring skin temperature. Four
of these measured skin temperature at different points inside
the capsule (T_{si}) while the other three measured skin
temperature outside it (T_{so}). The capsule was applied to
the skin of a calf exposed to an air temperature of $T_a \approx T_{so}$
$\approx 38°C$. Measurements of the temperatures of all seven skin
thermojunctions were made at frequent intervals.

The mean variation between individual skin temperatures
measured inside the capsule was $\pm 0 \cdot 132°C$ (S.D.) and that
between individual skin temperatures measured outside was
$\pm 0 \cdot 115°C$ (S.D.). Neither variation appeared to be affected
by altering air flow through the capsule up to rates of
4 l./min.

The relative difference between the two variations is
small, and it is concluded that any variation between the
four temperatures measured inside the capsule, due to uneven
ventilation of the area examined, are small compared with the
other sources of variation inherent in the method of
measurement.. The use of, say, eight junctions connected in
series opposition as four thermocouples for estimating

$(T_{si}-T_{so})$ is therefore justifiable.

(2) <u>The pressure applied to the capsule</u>

In order to provide adequate sealing between the rim of the capsule and the skin, a pressure of approximately 1 lb, applied to the capsule as a whole, is necessary for most regions, although considerably lower pressures may be acceptable on regions where the surface is smooth. This pressure was not normally measured, the tension of the belt securing the capsule, and the satisfactory contact of the capsule with the skin being gauged by visual and manual means; this normally resulted in a pressure of approximately 1 lb. The pressure applied to the skin by the rim of the capsule under these conditions is not known but must be considerable. After prolonged application of a capsule the pressure was sufficient to cause an annular depression in the skin surface which persisted for several minutes following removal of the capsule. The cutaneous blood flow under the rim of the capsule must therefore have been restricted to some extent, but there was no visual evidence of any abnormality in the skin at a distance further than 1 mm from the rim.

When the pressure was deliberately altered, no effect on evaporation rate was observed until the seal between capsule and skin was obviously broken at very low pressures. Deliberate variations in pressure did on occasion affect the measured value $(T_{si}-T_{so})$ especially when the pressure fell below 1 lb; this appeared to be due to alterations to the degree of contact of the thermojunctions with the skin, rather than to alterations in blood flow.

It is concluded that the evaporation results were not appreciably affected by blood flow changes resulting from the pressure at which the capsule was held in place. Frequent inspection of the capsules was however necessary to ensure that the seal remained unbroken.

(3) <u>Cooling and heating the capsule</u>

On a number of occasions at an air temperature of $T_a = T_{so}$, the local radiative conditions under the capsule were suddenly altered by applying a water-filled polythene bag to the outer surfaces of the capsule. In this way capsule temperatures were raised or lowered by up to 10°C above or below skin temperature. It was found that this resulted in no change in evaporation rate, except that occasionally cooling caused a small transient decrease in evaporation rate lasting approximately 5 min, after which the original level was re-established.

From these experiments it is concluded that alteration of the radiative heat loss, from the small area covered by the capsule, does not result in any permanent physiological adjustment which re-establishes the heat balance in that particular area, by adjusting the amount of water available for evaporation. The use of capsules for measuring evaporation when ambient temperature is not equal to skin temperature is therefore justified. The transient drop observed when the capsule was cooled may have been due to condensation of moisture on the walls of the capsule.

(4) <u>The effect of altering the air flow rate through the capsule (Experiment B)</u>

Four calves (Nos. 193, 196, 197 and 199) were each exposed

Table 7.   Evaporation rate $(g/m^2.hr)$ from the left mid flank (E_l) and right sacral back (E_r), and the difference (galvanometer scale divisions) between skin temperature inside and outside the capsule $(T_{si}-T_{so})$ on the left mid flank, for various air flow rates (l./min) (Experiment B)

Exposure No.	Nominal flow rate l./min	Calf 196			197			193			199		
		E_l	E_r	$T_{si}-T_{so}$	E_l	E_r	$T_{si}-T_{so}$	E_l	E_r	$T_{si}-T_{so}$	E_l	E_r	$T_{si}-T_{so}$
1.	0·5	83	–	0·7	69	96	1·5	90	112	2·8	95	53	1·0
	0·8	95	–	0·7	88	133	-1·4	112	141	1·0	89	44	2·1
	1·2	108	–	-0·4	89	128	-0·2	121	154	2·0	93	49	0·7
	1·8	144	–	0	103	171	-2·2	138	158	0·2	102	59	1·2
	2·6	131	–	-1·1	105	139	-2·0	144	158	0·7	95	62	0·1
	3·9	158	–	-0·6	116	198	-3·0	161	171	-1·5	110	72	0·1
2.	0·5	76	82	2·0	55	115	2·0	–	106	2·6	53	53	0
	0·8	83	89	0·9	73	131	0·8	–	132	1·5	62	59	-0·9
	1·2	90	91	1·0	73	138	1·0	–	144	1·0	66	65	-0·7
	1·8	105	98	0·1	70	148	1·2	–	159	0·6	69	60	-1·4
	2·6	98	102	0	72	182	1·1	–	148	1·0	73	66	-1·7
	3·9	120	121	-0·2	118	165	0·2	–	166	-0·1	85	72	-0·8
3.	0·5	73	77	0·4	42	93	2·4	89	108	–	20	–	0
	0·8	82	60	-0·3	47	108	1·7	108	131	–	23	–	0·4
	1·2	87	78	-0·8	54	122	2·2	113	140	–	23	–	0
	1·8	80	79	-1·0	59	128	2·4	126	146	–	23	–	-0·2
	2·6	96	83	-1·1	59	142	0·7	155	178	–	23	–	-0·4
	3·9	102	85	-1·3	67	146	0·8	148	164	–	23	–	-0·9
4.	0·5							92	106	2·4			
	0·8							100	129	1·7			
	1·2							126	149	1·0			
	1·8							132	165	0·2			
	2·6							148	177	-0·7			
	3·9							148	187	-1·1			

three times to an air temperature of approximately 38°C with
absolute humidity 18 mm Hg.   One extra exposure for calf 193
was included since failure of the measuring apparatus had
invalidated some results from earlier exposures.   A capsule,
fitted with eight thermojunctions, connected in series, for
measuring $(T_{si}-T_{so})$, was applied to the left mid-flank and
another capsule to the right sacral back region.   Flow rates
through both capsules were initially 1·2 l./min and, after a
2-hr waiting period, they were changed at half-hourly intervals
to cover the values 0·5, 0·8, 1·8, 2·6 and 3·9, finally
returning to 1·2 l./min.

Measurements were made every 5 min of air temperature,
skin temperature on left and right flanks, rectal temperature,
capsule temperature and of flow rates through the capsules.
Continuous recordings were made of wet bulb temperature
difference (w_o-w_1) for both capsules and of $(T_{si}-T_{so})$ for the
one capsule.   Occasional adjustments to the control system
of the climatic room were made to maintain air temperature at
the measured level of skin temperature.

The results for evaporation rate and for $(T_{si}-T_{so})$ at
various flow rates are given in Table 7.

Examination of the results shows that for any calf on any
day $(T_{si}-T_{so})$ fell as flow rate (F) was increased.   The fall
in $(T_{si}-T_{so})$ was approximately linear with log F.   The reason
why this linear relationship was not observed in Experiment A
(Fig. 4. p. 32) is not known.   It is possible that this
difference between the two sets of results is connected with
the fitting of baffled inlet tubes to the capsules, a

modification that was made only after the completion of Experiment A. The general level of $(T_{si}-T_{so})$ varied greatly from day to day, and so therefore did the estimate of critical flow rate F_o. $(T_{si}-T_{so})$ is a very small quantity, being the difference between two nearly equal temperatures and having a magnitude of $0 \cdot 2°C$ (3 scale divisions in Table 7) or less. Any local variation of skin temperature due to large blood vessels near the skin surface, or any form of poor contact of any of the eight thermojunctions with the skin would be likely to cause large errors in the estimate of $(T_{si}-T_{so})$. Large day-to-day variations in the measured values of $(T_{si}-T_{so})$ were therefore to be expected. However, with the capsule fixed in any one place, relative values of $(T_{si}-T_{so})$ on any one day were likely to be more consistent, as was indeed found. The day-to-day variations in the mean level of $(T_{si}-T_{so})$ showed no relation to day-to-day variations in evaporation rate, rectal, skin or air temperature or any other measured quantity; this strengthens the belief that such variations were in fact purely error from the causes mentioned above.

The regression equation of log F on $(T_{si}-T_{so})$ was calculated using the mean values of $(T_{si}-T_{so})$ averaged over all exposures for each flow rate. Hence the critical flow rate corresponding to $T_{si} = T_{so}$ was evaluated as $F_o = 1 \cdot 93$ l./min. The accuracy of this value for F_o, estimated from the 5% fiducial limits of log F_o in the regression equation, may be expressed as $1 \cdot 64 < F_o < 2 \cdot 25$ l./min. The error in F_o may be still greater than these limits suggest, since if individual values of log F_o are determined for each of the twelve exposures represented

Table 8.   Evaporation rates (E_o) corresponding to the
critical flow rate $F_o = 1 \cdot 93$ l./min, and
values of the regression coefficients,
$k = d \ (\log E)/d \ (\log F)$, used in computing
E_o (Experiment B)

Calf	Exposure No.	Left mid flank		Right sacral back	
		$E_o(g/m^2.hr)$	k	$E_o(g/m^2.hr)$	k
196	1	128	0·297	-	-
	2	100	0·209	103	0·173
	3	90	0·144	79	0·104
197	1	100	0·229	154	0·279
	2	80	0·275	154	0·207
	3	57	0·220	131	0·218
193	1	136	0·266	156	0·179
	2	-	-	149	0·194
	3	131	0·259	152	0·214
	4	131	0·247	162	0·265
199	1	99	0·084	59	0·203
	2	72	0·198	65	0·124
	3	23	0·050	-	-
Mean	-	96	0·206	124	0·196

by Table 7 and the standard deviation calculated, then the 5% confidence limits for F_o are found to be $1 \cdot 11 < F_o < 2 \cdot 70$.

The estimate of F_o may therefore be in error by approximately 75% of the true value.

The measured rate of evaporation E (see Table 7) rose as flow rate was increased. If log E is plotted against log F the relationship is approximately linear. The values of E_o corresponding to F_o were obtained by calculating linear regressions for log E on log F. The values of E_o are thus estimates of evaporation from the free skin surface under the conditions of air movement pertaining in the climatic room. In Table 8, E_o is given corresponding to $F_o = 1 \cdot 93$ l./min together with the values of the regression coefficient $k = d \ (\log_{10} E)/d(\log_{10} F)$. The mean of twenty-three determinations of k is $0 \cdot 202 \pm 0 \cdot 014$ (S.E.).

Computation of true evaporation rate when flow rate is not critical

If the relationship between evaporation rate and flow rate through the capsule is known it is not essential that experimental determination of evaporation rate be carried out at the critical flow rate. In fact in subsequent measurements the nominal flow rate $F = 1 \cdot 2$ l./min was chosen for experimental convenience.

If E is the observed evaporation rate at flow rate F, then the normal evaporation rate, E_o, at the critical flow rate, F_o, is given by

$$E_o = E(F_o/F)^k$$

and $\quad E = \dfrac{600mF}{A}$

where E and E_o are expressed in $g/m^2.hr$

F and F_o in $l./min$

A, the area of the capsule, in cm^2

m, the gain in absolute humidity of the

air as it passes through the capsule, in mg/l.

$\quad\quad k = 0.202$, for the capsule design employed.

The factor 600 is a dimensional constant.

Combining these two equations:

$$E_o = \dfrac{600mF(F_o/F)^k}{A}$$

or $\quad E_o = \propto m$

where $\propto$ is a factor, which for the standard conditions

employed, is dependent solely on the flow rate, F.

The estimate of normal evaporation rate (E_o) by this

method is subject to a systematic error which is associated with

the uncertainty of the estimate of the critical flow rate

$(F_o = 1.93 \; l./min)$. Since, for the capsule design used, k

is small compared with unity, a 75% error in F_o results in only

a 12% error in E_o. This fixed unknown error in E_o is in

addition to any random error associated with any one measurement.

<u>Summary of capsule method and errors</u>.

Capsules constructed as shown in Fig. 2 (p. 25) were

used to estimate the rate of evaporation from the skin E_o

that would normally occur from the area examined in the absence

of the capsule. This was done by measuring the gain in

absolute humidity $m(mg/l.)$ of the air as it passed through the

capsule, and the rate of air flow through the capsule $F(1./\text{min})$.
m was measured by means of wet and dry bulb thermocouples and
F by Rotameter flowmeters. The evaporation rate was then
obtained from

$$E_o = \propto m \ g/m^2.hr$$

where $\propto$ is a factor dependent solely on F.

For the nominal flow rate

$$F = 1\cdot2 \ 1./\text{min}$$

$$\propto = 19\cdot0 \ m/hr$$

The quantitative accuracy of this method is subject to
systematic error whose greatest possible magnitude is estimated
at 12%. In view of the possible large error it was decided as
a further quantitative check to compare the total cutaneous
evaporation, as measured by the capsule technique, plus the
respiratory weight losses with direct determination of the
total insensible weight loss. This comparison is described
in Chapter III.

Respiratory Analysis

Separation and collection of respiratory gases

The animal was made to wear a mask. The mask method
employed was designed to minimise the resistance to respiratory
gas flow. The use of any form of spirometer or collection bag
was avoided in order to eliminate inertia and the valves were
made as light as possible. The mask (Fig. 6) was constructed
of sheet metal at the lower end and sheet rubber at the upper
end. It was held in place by means of a leather strap that
passed over the back of the animal's head behind his ears.
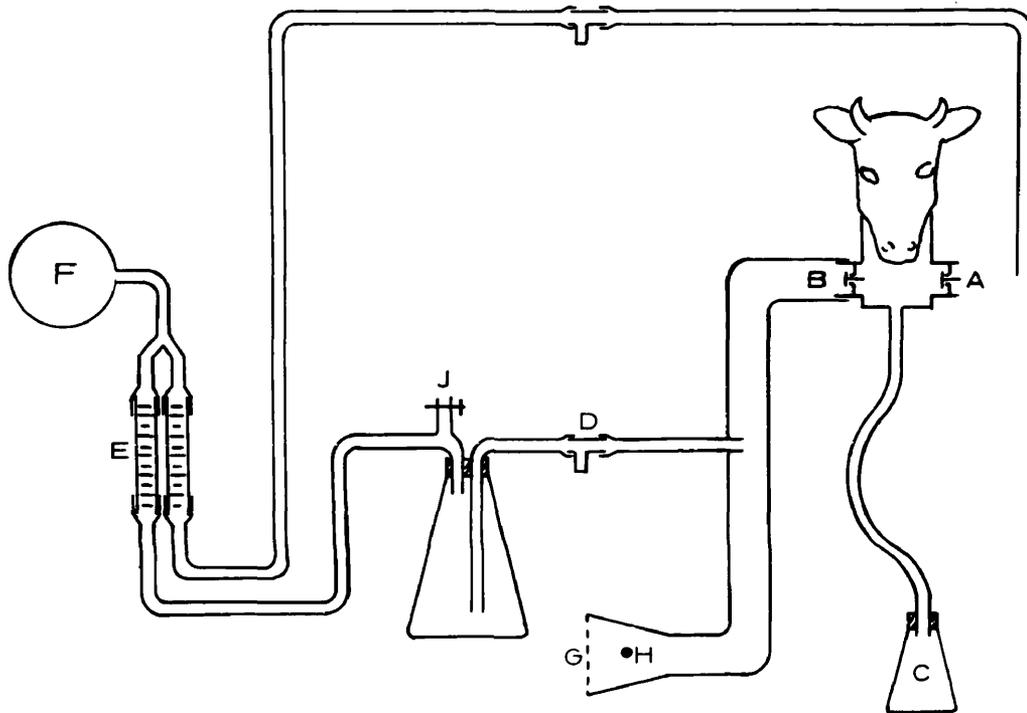
Fig. 6. The mask assembly for respiratory analysis. (A & B
    inlet and outlet valves, C saliva collection bottle,
    D wet and dry bulb apparatus, E Rotameter flowmeter,
    F air pump, G pneumotachometer gauze, H thermo-
    junction, J expired air sampling point.)

The mask was sealed onto the muzzle by means of an inflatable tube mounted inside the top opening, and by packing the joint with cotton wool. Inspired air entered the mask from the room via the valve A. Expired air passed through the valve B and then through a 1·2 m length of 8 cm diameter flexible tubing (Flexflyte) back into the room. A drainage tube fitted to the lower end of the mask allowed condensed moisture and saliva to be collected in a bottle C. A sample of the expired air passing down the flexible tubing was drawn continuously, from a point half way along the tubing at a rate of 1·2 l./min, through the wet and dry bulb apparatus D, a 3 litre mixing bottle and the Rotameter flowmeter E by the pump F. The remainder of the expired air passed out of the flexible tubing through a pneumotachometer gauze G (Nisbet, 1956). A 40 S.W.G. thermojunction H measured the mean temperature of expired air at the exhaust end of the flexible tubing. A second sampling tube was placed near the inspiratory valve, and through this and another wet bulb apparatus and Rotameter room air was drawn continuously by the same pump F. The junction J in the expired air sampling line was used for drawing off samples in tonometers for subsequent analysis on a Haldane apparatus. Inspired air samples were also collected in tonometers, from a position close to the inspiratory valve.

The construction of the valves* is shown in Fig. 7. The moving part of the valve is a 5 cm diameter mica disc A

* The design of the valves was by Mr. W. Nisbet.
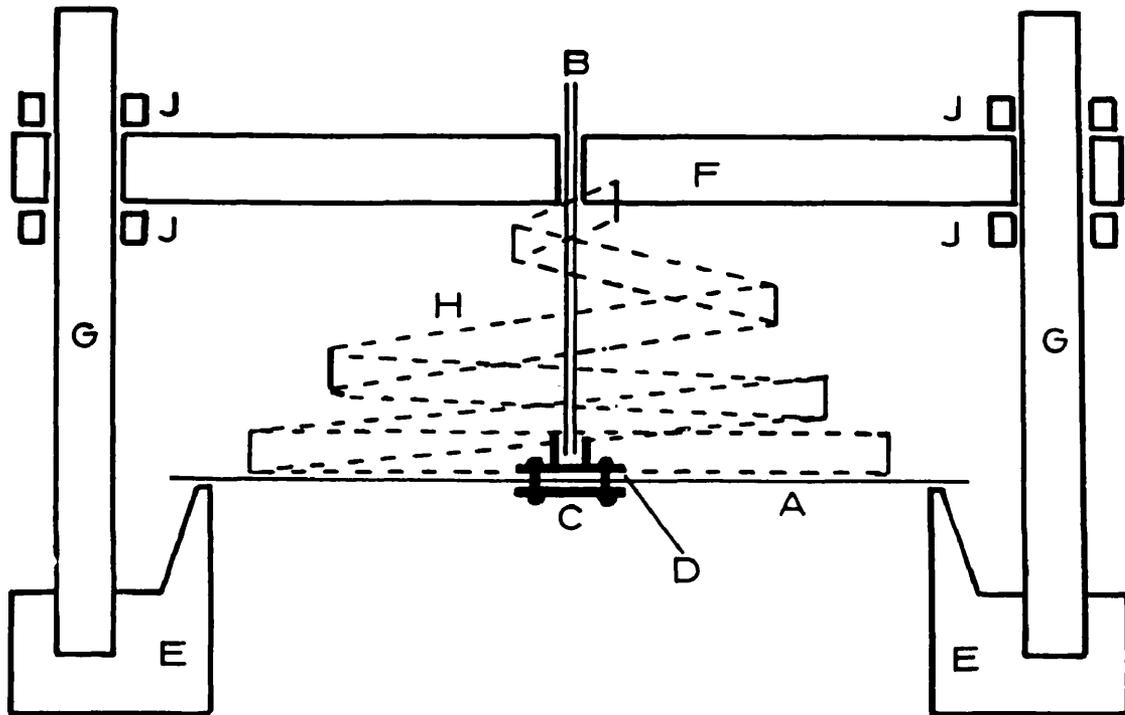
Fig. 7.   Construction of the valves used in the mask.   Scale -
    approximately twice actual size.   (A mica disc, B
    stainless steel guide tube, C brass washer, D brass
    collar, E valve seat made from perspex, F brass rod,
    GG threaded brass posts, H watch spring, JJ
    clamping nuts.)

with an axial guide rod B made from stainless steel capillary tubing of 1 mm outside diameter. A washer C and collar D, both made from brass are fixed centrally on either side of the mica disc by means of rivets. The guide rod is push-fitted into the collar. The fixed part of the valve is a perspex annulus E, the valve seat being a plane annular surface of 4·5 cm internal diameter and 0·7 mm width. This design is a compromise between the conflicting requirements of airtightness, which calls for a valve seat of large area, and of non-stickiness which would be best effected by a knife-edged seat. The guide rod slides loosely through a hole drilled in a brass rod F which is clamped onto two threaded brass posts GG mounted on the perspex annulus. A shaped watch spring H is soldered onto the rod F and the position of the spring is adjusted by means of clamping nuts JJ so that the mica is just held onto the valve seat against gravity when the valve assembly is inverted. The pressure required to hold these valves fully open is approximately 0·1 mm Hg. They operate satisfactorily in any position and whether wet or dry.

Difficulties were occasionally experienced due to leaks developing at the seal of the mask to the face of the animal and due to the outlet valve sticking when saliva had accumulated on it. On most occasions these faults were obvious by an apparent decrease in minute volume or increase in the vapour pressure of expired air, and they could be corrected immediately.

Measurement of respiratory rate and volume

The quantity of air passing out of the mask assembly through the gauze G (Fig. 6, p. 45) was measured by a pneumotachometer (Nisbet, 1956). This is an electronic instrument which measures instantaneous air flow rates by detecting minute pressure changes, induced across a fine meshed gauze, as air passes through it. An electronic integrator can present the results in terms of either the volume of a single expiration or the integrated volume of all expirations during any convenient period. A modification to the relay system of the pneumotachometer was made by Mr. W. Nisbet so that the instrument would operate with the unidirectional air flows occuring in the present mask assembly as well as with reversing respiratory flows in the original pneumotachometer mask.

The integrated air flow through the gauze during one minute added to that drawn down the expired air sampling tube represented the expiratory minute volume.

Respiratory rate was counted by observation of the pneumotachometer indicators using a stop watch. On occasions when the mask assembly was not in use, respiratory rate was measured with a mechanical counter (Nisbet, 1958), operated by flank movements of the animal.

Composition of respiratory gases.

The gain in absolute humidity of air as it passed through the respiratory apparatus was measured using wet and dry bulb thermocouple apparatuses as already described for capsules. This quantity added to the absolute humidity of room air was

used to estimate the absolute humidity of expired air for the
purposes of correcting minute volume into terms of the total
volume of dry air expired at s.t.p.

Oxygen and carbon dioxide percentages in expired and
inspired air samples were measured on Haldane gas analysers.
It was found that the variation in composition between
individual samples of inspired air was unrelated to temperature
and humidity levels or to the presence or absence of an animal
in the climatic chamber.   The variation, which was random,
was attributed to sampling and analysis errors, more particularly
to errors due to the presence of the observer in proximity to
the tonometers when collecting samples.   The composition of
inspired air was therefore assumed to be constant and equal to
the mean level obtained from all inspired air analyses (71 in
all).   The composition of inspired dry air in the general
purpose chamber, where all experiments with the mask were
conducted, was thus estimated as follows:

Carbon dioxide	0·085%
Oxygen	20·88%
Nitrogen	79·035% (by difference)

For the purposes of calculations it was assumed both
for expired and inspired dry air that carbon dioxide, oxygen
and nitrogen were the only constituents.

Heat production and metabolic weight loss

Heat production H_p was calculated from the respiratory
data using the equation of Brouwer (1958):

$$H_p = 3 \cdot 869 . O_2 + 1 \cdot 195 . CO_2 \text{ (kcal/hr)}$$

where O_2 and CO_2 represent the volumes (l./hr) of oxygen

consumed and carbon dioxide produced at s.t.p.   Brouwer

showed that for ruminants, the omission from the equation of

additional terms containing the weight of protein metabolised

and the volume of methane produced, results in an error of

not more than 2% in the estimate of heat production.

The weight loss due to oxygen-carbon dioxide exchange,

or metabolic weight loss W_m, may be calculated from the gas

molecular weights and the volumes consumed and produced;   it

is given by the equation:

$$W_m = 1 \cdot 964.CO_2 - 1 \cdot 429.O_2 \quad (g/hr)$$

The values of the quantities O_2 and CO_2 were obtained from

the volume of dry air expired at s.t.p. V(l./hr) and the

percentages of oxygen (x) carbon dioxide (y) and nitrogen

(z) in inspired (subscript l) and expired (subscript O) air

as follows:

$$CO_2 = (y_0 - y_1 z_0 / z_1) \, V/100 \quad l./hr$$
$$O_2 = (x_1 z_0 / z_1 - x_0) \, V/100 \quad l./hr$$

Respiratory evaporation

The quantity of moisture evaporated from the respiratory

passages E_r was obtained from the product of the expiratory

minute volume V_m (litres) and the gain in absolute humidity

of the air passing through the mask assembly m(milligrams

per litre of expired air).   Including dimensional constants

the equation is:

$$E_r = 0 \cdot 06 \, m \, V_m. \quad (g/hr)$$

This method of estimating respiratory moisture loss,

hereafter described as 'the direct method' was found unsuitable

at air temperatures below 30°C due to condensation of respiratory
moisture in the tube leading to the wet and dry bulb apparatus.
When the environmental conditions were such that condensation
occured, respiratory evaporation was estimated by 'the
difference method' as follows:

$$E_r = W_t - W_m - E_s$$

where W_t = total insensible weight loss

W_m = metabolic weight loss

E_s = weight loss by cutaneous evaporation

Insensible Weight Loss

The animal was tethered standing in a stall made of
galvanised tubing and timber.   Urine was collected by means
of a polythene funnel, which was screwed into the neck of a
polythene bottle and which was supported by harness passing
round the trunk.   Faeces were collected in a bag, constructed
from a motor tyre inner tube, and supported by other harness.

The order of magnitude of the weight loss due to
evaporation of water from the accumulated urine and faeces
in the funnel and bag was determined experimentally with the
open collectors placed on a small balance.   The loss was
3 g/hr or less under all environmental conditions employed.
Another error arose due to inhibition of cutaneous evaporation
from the skin regions covered by the collectors and harness.
This was kept small by making the harness wherever possible
from plastic covered elastic wire curtain rod.   These two
sources of error tended to be mutually self-cancelling and
no correction was made for them.

The stall containing the animal, excreta collectors, mask assembly, capsules and harness normally rested on wooden blocks above the platform of an Avery balance. The blocks were removed when weighing was required and the ventilating tubes to the capsules temporarily disconnected. The only connections between the stall and its surroundings during weighings were five thermocouple leads which hung loosely between a certain point on the stall and a fixed support; the drag of the leads was therefore constant. It was found by experiment in the absence of the animal that the weight of the stall was not affected, within the limits of accuracy of the balance, by alterations in room air temperature and humidity. The balance scale was marked in divisions of 2 oz but readings were estimated to the nearest $\frac{1}{2}$ oz. The overall difference between two weighings was estimated to have an accuracy of 1 oz or 28 g. Measurements of insensible weight loss were normally made over periods of approximately 2 hr except at ambient temperatures of 20°C or less, when the weight change was so small that periods of 4 hr were necessary. The probable accuracy of the insensible weight loss measurements was thus approximately 14 g/hr.

Other Estimations

Heat storage

The rate of heat storage H_s by the animal during an exposure was estimated from the rise in rectal temperature per hour ΔT_r (°C), the rise in skin temperature per hour ΔT_s (°C), the weight of the animal W(kg) and the specific heat.

Table 9.　A table of the factors, expressing the
heat derived from the animal in the
evaporation of 1 g of water, as used
for computing cutaneous and respiratory
evaporative heat losses

Environmental condition (see p. 56)	Heat of vaporization (kcal/g)	
	Cutaneous	Respiratory
15	0·616	0·575
20	0·620	0·575
25	0·626	0·575
30	0·631	0·575
35L	0·636	0·575
40	0·641	0·575
35M	0·605	0·575
35H	0·587	0·575

The equation used was that derived for man (Hardy & Dubois, 1938):

$$H_s = (4 \, \Delta T_r + \Delta T_s) \, hW/5 \quad (kcal/hr)$$

where $h = 0 \cdot 83 \, cal/g$

Evaporative heat loss

Evaporative heat loss H_e was estimated by multiplying the evaporative weight loss by a suitable factor expressing the heat derived from the animal in the process of evaporating 1 g of moisture to the atmosphere. The value of the factor depends on the environmental conditions and on the temperature at the site of evaporation (Hardy, 1949). For cutaneous evaporation the factor includes the latent heat of vaporization at skin temperature, the heat absorbed on cooling and expanding the vapour to saturation at room air temperature and the heat absorbed on further expanding the vapour to room air vapour pressure. For respiratory evaporation the factor includes only the latent heat of vaporization at body temperature. This assumes that the animal expires air saturated with moisture at body temperature; an assumption that was subsequently found to be justified as a close approximation to what occurs in practice. The practical values of these factors used in computing the heat losses by cutaneous and respiratory evaporation are given in Table 9; they are based for each environmental condition on the mean levels of rectal and skin temperatures observed during the experiments.

Non-evaporative heat loss

Non-evaporative heat loss H_n was estimated by difference

from the heat production H_p, evaporative heat loss H_e and
heat storage H_s:

$$H_n = H_p - H_e - H_s$$

Surface area

The total surface area $A(m^2)$ of the animal was estimated
from the body weight $W(kg)$, using the equation of Brody (1945,
p. 403):

$$A = 0.15 \ W^{0.56}$$

CHAPTER III
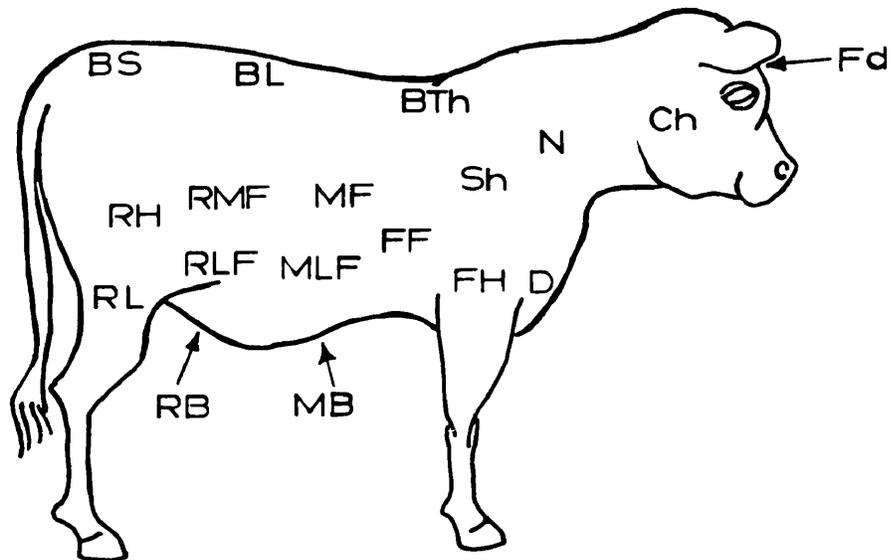
Fig. 8.   Skin regions where rate of cutaneous evaporation was measured.

BL	Back lumbar	MF	Mid flank
BS	Back sacral	MLF	Mid lower flank
BTh	Back thoracic	N	Neck
Ch	Cheek	RH	Rear haunch
D	Dewlap	RL	Rear leg
Fd	Forehead	RB	Rear belly
FF	Fore flank	RLF	Rear lower flank
FH	Fore haunch	RMF	Rear mid flank
MB	Mid belly	Sh	Shoulder

PHYSIOLOGICAL EXPERIMENTS AND RESULTS

The experimental work described in this thesis consists of a series of preliminary experiments and three physiological experiments. The preliminary experiments, already described, were mainly concerned with developing techniques for measuring cutaneous evaporation. This chapter first describes the objects and the procedures employed in the three physiological experiments, and then reports the results.

Experiment C

The object of this experiment was to compare the relative rates of cutaneous evaporation from a number of skin regions on different calves at various environmental temperatures. This information was required as a guide to the selection of a smaller number of skin regions, which taken together would be representative of evaporation from the whole surface of the animal.

Three calves (Nos. 196, 197 and 199) were used. They were each exposed in the large climatic room to various air temperatures in the range 15 to 42°C. Each exposure lasted approximately 4 hr and consisted of a waiting period of 2 hr, followed by a 2-hr period during which capsules were placed in turn on various skin regions for approximately 12 min at a time. Measurements were made on the eighteen skin regions (all on the right hand side) shown in Fig. 8 and on one region (mid flank) on the left hand side. A nominal air flow rate of 1·2 l./min was maintained through all capsules. Rectal temperature and respiratory rate were also measured.

Experiment D

The objects of this experiment were as follows:-

(1)   To make quantitative comparisons of the evaporative heat losses from animals in approximate thermal equilibrium with different environmental temperatures at a fixed low level of absolute humidity.

(2)   To make quantitative comparisons of the evaporative heat losses from animals in approximate thermal equilibrium with different environmental humidities at a fixed high level of air temperature.

(3)   To compare the responses of cutaneous evaporation to long term and to short term variations in environmental humidity.

(4)   To compare the partition of total heat losses between cutaneous evaporative, respiratory evaporative and non-evaporative channels at different environmental conditions.

(5)   To obtain a quantitative check on the systematic errors of the ventilated capsule method by comparison with insensible weight loss.

Three calves (Nos. 210, 221 and 226) were used.   They were each exposed in the large climatic room on successive days to nominal air temperatures of 15, 20, 25, 30, 35 and 40°C all at a humidity of 8 mm Hg, and also to nominal humidities of 20 and 35 mm Hg at an air temperature of 35°C.   These environmental conditions are hereafter referred to by the abbreviations 15, 20, 25, 30, 35L, 40, 35M and 35H, where L, M and H denote the low, medium and high humidity levels.   The exposures were not necessarily on consecutive days, and the schedule of eight climatic conditions was applied three times to each animal.

Calf 221 was exposed to the complete schedule one extra
time because failure of the measuring apparatus had invalidated
many of the earlier readings. Each exposure lasted approximately
4 hr and consisted of a 2-hr waiting period followed by a 2-hr
period in which measurements were made. During the measuring
period capsules were placed for up to 30 min at a time on each
of the following regions, all on the left hand side: back
thoracic, mid flank, rear leg, mid belly, shoulder and dewlap
(see Fig. 8, p. 55). These six regions were chosen, following
Experiment C, as being representative of the mean rate of
cutaneous evaporation from the whole skin surface. At
approximately 15-min intervals measurements were made of room
air dry and wet bulb temperatures, of dry bulb temperatures
of airstreams associated with capsule and mask measurements,
of airflow rates through capsules, and of respiratory rate
and minute volume. Expired air gas samples were collected
at 30-min intervals, and one inspired air sample was collected
during each exposure. Weight measurements of the stall
containing the animal and all equipment were made at the
beginning and at the end of each 2-hr measuring period except
for exposures at 15 and 20°C when the initial weighing was
made at the start of the exposure. Following each exposure
to the environment 35M each animal was kept in the climatic
room for a further 3 hr. During this time the air temperature
was maintained as nearly as possible at the same level as
before but the air humidity was altered at 20-min intervals
from the original level of 20 mm Hg to 26, 14, 32, 8 and
finally back to 20 mm Hg. Throughout every exposure

continuous recordings were made of wet bulb temperature
difference $(w_o - w_1)$ from capsules and from the respiratory
gas sampling apparatus.   Skin temperature under one of
the capsules was also recorded automatically.

Experiment E

The object of this experiment was to investigate the
variation in the rate of cutaneous evaporation from calves,
exposed to a hot dry environment, with increasing age from
10 to 34 weeks.

Three calves (Nos. 219, 220 and 222) were exposed in
the large climatic room to a nominal air temperature of 38°C
and absolute humidity 17 mm Hg for periods of 3 hr at a
time.   Each calf was subjected to hot room exposures on
three successive days each 'month'.   For the purposes of
describing this experiment the term 'month' is used to denote
an interval of 28 days.   On the first exposure day of each
'month' calf 219 entered the climatic room at 9 a.m., calf
220 at 11 a.m. and calf 222 at 1 p.m.   In order to ensure
that possible acclimatisation effects and differences between
animals could not be confused with effects due to diurnal
variations, the order of entry was varied on the two succeed-
ing days;   thus over the 3-day period of exposures in each
'month', each calf entered only once at each time of day.
All calves were first exposed in the climatic room at the
age of 10 to 11 weeks and further 3-day exposure series
followed at six successive 'monthly' intervals.   The final
3-day exposure series for calf 222 followed only 3 weeks
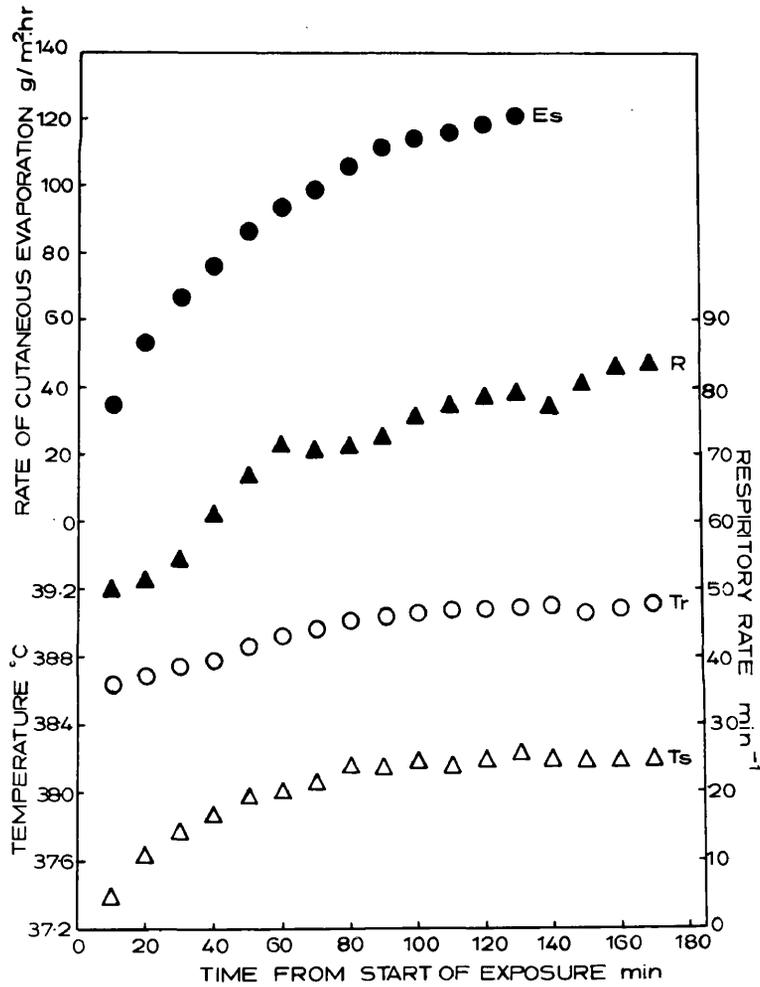
Fig. 9.   The variation, following the start of an exposure to
an air temperature of 38°C, in the mean levels of
skin temperature (T_s) and rectal temperature (T_r),
respiratory rate (R) and mean rate of cutaneous
evaporation (E_s) (Experiment E).

after the penultimate one.

Each exposure consisted of a 2-hr waiting period
followed by an hour-long measuring period.   During the
measuring period capsules were placed for approximately
15 min at a time on each of the following skin regions,
all on the right hand side: back sacral, back thoracic,
rear haunch, mid flank, mid belly, neck, dewlap and cheek
(see Fig. 8, p. 55).   Rectal temperature, skin temperature
on the left and right fore flanks and respiratory rate
were also measured.

Short Term Adjustments to Thermal Stress

Whenever an animal was taken from the byre and placed
in a warm environment there followed a period during which
heat losses were adjusted until the animal had reached an
approximately steady thermal state.   During this period
rectal temperature, skin temperature, respiratory rate and
evaporative heat losses all increased.   These adjustments
were usually completed within the first 2 hr, but in some
instances the increase continued very slowly for several
hours and in others the initial increase was followed by a
prolonged gradual fall.   The adjustments are illustrated
in Fig. 9, which shows the mean levels (averaged over all
animals and all exposures in the last three 'months' of
Experiment E) of rectal and skin temperatures, of respiratory
rate and of cutaneous evaporation at successive 10-min
intervals.

A waiting period of 2 hr following the start of each
exposure was therefore allowed in all experiments before the
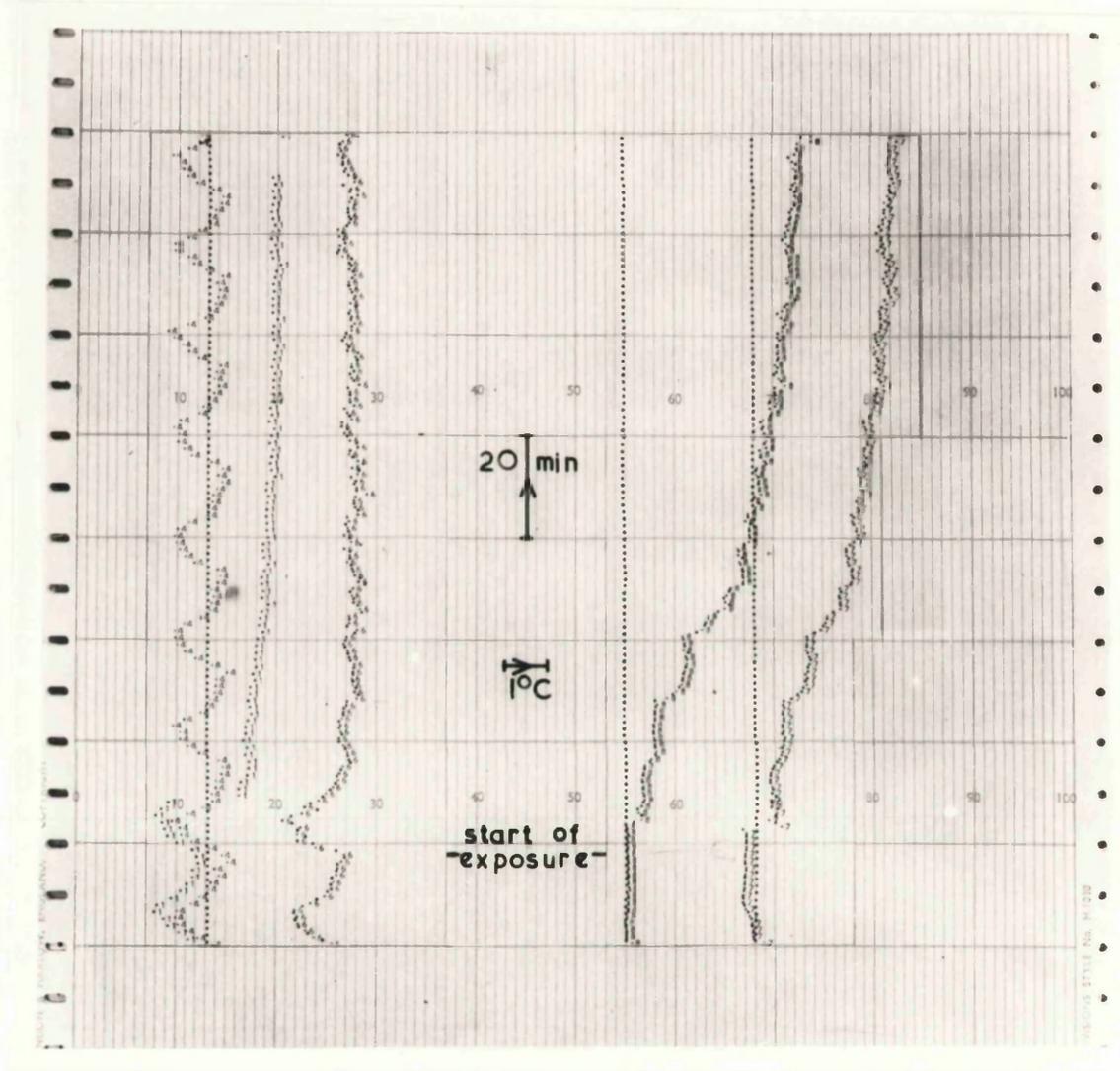
Fig. 10.   Photograph of a typical recorder chart showing
            stepwise increases in cutaneous evaporation
            (Calf 193, 38°C).

            1.   Rectal temperature
            4.   Air temperature
            6.   Skin temperature (fore flank)
            7.   Left mid flank   ) wet bulb temperature
            8.   Right sacral back) difference $(w_o - w_1)$

        The un-numbered rows of dots, from which records

        7 and 8 diverge, represent $w_o - w_1 = 0$.

main series of measurements was begun.   The results for the

period beginning at the end of the second hour of exposure

in Experiments C, D and E are given in Appendices I, II and

III.

Rapid Fluctuations in Cutaneous Evaporation

Examination of the printed records of evaporation from

the skin (i.e. of the lines displaying the quantity $w_o - w_1$)

shows that in most instances evaporation rate rose during

the first 2 hr in a series of steps.   Each step was character-

ised by a sharp rise, frequently occuring in the interval of

40 sec between successive printings of the recorder, of up to

25 g/m^2.hr in the rate of evaporation.   The steps occurred

at irregular intervals of 3 to 20 min.   They were observed

on many different body regions and their appearance was

coincident on all regions.   Between the steps evaporation rate

usually remained constant but sometimes rose or fell gradually.

In many instances each stepwise increase in evaporation rate

coincided with a sharp rise in skin temperature of up to $0 \cdot 5°C$,

followed by a gradual fall to its previous level during the

next 2 or 3 min.   The magnitude of the skin temperature effects

appeared to be positively correlated with the magnitude of the

coincident steps in cutaneous evaporation.   The magnitude of

both effects varied widely between exposures and between

animals.   The steps were first observed on calf 193 and were

later observed on all calves used in Experiments B, C, D and

E which followed.   Fig. 10 is a photograph of a typical chart

showing these steps.   This record was made during the first
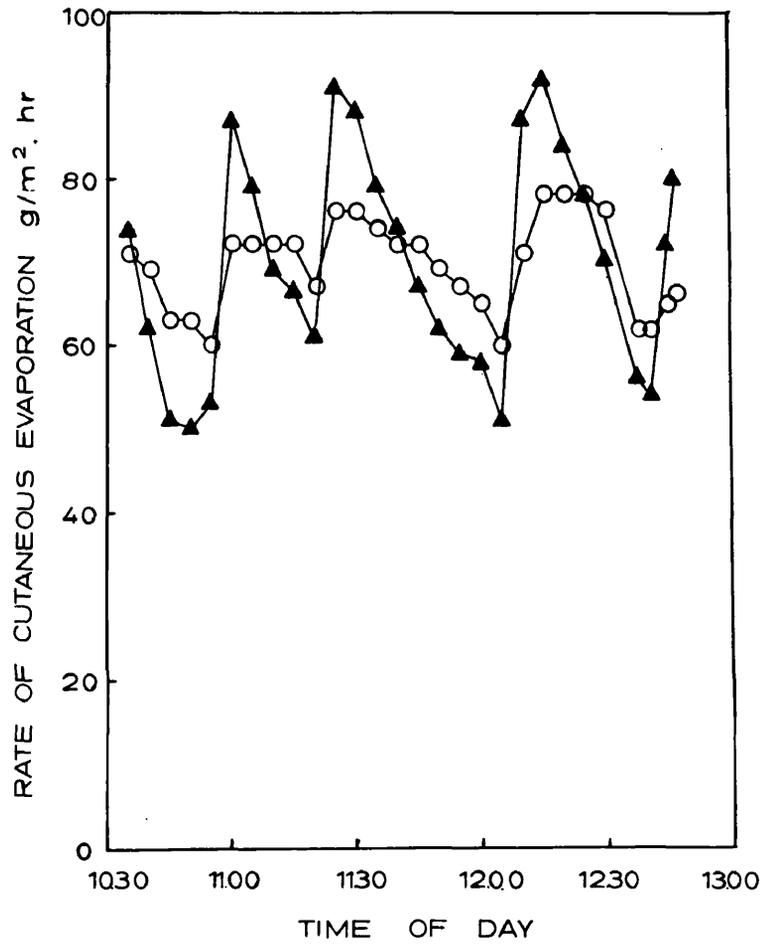
Fig. 11. The fluctuating rates of cutaneous evaporation observed from shorn (▲) and unshorn (o) regions of the foreflank of one (heifer) calf only, when exposed to an air temperature of 20°C.

2 hr of an exposure of calf 193 to 38°C air temperature.

Fig. 11 illustrates exceptionally large fluctuations in
the rate of cutaneous evaporation that were observed in only
one animal, a heifer calf which belonged to the farm herd at
the Hannah Dairy Research Institute. This calf was frequently
observed under normal conditions to have a damp coat; i.e.
it appeared to be bathed in sweat. It was decided, despite
the known inadequacies of the capsule technique used at the
time, to make some measurements of cutaneous evaporation while
this apparently exceptional animal remained available.
Flanged capsules were used and automatic recording was not
employed. The fluctuations in cutaneous evaporation shown
in Fig. 11 were observed on two body regions, from one of
which the coat was clipped; the clipped region showed the more
marked fluctuations. Such fluctuations were observed at air
temperatures of 20 and 30°C but not at 40°C. The mean levels
of evaporation rate from this animal were approximately twice
as great at 20 and at 30°C air temperatures as those obtained
from the other animals to which the same technique was applied;
at 40°C this animal did not lose appreciably more moisture
from the skin than did the others.

Evaporation from Different Skin Regions

The results of Experiment C are given in detail in
Appendix I and are summarised in Table 10. At air temperatures
of 15 to 20°C the rate of cutaneous evaporation was approximately
8 g/m^2.hr from all regions. At successively higher temperatures
evaporation from all regions increased, but more markedly from

Table 10. Mean rates of cutaneous evaporation (g/m².hr) averaged over three animals for various skin regions at temperatures between 15 and 42°C. (Experiment C).

Air temp D.B. °C	16 - 20	25	30	35	40 - 42
Air temp W.B. °C	10 - 16	18	23	25	27
Right hand side regions:					
Dewlap	8	42	114	153	174
Front haunch	8	29	103	121	149
Shoulder	7	24	83	108	151
Neck	7	24	74	93	114
Back thoracic	8	21	59	63	103
Foreflank	9	19	56	61*	91
Rear haunch	9	21	54	60	81
Rear midflank	10	15	46	36*	84
Back lumbar	6	14	33	46	84
Back sacral	4	8	32	48	81
Mid flank	7	12	42	38	72
Rear lower flank	10	20*	38	40*	58
Cheek	8	14	21	37*	66
Rear leg	11	19	41	31	44
Forehead	9	20	31	39	39
Mid lower flank	6	12	26	17	40
Rear belly	11	11*	14	11	24
Mid belly	9	11	10	11	16
Left mid flank	5	9	35	45	69

* Mean evaporation rates marked by an asterisk correspond to conditions when the data (see Appendix I) were incomplete. For the purposes of compiling this table missing values in Appendix I were computed by the method of Allan & Wishart, (1930), using all data obtained for all three calves at one environmental temperature.

Table 11. Cutaneous evaporation from different skin
regions expressed as percentages of the
mean level from four regions (dewlap,
back thoracic, mid flank and mid belly)
(Experiments C, D and E)

Experiment Temperature °C	C 35 – 40			D 38			E 35 – 40			Weighted mean over all calves
No. of exposures	2	2	2	6	7 to 8	6	21	21	21	
Calf	196	197	199	210	221	226	219	220	222	
Fore haunch	163	149	216							176
Rear haunch	114	77	69				172	152	160	155
Neck	124	152	113				173	135	139	147
Shoulder	145	210	136	141	139	140				146
Dewlap	159	220	274	133	100	127	125	149	125	136
Back thoracic	132	99	65	111	150	141	148	128	145	136
Back sacral	95	98	33				134	93	124	113
Rear leg	33	65	47	149	98	110				101
Mid flank	92	65	43	101	112	109	102	94	103	99
Cheek		77	33				71	89	101	85
Foreflank		75	90							82
Back lumbar	104	79	47							77
Rear mid flank		80	38							59
Forehead	42	61	71							58
Rear lower flank		31	83							57
Mid lower flank	62	15	21							33
Mid belly	17	17	19	54	33	22	25	30	27	29
Rear belly	18	22	29							23

some than from others.   When the skin regions are listed in order according to their rates of evaporation the order is similar at all temperatures above 20°C and for all three animals.

The results of Experiment C were used as a basis for choosing six regions whose mean rate of evaporation was estimated to be representative of the overall mean rate from the whole animal.   Evaporation from these six regions was studied more fully in Experiment D; and in Experiment E measurements were made on a further selection of eight regions.

Table 11 shows the relative rates of evaporation at air temperatures between 35 and 40°C from various skin regions of the nine animals used in the three experiments.   The rates of evaporation are presented as percentages of the mean rate from the four skin regions (dewlap, back thoracic, mid flank and mid belly) that were studied in all three experiments. The regions are listed in order of decreasing evaporation and the general trend common to all animals is apparent despite inconsistencies, which are particularly marked for calves 197 and 199.   The number of exposures on which each value in the table is based (shown in the third row of the table) is less for Experiment C than for Experiments D and E; the evaporation rates for calves 196, 197 and 199 are therefore of lower accuracy than the rates for the others.   The final column in the table was calculated by weighting the values obtained according to the number of measurements on which each estimate was based.

Fig. 12, which is based on Table 10, gives a pictorial representation of the relative rates of evaporation from the
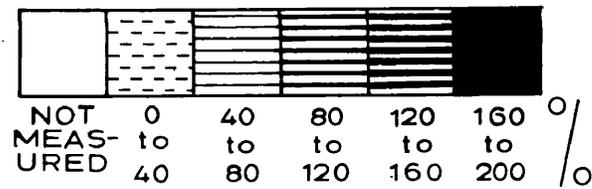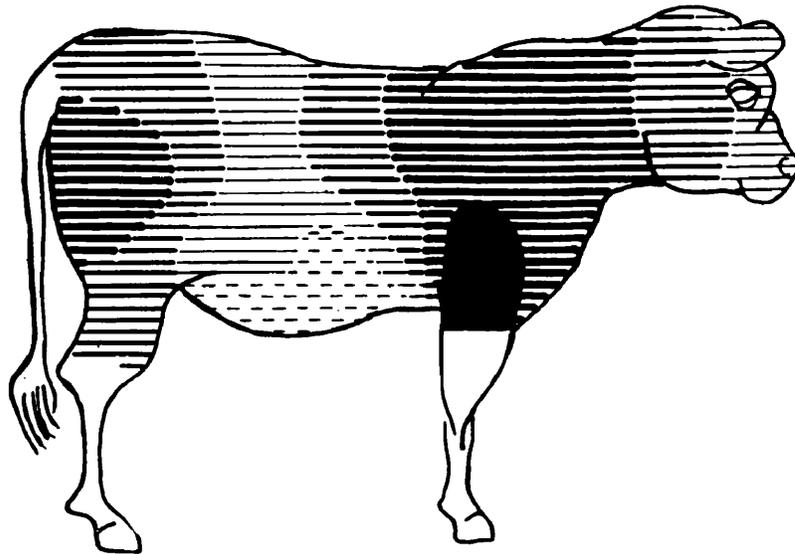
Fig. 12. Pictorial representation of the relative rates of evaporation from different skin regions of Ayrshire calves exposed to air temperatures of 35 to 40°C. The rates are expressed as percentages of the mean rate from four specific regions (dewlap, back thoracic, mid flank and mid belly) (Experiments C, D & E).

different parts of the skin at high air temperatures.   No measurements were made on the lower parts of the limbs.

The Effects of Environmental Temperature and Humidity
(Experiment D)

The detailed results of Experiment D are given in Appendix II.   As described earlier, faults in the apparatus such as a break in the seal of the mask to the face or a sticking valve were in most instances readily apparent and therefore corrected immediately.   It is, however, only to be expected that some faults were not detected.   These may account for the apparently anomalous results that were occasionally obtained for those quantities whose evaluation depends on the rate of pulmonary ventilation (e.g. respiratory evaporation, heat production and metabolic weight loss). There was, however, no means of proving that such results were invalid and they were included in the computation of the average values for each animal.   The only results excluded from the averages were those for which the data were incomplete;   i.e., if in any exposure the data were missing, for any of the four categories of weight loss measured, then all the data for that exposure were excluded from the averages of weight losses, heat exchanges, respiratory quantities, and body temperatures.

In order to avoid weighting the results in favour of any animal, the available data were first averaged for each animal over the two, three or four exposures at each environmental condition.   The overall mean results for each
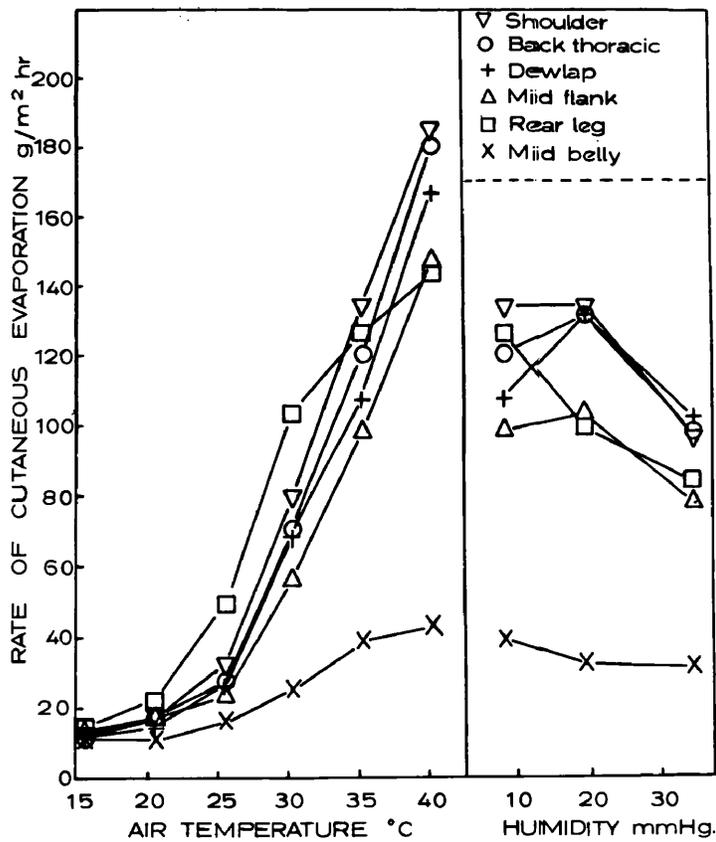
Fig. 13. The effects of environmental temperature and humidity on the rates of evaporation from six regions (Experiment D).
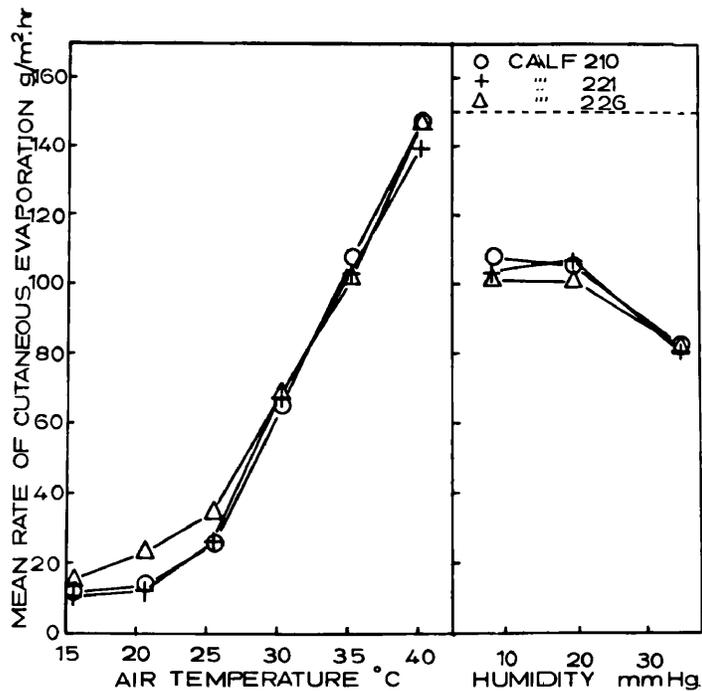
Fig. 14. The effects of environmental temperature and humidity on the mean rates of cutaneous evaporation from three calves (Experiment D).

environmental condition were then calculated by averaging the three calf means so obtained. These overall means are presented in Figs. 13 and 15 to 19 which follow.

Cutaneous evaporation

The effects of environmental temperature and humidity on the rate of evaporation from six different skin regions are shown in Fig. 13. The rate of evaporation from all regions was approximately 12 g/m^2.hr at 15°C and increased with increasing air temperature. At an air temperature of 35°C, evaporation rate was not greatly altered by increasing humidity from 8 to 20 mm Hg, but was appreciably reduced by a further increase in humidity to 35 mm Hg. The relative contribution of each region to the total evaporation varied systematically with both temperature and humidity, except for the rear leg and possibly the mid belly regions. The exceptional behaviour of the rear leg region which was exhibited by all three calves in Experiment D was not observed in Experiment C.

In Fig. 14 the mean rate of evaporation averaged over all six regions is given for each of the three calves. The mean rate of cutaneous evaporation per unit area from calf 226 was greater at low air temperatures than that from calves 210 and 221, but at all other environmental conditions mean evaporation rate was similar for all three calves.

Evaporation and insensible weight loss

The effects of environmental temperature and humidity on the weight losses by respiratory and cutaneous evaporation, on metabolic weight loss and on total insensible weight loss
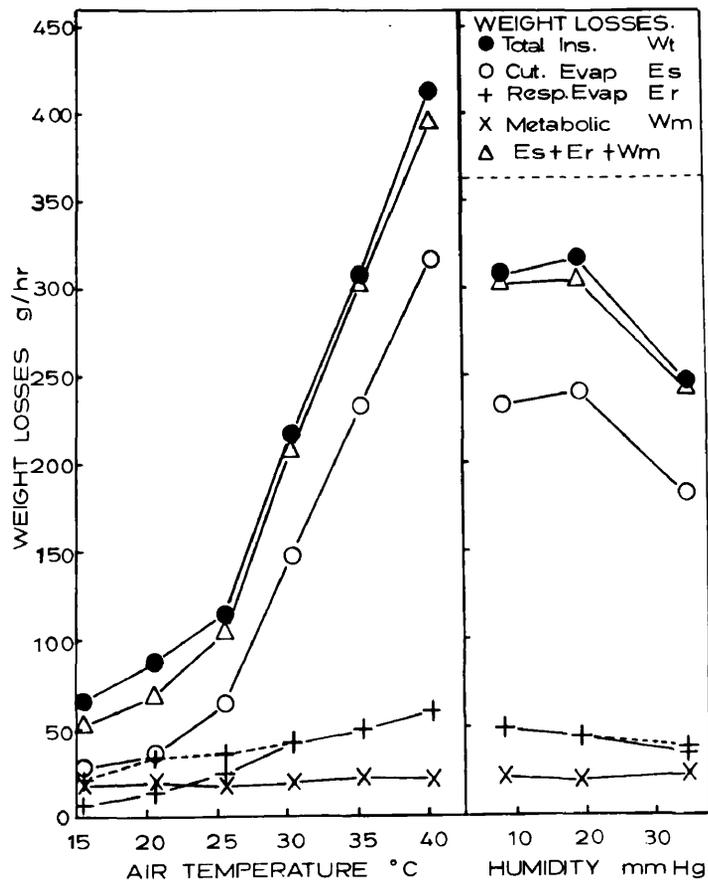
Fig. 15. The effects of environmental temperature and humidity on the weight losses by respiratory evaporation (E_r) and cutaneous evaporation (E_s), on metabolic weight loss (W_m) and on total insensible weight loss (W_t). The broken line indicates E_r calculated by the difference method $(W_t - E_s - W_m)$ (Experiment D).

are shown in Fig. 15. The difference between insensible weight loss as measured directly and the sum of its three components is discussed fully in the next chapter. It is shown that at the environmental conditions 15, 20 and 25 the difference resulted from errors in the direct estimate of respiratory evaporative weight loss. At these environmental conditions and also at 35H condensed moisture was always visible in the sampling tube leading to the respiratory wet and dry bulb thermocouple apparatus. The measured value of respiratory evaporation at these environmental conditions by the direct method was therefore limited to that corresponding to saturation at air temperature. Respiratory evaporation must in fact have been greater. Since the temperature of the expired air passing through the gauze was higher than that of room air, more moisture may be assumed to have been lost from the balance than the amount recorded by the respiratory wet and dry bulb apparatus. For the environmental conditions 15, 20, 25 and 35H respiratory evaporative weight loss was therefore estimated also by the difference method (i.e. $W_t - E_s - W_m$). Respiratory evaporation so estimated is represented by the broken lines in Fig. 15.

A further source of error resulted from condensation of respiratory moisture in the mask itself. This condensation could have been prevented by heating the mask, but since this would have inevitably heated the inspired air, it was deemed inadvisable. Attempts were made to estimate the quantity of moisture condensed, by weighing the mask assembly before and after each exposure. This proved unsatisfactory because even

at the lowest air temperatures appreciable quantities of saliva were sometimes produced, and it was not possible to distinguish the weight increase due to saliva from that due to condensed moisture. The lowest recorded weight increases of the mask assembly were 11, 7 and 6 g/hr at 15, 20 and 25°C respectively, and it may be that these minimum figures represent exposures where salivation did not occur or was minimal. The quantity of condensed moisture in the mask represents a correction that should be added both to the measured value of respiratory evaporation and to that of insensible weight loss. Condensation of moisture within the mask does not therefore account for the disparity between insensible weight loss and the sum of its three components, since it results in equal errors in both. At air temperatures of 30°C and above, except at the highest humidity level at 35°C, the wet bulb temperature of expired air was always 1·5°C or more below air temperature. In two exposures at 30°C the weight gain of the mask assembly was less than 2 g/hr, indicating that the combined quantities of saliva and condensed water were small. It may therefore be assumed that condensation of respiratory moisture was negligible for these environmental conditions.

Condensation of moisture did not limit the measured values of evaporation from the skin. At no time in any of the exposures was the outlet air from any capsule saturated with moisture, nor did it ever attain the humidity corresponding to the saturation vapour pressure at skin temperature. The limiting condition was however nearly reached at the highest humidity level at 35°C. At this environmental condition the
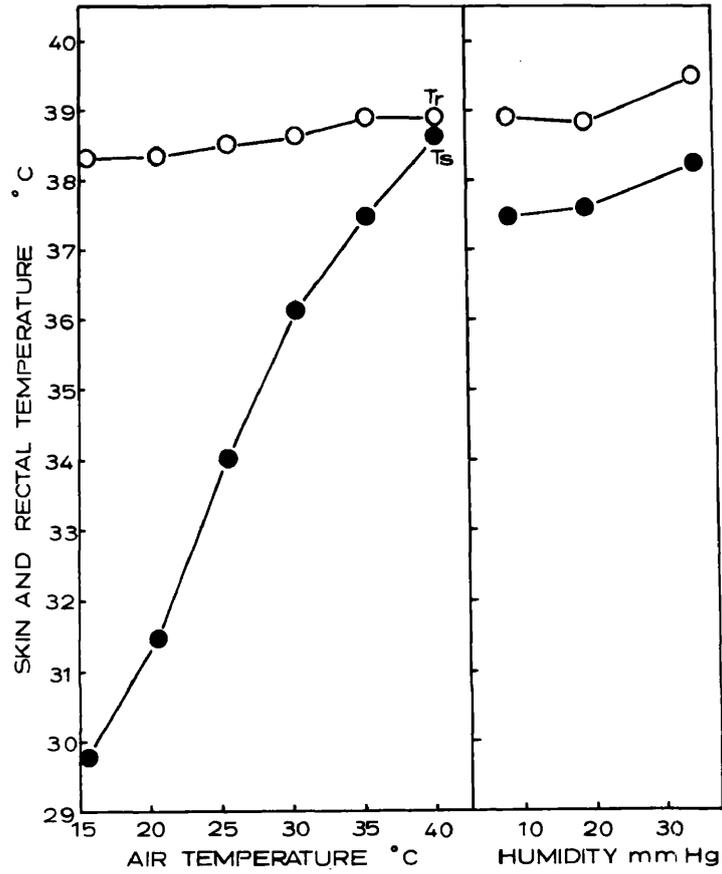
Fig. 16. The effects of environmental temperature and humidity on skin (T_s) and rectal (T_r) temperatures (Experiment D).

relative humidity of outlet air from capsules, placed on the
regions normally associated with high rates of cutaneous
evaporation, frequently exceeded 90%.

Both cutaneous and respiratory evaporation increased with
increasing air temperature, but the former contributed an
increasingly great proportion to the total evaporative loss.
At 40°C cutaneous evaporation accounted for 84% of the total.
There was an elevenfold increase in cutaneous evaporation at
40°C over that at 15°C.   At 35°C cutaneous evaporation was,
if anything, higher at a vapour pressure of 20 mm Hg than at
8 mm Hg.   A vapour pressure of 35 mm Hg, however, resulted
in a markedly lower rate of cutaneous evaporation.   Respiratory
evaporation fell with increasing air humidity over the whole
range.

Body temperature

After the initial increase during the first 2 hr of
exposure rectal and surface temperatures altered by only small
amounts.   The effects of environmental temperature and
humidity on the mean levels attained by rectal temperature
and by surface temperature of the sacral region of the back
are shown in Fig. 16.   Rectal temperature increased slightly
with increasing air temperature, being approximately 0·6°C
higher at 40°C than at 15°C.   Skin temperature on the sacral
region rose from approximately 9°C below rectal at 15°C to
approximately 0·3°C below at 40°C.   At 35°C neither rectal
nor skin temperature was appreciably altered by increasing
vapour pressure from 8 mm Hg to 20 mm Hg, but a vapour pressure
of 35 mm Hg resulted in markedly higher rectal and skin

Table 12. Analysis of variance of heat production data (Experiment D).

| Environment | Heat production kcal/hr | | | |
	Calf 210	221	226	Means of 3
15	223	185	174	194
20	231	175	185	197
25	205	183	164	184
30	234	172	184	197
35L	236	195	191	207
40	244	178	172	198
35M	289	208	174	224
35H	297	220	218	245
Means of 8	245	189	183	

Variable	Degrees of freedom	Sums of squares	Mean squares	F	
Environments (E)	7	8083	1155	5.40	0.01>P>0.001
Calves (C)	2	18591			
E x C	14	2991	214		
Total	23	29665			

Standard error for difference between two means of 3 = S.E.

$$S.E. = \pm\sqrt{(214 \times \tfrac{2}{3})} = \pm11.9 \text{ kcal/hr}$$

t(5%) = 2.14   t x S.E. = ±25.5 kcal/hr
t(1%) = 2.97   t x S.E. = ±35·3 kcal/hr
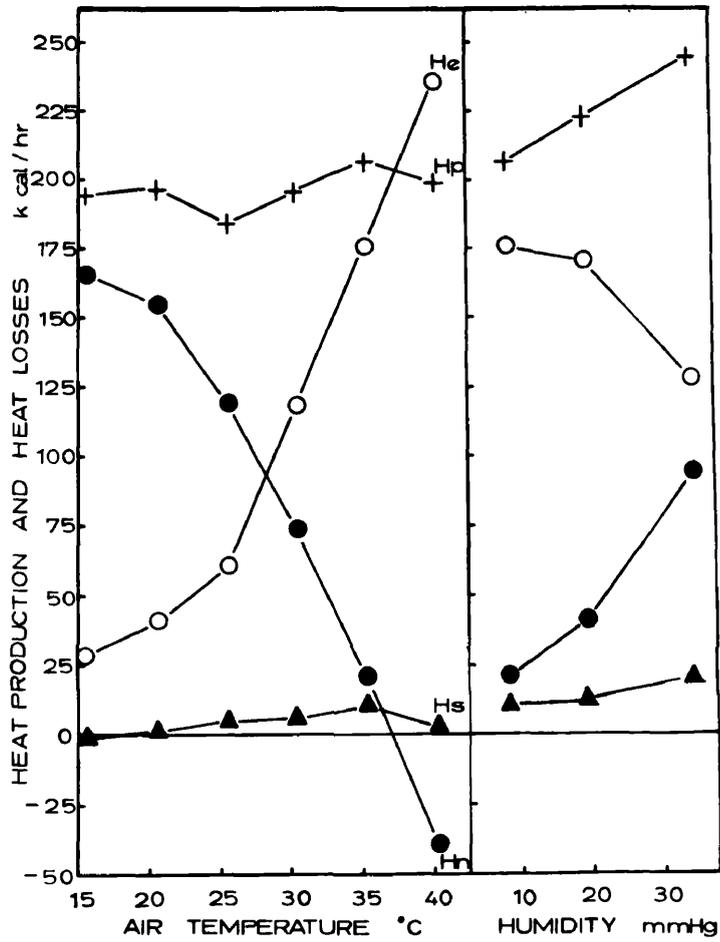
Fig. 17.   The effects of environmental temperature and
            humidity on heat production (H_p), on total
            evaporative heat loss (H_e) on non-evaporative
            heat loss (H_n) and heat storage (H_s) (Experiment
            D).

temperatures. The difference between rectal temperature and skin temperature on the sacral region was not greatly altered by changes in environmental humidity, at an air temperature of 35°C.

Heat production and heat losses

The effects of environmental temperature and humidity on heat production, on total evaporative heat loss, on non-evaporative heat loss and on heat storage are shown in Fig. 17. The total evaporative heat loss at 15, 20 and 25°C and at the highest humidity level at 35°C is based on respiratory evaporation computed by the difference method from insensible weight loss. The analysis of variance of the heat production data is given in Table 12. The variation of heat production with air temperature was not statistically significant, but the variation of heat production with humidity was significant.

At air temperatures above 25°C evaporative heat loss rose linearly with increasing air temperature at a rate of 11·9 kcal/hr.°C, and at approximately 37·5°C it was equal to heat production. At air temperatures below 25°C the rate of change of evaporative heat loss with air temperature was not as great as above 25°C. The relationship between non-evaporative heat loss and air temperature was approximately the reverse of that between evaporative heat loss and air temperature, being modified only by the relatively small variations of heat production and of heat storage. Non-evaporative heat loss thus fell with rising air temperature above 25°C at a rate of 10·5 kcal/hr.°C.

Evaporative heat loss was not appreciably affected by
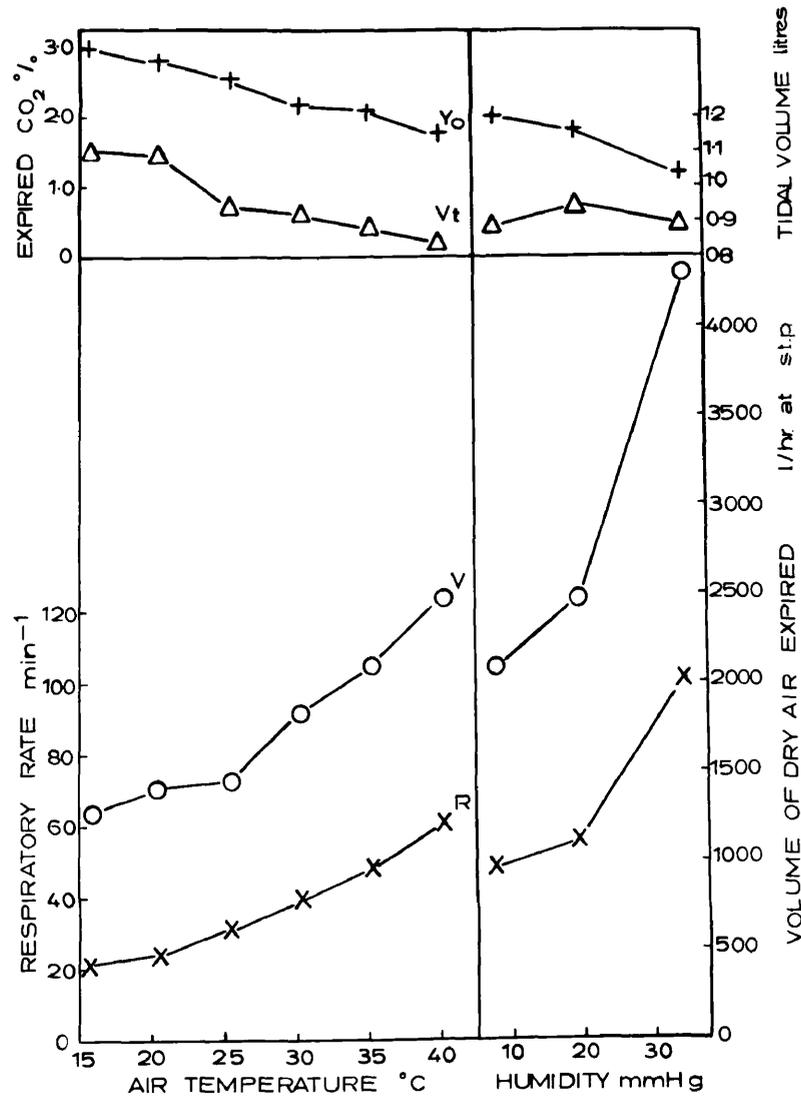
Fig. 18.   The effects of environmental temperature and
           humidity on respiratory rate (R), on tidal volume
           (V_t), on pulmonary ventilation rate (V) and on
           the mean percentage of carbon dioxide in dry
           expired air (y_o) (Experiment D).

increasing humidity from 8 to 20 mm Hg at an air temperature
of 35°C. A humidity of 35 mm Hg, however, resulted in a
lower rate of evaporative heat loss. The corresponding
increase in non-evaporative heat loss was enhanced to balance
the increased heat production.

Analysis of respiratory changes

The respiratory reactions to different levels of air
temperature and humidity are shown in Fig. 18. There was a
threefold increase in mean respiratory rate at 40°C over that
at 15°C, but this was accompanied by a fall in the tidal volume.
The result of these changes was that the total volume of
expired air increased over the temperature range by a factor
of only two. The concentration of carbon dioxide in the air
expired from the mask also decreased with rising air temperature.
As a result, the total amount of carbon dioxide exhaled, which
is an approximate measure of the heat production, remained
constant.

Respiratory rate and the total volume of air breathed at
an air temperature of 35°C both increased with rising humidity,
the increases being very marked between 20 and 35 mm Hg. Tidal
volume, however, was not appreciably altered by changes in air
humidity, and the fall in the concentration of carbon dioxide
in expired air was not great enough to prevent the total output
of carbon dioxide from rising.

Fig. 19 shows the humidity of air expired from the mask at
different air temperatures and humidities. Curves m_2 represent
the humidity of air passing through the respiratory wet and dry
bulb apparatus; this quantity approximates to saturation
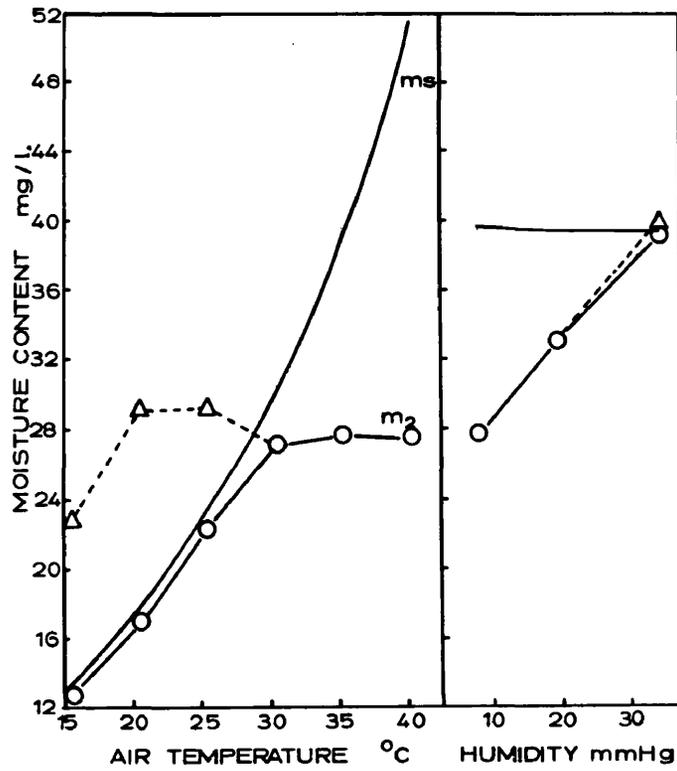
<u>Fig. 19.</u>   The effects of environmental temperature and
     humidity on the moisture content (m_2) of air
     passing through the respiratory wet and dry bulb
     apparatus.   The broken lines represent the
     moisture content of air expired from the mask as
     calculated from respiratory evaporation computed
     by the difference method.   The solid line (m_s)
     represents saturation moisture content of air
     at room temperature (Experiment D).

humidity (curves m_3) for air temperatures of 15, 20 and 25°C
and for the highest humidity level at 35°C.   At these
environmental conditions, respiratory evaporation was calculated
by the difference method.   From the respiratory evaporation so
estimated the quantity of moisture that must have been present
in air expired from the mask assembly was calculated.   The
broken lines in Fig. 19 represent these corrected levels of
the humidity m_3 of air expired from the mask.   The corrected
levels of m_3 show that over the temperature range 20 to 40°C
with a fixed room air humidity, the humidity of air expired
from the mask was nearly constant at 28 mg/l.   This humidity
corresponds to saturation at 29°C or to 60% saturation at body
temperature.   At 35°C, however, the humidity of air expired
from the mask increased with increasing humidity of the room
air.

Short term changes in environmental humidity

On days when the animals were exposed to the intermediate
humidity level at 35°C they were kept in the climatic room
after the measurements described in the preceding sections had
been completed and a further series of measurements were made
while the room humidity was altered at 20-min intervals.   The
effects of these short term humidity changes are compared with
corresponding effects of day-to-day humidity changes in Fig.
20.

Since the intermediate humidity level at 35°C represented
a relatively severe thermal stress, the animals tended to store
heat.   This resulted in the mean level of rectal temperature
being higher during the afternoons when the short term humidity
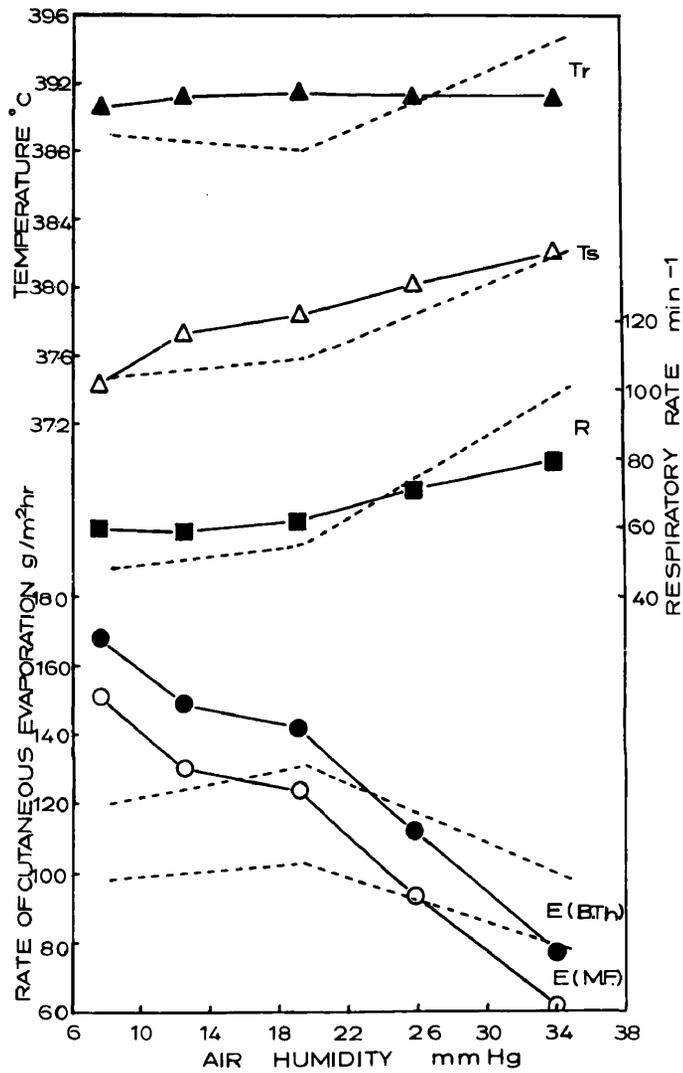
Fig. 20. The effects of short term alterations (solid lines) and day-to-day alterations (broken lines) in air humidity at 35°C on rectal (T_r) and skin (T_s) temperatures, on respiratory rate (R) and on the rate of cutaneous evaporation (E) from the back thoracic and mid flank skin regions (Experiment D).

changes were effected than they had been in the mornings when the main series of measurements were made. Respiratory rate, cutaneous evaporation and skin temperature were also observed to be greater in the afternoons than they had been at the same humidity level in the mornings.

The short term humidity alterations did not affect rectal temperature and their effect on respiratory rate was approximately one-third as great as that of the day-to-day humidity alterations. Skin temperature was affected in a similar manner both by short term and day-to-day humidity changes. The rates of cutaneous evaporation from the two regions studied were in the same ratio for both short term and day-to-day humidity changes; but for the short term changes the rate from both regions fell approximately linearly with increasing humidity, in marked contrast to the response to the day-to-day humidity variations.

The Effect of Age
(Experiment E)

The detailed results of Experiment E are given in Appendix III.

Cutaneous evaporation

The analysis of variance of the measurements of cutaneous evaporation is given in Table 13 and the major statistically significant trends are shown in Figs. 21 and 23.

The overall mean rates of cutaneous evaporation measured on the three successive days during which measurements were made every 'month' were 81·8, 87·9 and 90·2 g/m^2.hr for the first, second and third days respectively. These differences

<u>Table 13</u>.   Analysis of variance of cutaneous
evaporation data (Experiment E)

Units - $g/m^2 . hr$

Variable	Degrees of freedom	Sum of Squares	Mean Square	Error variance	F	Probability
Calves (C)	2	140059	70030			
Days (D)	2	6345	3172	e_3^2	9.88	P>0.05
CxD	4	2076	519	e_1^2	1.77	P>0.05
'Months' (M)	6	293510	48918	CxM	7.09	0.01>P>0.001
CxM	12	82840	6903	e_1^2	23.48	0.001>P
DxM	12	4297				
CxDxM	24	6272	$e_1^2 = 294$			
Regions (R)	7	464785	66398	CxR	24.32	0.001>P
CxR	14	38223	2730	e_2^2	21.84	0.001>P
DxR	14	1593	114			
CxDxR	28	5598	200			
MxR	42	68140	1622	CxMxR	3.17	0.001>P
CxMxR	84	42966	512	e_2^2	4.10	0.001>P
DxMxR	84	11050				
CxDxMxR	168	20541	$e_2^2 = 125$			
Total	503	1188295				
Times (T)	2	1434	717	e_3^2	2.23	P>0.05
CxD - T	2	642	$e_3^2 = 321$			
CxD	4	2076				

(Days) are not statistically significant when tested against the residual error variance $e_3{}^2$, but are significant ($P < 0 \cdot 001$) when tested against the residual error variance $e_1{}^2$. The numerical difference between the two error variances is small, but the estimate of the first $e_3{}^2$, being based on only two degrees of freedom, does not allow a reasonable assessment of significance. The results therefore indicate that cutaneous evaporation rate for this group of three calves was lower on the first day of each 'month' than on the next two days, suggesting some form of acclimatisation, but they do not permit the extension of this statement to Ayrshire calves in general. The overall mean rate of cutaneous evaporation recorded from observations on animals that had entered the climatic room at different times of day were $89 \cdot 0$, $85 \cdot 4$ and $85 \cdot 5$ g/m^2.hr for entry at 9 a.m., 11 a.m. and 1 p.m. respectively. These differences (Times) are not statistically significant when tested against either of the error variances, $e_3{}^2$ and $e_1{}^2$. There is therefore no evidence of the results being influenced by any diurnal variation.

The differences between the overall mean rates of cutaneous evaporation measured in separate 'months' (Months) and the degree to which this monthly variation differed between calves (CxM) were both statistically significant. The trends are shown in Fig. 21. Evaporation rate tended to rise with increasing age from 10 to 34 weeks for all three calves but there was a marked drop in evaporation rate for calf 222 in the last 'month', and for calf 220 cutaneous evaporation was higher in the first than in the second 'month'. Results
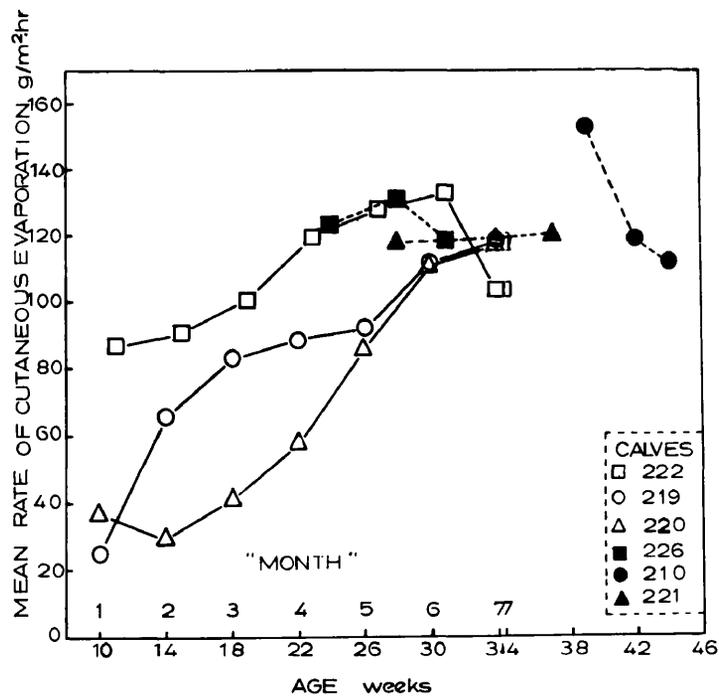
Fig. 21. The variation with increasing age of the mean rate of
cutaneous evaporation from six calves when exposed
to air temperatures of 38°C (Experiment E, solid
lines and open symbols; Experiment D, broken lines
and closed symbols).
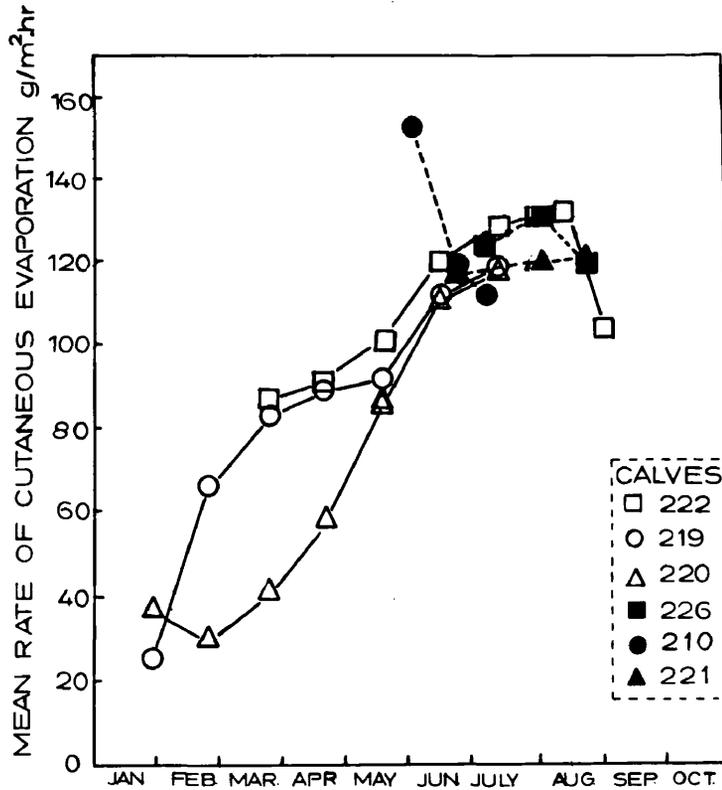
Fig. 22. The variation with time of year of the mean rate of
cutaneous evaporation from six calves when exposed
to air temperatures of 38°C (Experiment E, solid
lines and open symbols; Experiment D, broken
lines and closed symbols).

from the measurements on calves 210, 221 and 226 (Experiment
D) are included in Fig. 21 for comparison. The mean levels
of evaporation for these three animals are not quantitatively
comparable with those for calves 219, 220 and 222 since
evaporation was not measured on the same set of body regions
in each experiment. Also the results plotted for calves 210,
221 and 226 are each averaged from observations during two
exposures, one to 35°C and the other to 40°C air temperature,
whereas those for calves 219, 220 and 222 refer only to
exposures to 38°C. Calves 221 and 226 whose ages during the
experiments were between 24 and 37 weeks both showed little
change in cutaneous evaporation with age; calf 210, which was
older, showed a progressive decline in cutaneous evaporation.

Calf 222 was born approximately 7 weeks later than the
other two used in Experiment E and measurements on this animal
were made 8 weeks later than the corresponding measurements
on calves 219 and 220 for the same 'month' of age. In Fig.
22 the same data as in Fig. 21 are replotted against time of
year without regard to age. The increases in cutaneous
evaporation rate for calves 219, 220 and 222 all occurred
during the period February to June and the later decrease for
calf 222 occurred in August. Calves 221 and 226 showed nearly
constant cutaneous evaporation rates during July and August
and calf 210 showed a decreasing rate during June and July.
All measurements on all six calves took place in the same
year (1960).

The differences between cutaneous evaporation rates
recorded from separate skin regions (Regions) and the degree
to which these differences varied between 'months' (MxR) were
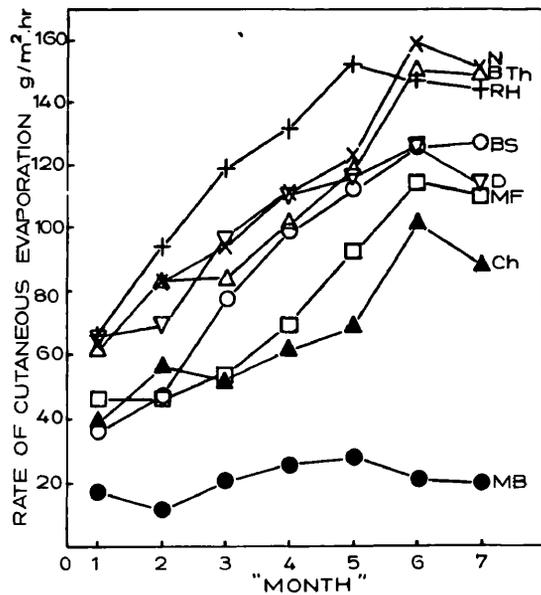
Fig. 23. The variation with increasing age of the rate of
cutaneous evaporation observed from eight skin
regions of calves when exposed to air temperatures
of 38°C (Experiment E).

BS	Back sacral	MB	Mid belly
BTh	Back thoracic	MF	Mid flank
Ch	Cheek	N	Neck
D	Dewlap	RH	Rear haunch
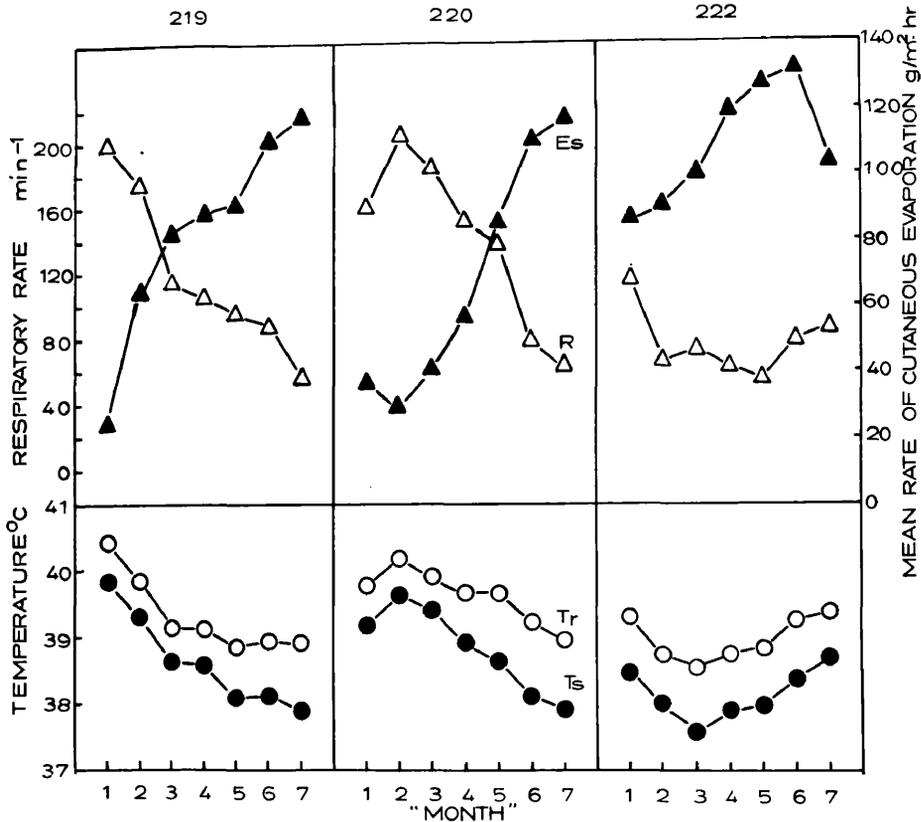
Fig. 24. The mean levels of rectal (T_r) and skin (T_s) tempera-
tures, respiratory rate (R) and rate of cutaneous
evaporation (E_s) observed from calves when exposed
to air temperatures of 38°C in successive 'months'
(Experiment E).

both statistically significant.   The trends are shown in
Fig. 23.   Evaporation increased from all regions as the
animals grew older but appeared to reach a maximum value at
about 30 weeks of age and then to decline.   The decline
during the last month was however largely due to the influence
of the results for calf 222.

The variation between calves of the difference between
cutaneous evaporation rates on separate regions (CxR) was
statistically significant, but this variation was small
compared with the differences themselves.   The relative
trends have already been presented and discussed (Table 11,
p. 63).

Rectal and skin temperature and respiratory rate

Rectal and skin temperature and respiratory rate all
altered for each animal with increasing age (Fig. 24), but
the form of the trends differed markedly between animals.
All three quantities tended to fall as the calves grew older,
but for calf 222 there was a reversal of these trends after
the third 'month' and for calf 220 all three quantities were
lower in the first 'month' than in the second.

Cutaneous Evaporation in Relation to Body Temperature

In Fig. 24, which was described in the preceding section,
the variation of cutaneous evaporation rate with increasing
age is included for comparison with the other variables.
From observation of Fig. 24 it can be concluded that there was
a striking positive correlation between both rectal and skin
temperatures and respiratory rate for each calf; moreover

Table 14. Comparison between animals for exposures to air temperatures 35 to 40°C (See p. 80). (Experiments C, D and E).

Calf	Cutaneous evaporation g/m².hr	Rectal temperature °C	Age weeks	Date of measurements
199	56	40·1	29	December
197	83	39·9	36	December
222	97	39·2	31-34	August
196	99	39·3	37	November
219	100	38·9	30-34	June/July
220	104	39·1	30-34	June/July
210	111	38·6	39-44	June/July
221	113	38·7	28-37	June/August
226	115	39·3	28-31	August

cutaneous evaporation, especially for calves 219 and 220,

appeared to be negatively correlated with each of the other

three variables.   Table 14 shows the mean rate of cutaneous

evaporation and the mean rectal temperature in warm environ-

ments for the nine calves used in Experiments C, D and E.

Evaporation rate in all instances is the mean rate from the

four body regions that were studied in all experiments.   For

calves 196, 197 and 199 (Experiment C) and for calves 210,

221 and 226 (Experiment D) each value represents the mean over

pairs of exposures, one to 35° and one to 40°C air temperature;

the two exposures, in all except one instance (calf 197), being

separated in time by not more than one week.   For calves 219,

220 and 222 (Experiment E) each value represents the mean over

six exposures to 38°C.   In order to eliminate so far as possible

the effects of age the results for the first five 'months' of

Experiment E and the first set of measurements on calf 226 were

excluded in the computation of the table.   The values given

in Table 14 thus summarise the mean levels of cutaneous

evaporation rate and of rectal temperature from nine animals,

which were all aged 27 weeks or over at the time of the

observations.   The ages of the animals and the time of year

are also included in the table.   The animals are listed in

order of increasing evaporation and this results in those

with the highest rectal temperatures tending to be grouped at

the top of the table.   The final column of the table shows,

however, that the two lowest rates of cutaneous evaporation

and highest levels of rectal temperature were recorded during

the coldest month.

CHAPTER IV

DISCUSSION

The Ventilated Capsule Method

Measurement of cutaneous evaporation by the ventilated capsule method has been discussed theoretically in Chapter II. The experimental findings show that the figure obtained for the evaporation rate from the skin is influenced by the geometry of the capsule and the rate of ventilation. In order to estimate the rate of cutaneous evaporation E_o from undisturbed skin (i.e. in the absence of a capsule) it is necessary either to employ a critical flow rate F_o, or to interpolate to F_o. It was estimated that

$$E_o = E (F_o/F)^k$$

where E is the observed evaporation rate at the flow rate F employed. For the particular design of capsule and under the conditions of air movement pertaining in the climatic room F_o was estimated to be 1·93 l./min and k to be 0·202. The estimate of F_o is of poor accuracy but the equation shows that even a 100% error in F_o would only affect E_o by 15%: this is due to the fact that k is small compared with unity.

For any alternative design of capsule the values of both F_o and k would have been different. The earlier experiments in which capsules without baffled inlet ports were used on clipped skin areas (Table 4, p. 28), suggest a value of approximately 0·4 for k. Under such conditions a 100% error in F_o affects E_o by approximately 30%. Kibler & Yeck (1959) used ventilated capsules similar in size to those used in the present experiments. They also found increasing rates of evaporation as ventilation rate rose, and their results suggest a value for k of approximately

0·5.   Taneja (1959), who used hemispherical capsules of area

19·6 cm², stated that on increasing flow rate from 0·5 to

2 l./min evaporation rose from 75 to 200 g/m².hr at the same air

temperature; this corresponds to k = 0·71.   The quantity k,

which represents the degree to which evaporation is affected by

ventilation rate, appears to be kept small if the area and depth

of the capsule are large and the design ensures an even

distribution of air over the skin area under examination.   The

value of k appears also to be higher for observations on clipped

as against normal areas of skin.

It seems probable that choice of capsule designs and flow

rates may account for some of the exceptionally high rates of

cutaneous evaporation previously reported for cattle.   McDowell,

Lee & Fohrman (1954) who used small capsules (5 x 2 cm by ½ cm

high) ventilated at 4 l./min found rates (Table 1, p. 9) which

were in excess of those reported here by factors of 2·5 to 10,

and which greatly exceeded any reasonable estimate of the heat

production per unit area.   McDowell et al. (1954) and also

Taneja (1959) both used flanged capsules fixed to the skin by

means of adhesives, and the possibility of collection of moisture

from the area covered by the flange cannot be ruled out.   This

could also result in overestimation of evaporation rate per unit

area.   For the small capsules used by McDowell, the area

covered by the flange was approximately twice as great as the

test area.

As a result of the work on capsule techniques, the general

principles that appear most likely to provide quantitatively

accurate estimates of the normal rate of cutaneous evaporation

may be summarised as follows:-

1.   The capsule should not have a flange and it should be pressed lightly against the skin.

2.   The design should ensure uniform air velocity over the test area, i.e. the capsule should not be shallow compared with the linear dimensions of the test area and the inlet ports should be large and baffled, or numerous and dispersed.

3.   Ambient air should be drawn into the capsule.

4.   The rate of air flow should give ventilation inside the capsule equivalent to that outside, or else interpolation to these conditions should be made.

The systematic error of the capsule method described here has been estimated to have a possible magnitude of ±12%. In addition to the systematic error statistical errors exist due to the random variation between measurements.   The analysis of variance of the data for Experiment E (Table 13, p. 75) provides two estimates of these errors.   The error variance $e_2{}^2 = 125$ (S.D. = ±11·2 g/m^2.hr) is the best estimate available of the statistical error attached to a single observation of the rate of evaporation from a particular skin region of a particular calf exposed on a particular day to the specified thermal environment of the experiment.   This error variance contains three components of variation, one due to the instrumental error of the wet and dry bulb apparatus, another due to the error involved in placing the capsule securely and accurately on the chosen region and a third due to any short term fluctuations in evaporation rate with time, i.e. any fluctuations occurring within one day.   The precision of the wet and dry bulb apparatus has been estimated as being within

extreme limits of $\pm 0 \cdot 2$ mg/l. which is equivalent to approximately ± 4 g/m^2.hr. This corresponds to a standard deviation of approximately ± 2 g/m^2.hr. The remaining two components are not distinguishable from one another, but together they make the major contribution to the error variance e_2^2.

The error variance $e_1^2 = 294$, represents the statistical error attached to the sum of eight single estimates of the rate of evaporation from eight separate regions of any particular calf exposed to the specified environment. The error variance $e_1^2/8$ thus represents the statistical error attached to the mean rate of evaporation assessed from the eight regions. This variance, from which the components of variation due to the major calf x time trends studied in Experiment E have been removed, contains an estimate of the residual random day-to-day variation E^2 in the rate of cutaneous evaporation from calves exposed to the specified thermal environment of the experiment. It also contains one eighth of the variance e_2^2:

$$\frac{e_1^2}{8} = \frac{e_2^2}{8} + E^2$$

Hence $E^2 = (294 - 125)/8 = 21$

For any other experiment carried out under similar conditions but with estimates of evaporation rate from n regions the statistical error e_n^2 attached to a determination of the mean rate of cutaneous evaporation is therefore given by:

$$e_n^2 = E^2 + e_2^2/n = (21 + 125/n)$$

The information available from Experiment E and from the preliminary experiments, concerning the accuracy of the capsule method may thus be summarised as follows:-

1)   There is a systematic error whose maximum possible magnitude is ±12%.

2)   The standard deviation of single measurements by the capsule method described, i.e. the instrumental and other random variations that are inherent in the method itself, is estimated at ±11 g/m^2.hr.

3)   The standard error of an estimate of the mean rate of cutaneous evaporation from a particular calf based on n individual regional measurements, and including random day-to-day variations, is estimated at ±$\sqrt{(21 + 125/n)}$ g/m^2.hr.

These estimates of variation are based on measurements made on calves exposed to an air temperature of 38°C. It may be that at lower air temperatures, where evaporation rates are generally smaller, the errors are also smaller, and at higher air temperatures the errors may be greater.

Since the data from Experiment D are not orthogonal, a full statistical analysis of the determinations of cutaneous evaporation rates in individual exposures would be complex and unlikely to provide further information on the accuracy of the capsule method. The information already available may however be used to aid the interpretation of the results of Experiment D. The probable standard error of a single determination of the mean rate of cutaneous evaporation based on six regional measurements during a single exposure in Experiment D is ±$\sqrt{(21 + 125/6)}$ = ±6·5 g/m^2.hr. Similarly the probable standard error of an estimate, based on eight to ten individual exposures, of the mean rate of cutaneous evaporation from the group of calves in Experiment D is approximately ±6·5/$\sqrt{9}$ = ±2·2 g/m^2.hr. These errors apply at an air temperature of 38°C
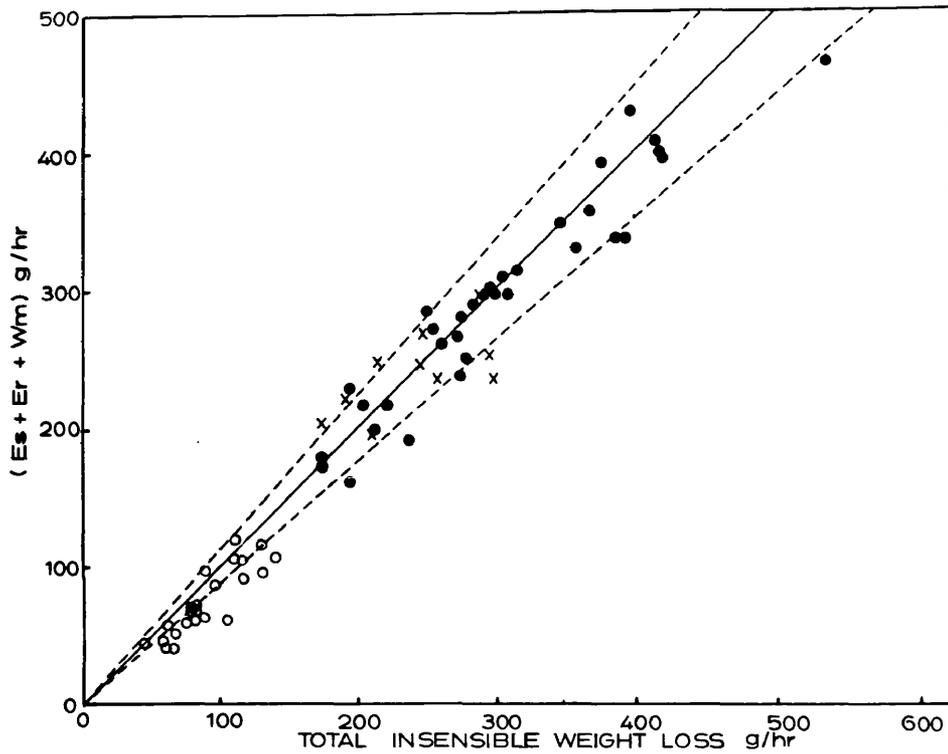
Fig. 25. The sum of the three forms of weight loss (cutaneous evaporative E_s and respiratory evaporative E_r and metabolic W_m) plotted against total insensible weight loss for individual exposures to the environmental conditions 15, 20 and 25 (o), 30, 35L, 35M and 40 (●) and 35H (x) (Experiment D).

at lower temperatures the errors may be less.

The Accuracy of Weight Loss Determinations

In Fig. 25 the sum of the three separate forms of weight loss is plotted against total insensible weight loss, each point referring to an individual climatic room exposure in Experiment D.   The lines drawn on the graph represent the theoretical equality that should exist between these two independent estimates of the same quantity, and error limits of ±12%.   The departure of any point on the graph from the line of equality between the two estimates may arise from a combination of the following:

Systematic errors which include:

a.   The systematic error of the capsule method employed (±12%).

b.   The error attached to the selection of the six regions studied as being representative of the overall mean rate of cutaneous evaporation (unknown magnitude).

c.   Errors, resulting from condensation in the tube leading to the respiratory wet and dry bulb apparatus, which result in systematic underestimation of respiratory moisture loss (unknown magnitude at the environmental conditions 15, 20, 25 and 35H, but known to be non-existent at other environmental conditions).

Random errors which include:

d.   The estimated standard deviation of a single determination of cutaneous evaporative weight loss (±6·5 g/m^2.hr x surface area, or approximately ±15 g/hr).

Table 15.   Statistical analysis of the difference between insensible
            weight loss and the sum of its three components
            $(W_t - E_s - E_r - W_m)$, (Experiment D).   Units: g/hr.

Environmental conditions	30, 35L, 35M & 40	15, 20, 25	35H
Symbol used in Fig. 25 (p. 86)	●	o	x
Number of observations	34	23	10
Mean difference	8·4	14·9	1·3
Standard deviation of an individual estimate	25·1	12·9	32·9
Standard error of mean	4·3	2·7	10·4
Mean difference expressed as a percentage of E_s	3·6	35·3	0·7
Statistical significance of mean difference	0·1 > P > 0·05	0·001 > P	P > 0·25

e.   The error of an insensible weight loss
determination (estimated to be within extreme limits of ±14
g/hr, which corresponds to a standard deviation of approximately
±8 g/hr).

f.   The statistical errors of the respiratory
evaporative and metabolic weight loss determinations (magnitude
for a single observation unknown).

The statistical analysis of the difference between the
insensible weight loss as measured directly and as calculated
from determinations of cutaneous and respiratory evaporative
and metabolic weight losses is given in Table 15.   For
exposures to conditions where condensation was known not to
occur in the respiratory gas sampling tube the standard
deviation of the difference between the two estimates is
±25·1 g/hr.   The errors (d) and (e) account for approximately
half this variation and it therefore appears that the errors
associated with the mask measurements are of the same order
of magnitude as those associated with the measurement of
cutaneous evaporative loss.   The mean difference between the
two estimates is 8·4 (±4·3 S.E.) g/hr or 3·6% of the mean
cutaneous weight loss.   This difference is of doubtful
significance and is well within the maximum possible systematic
error (a) of the capsule method.   The possibility cannot be
excluded that a systematic error of up to ±12% in the capsule
method is cancelled by a nearly equal and opposite systematic
error (b) in the selection of skin regions.   It is however
more probable that both errors (a) and (b) are well within
the ±12% limits.

For exposures to the environmental conditions 15, 20 and 25 when condensation was always visibly evident in the respiratory gas sampling tube the standard deviation of the difference between the two insensible weight loss estimations is $\pm 12 \cdot 9$ g/hr. This lower value for the standard deviation than the previous estimate probably results from smaller numerical errors in the determinations of cutaneous evaporative and of respiratory weight losses at the lower environmental temperatures. The mean difference under these conditions is $14 \cdot 9$ ($\pm 2 \cdot 7$ S.E.) g/hr or $35 \cdot 3\%$ of the mean cutaneous weight loss. This difference is highly significant and well outside the possible systematic error of the capsule method. There is little doubt that the main cause of the difference lies in errors (c) in the estimate of respiratory evaporative loss due to condensation in the respiratory gas sampling tube. For this reason respiratory evaporative weight losses were estimated, for the environmental conditions 15, 20 and 25, by the indirect method, i.e. $E_r = W_t - E_s - W_m$.

For exposures to the environmental condition 35H the scatter of the data is too great to permit any conclusions being drawn with regard to systematic errors. At this environmental condition the mean difference between the two estimates of insensible weight loss is negligible. Since at this condition condensation was visible in the respiratory gas sampling tube, the data, for consistency, were interpreted in the same manner as that for the conditions 15, 20 and 25.
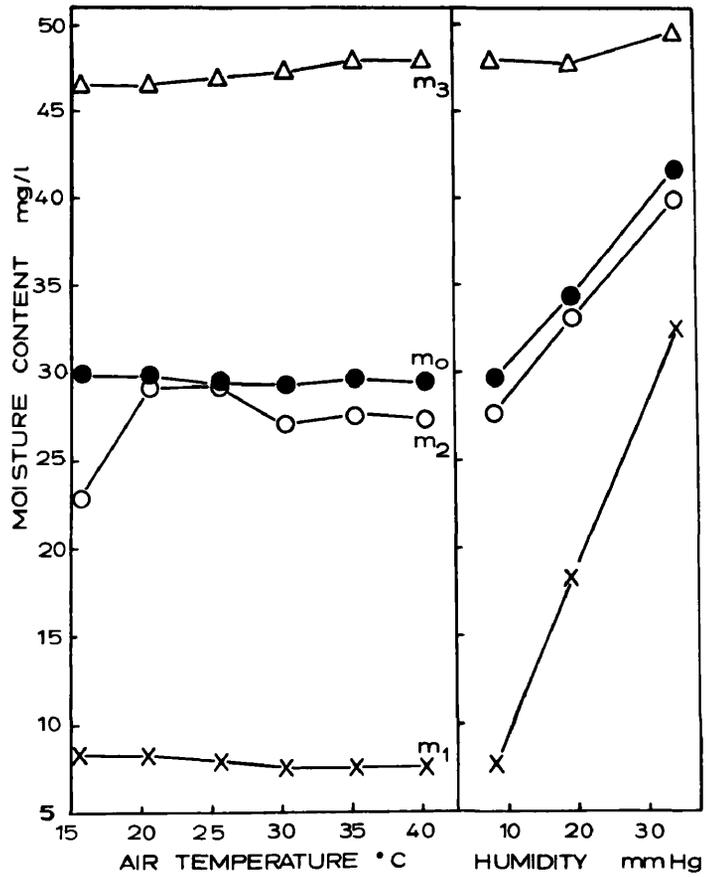
Fig. 26. The effects of environmental temperature and
humidity on the moisture content of respiratory
gases (Experiment D).

m_1 moisture content of air entering the mask
m_2 observed moisture content of air leaving the
   mask
m_3 saturation moisture content at body temperature
m_0 calculated moisture content of air leaving the
   mask, assuming expiration of air at m_3 by the
   animal.

The Mask Method for Respiratory Analysis

The mask method used for estimating respiratory evaporation (the direct method) is clearly inadequate when condensation occurs in the tube leading to the respiratory wet and dry bulb apparatus. The difference method is not of great accuracy since the errors of all three components (insensible, cutaneous and metabolic weight losses) are additive and respiratory evaporation represents only a small proportion of the total insensible weight loss. In addition, the accumulation of an unknown quantity of condensed water in the mask assembly during the course of the experiment represents a further source of error. The moisture content of air expired from the mask was, however, nearly constant over the air temperature range studied, despite the fact that it was estimated by the direct method at higher temperatures and by the difference method at lower temperatures. The moisture content of air expired from the mask was approximately 28 mg/l. at all air temperatures when room air humidity was held at 8 mg/l. but rose to 33 and 40 mg/l. when room air humidity was increased to 18 and 32 mg/l. at an air temperature of $35°C$. These levels are shown in Fig. 26 by the curves m_1 and m_2, the latter being replotted from Fig. 19 (p. 73). The levels of curves m_2 may be shown to result from mixing of the respiratory gases in the mask if it is assumed that under all environmental conditions the animal breathes out air into the mask with a moisture content corresponding to approximately 90% of saturation at body temperature. In Appendix IV it is shown that if the ratio of the respiratory tidal volume to the volume
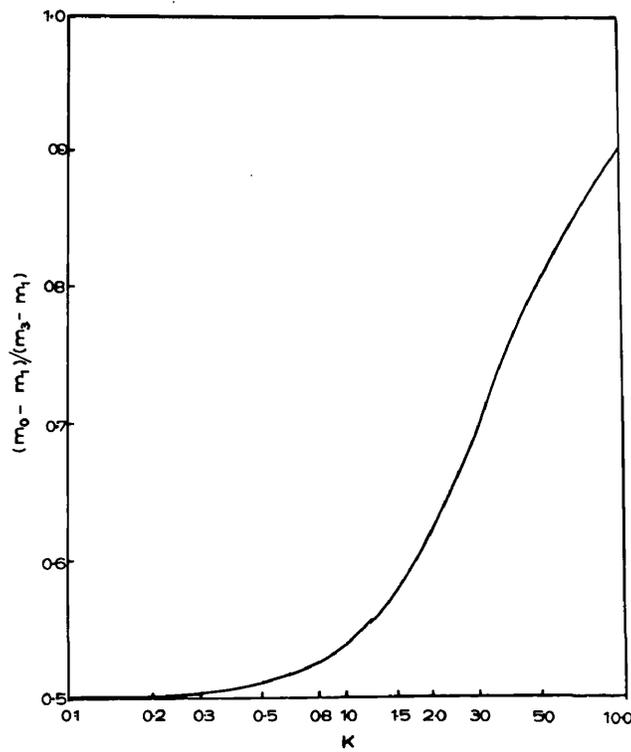
Fig. 27. Graph of the equation $m_0 = m_1 + (m_3 - m_1)[1 - \frac{1}{K}(\frac{e^K-1}{e^K+1})]$ (see text p. 91).

of the ventilated dead space of the mask is K, and if air
enters the mask from the room at absolute humidity m_1 and
is expired by the animal into the mask at m_3, then the mean
level of humidity of air expired from the mask is m_0 where

$$m_0 = m_1 + (m_3 - m_1) [1 - \frac{1}{K} \frac{(e^K - 1)}{(e^K + 1)}]$$

and e is the exponential function.

The graph of this equation is shown in Fig. 27, in which
m_0 is plotted, as a fraction of the difference between m_3 and
m_1, against K. The humidity of the air expired from the
mask falls from the true expired humidity m_3 when K is
infinite (zero dead space) to a level mid way between m_3 and
room humidity m_1 when K = 0 (an infinitely large mask).
The dead space of the mask used in the experiment was
estimated to be approximately 0·8 litres and the mean tidal
volumes at the various environmental conditions were in the
range 0·85 to 1·1 litres, hence K was of the order of 1·2
for which

$$m_0 = m_1 + 0·55 (m_3 - m_1).$$

A theoretical computation may thus be made of the
humidity of the air leaving the mask m_0 at each environmental
condition by assuming that the air expired into the mask by
the animal is always saturated at body temperature m_3. These
two humidity levels (m_3 and m_0) are shown by the upper two
curves of Fig. 26. The agreement between the theoretical
curve for m_0, and the measured values of humidity of air
expired from the mask m_2 is close, although the former is
always slightly in excess of the latter. The small difference

of the theoretical from the practical estimate of expired air humidity may be eliminated by assuming that the humidity level of air expired by the animal into the mask corresponds to approximately 90% saturation at body temperature. This last assumption may in turn by a similar argument be explained by postulating a second dead space, in the upper respiratory tract of the animal, the volume of this dead space being approximately one-eighth of the tidal volume. This dead space is not the same as the 'respiratory dead space' commonly referred to in studies concerning oxygen-carbon dioxide exchange; nor is it suggested that any anatomically defineable region exists as a true dead space in which moisture evaporation does not occur at all. It is probable that the air representing the final portion of each inspiration is not retained in the upper region of the respiratory tract for long enough to attain equilibrium in temperature and humidity, and that this results in the mixed air of the expiration having a humidity level slightly less than that corresponding to saturation at body temperature.

Although the animals in this experiment expired air into the mask at a considerably higher humidity level than that of the air leaving the mask, this does not mean that the respiratory evaporative loss was incorrectly estimated, because it also follows that the humidity of the air inspired by the animal from the mask was increased above the level of room air humidity by a corresponding amount. The respiratory evaporative loss measured was therefore the true quantity of respiratory moisture lost by the animal under the experimental conditions. The quantity of water vapour added to each litre of respired air was,

however, limited to approximately 55% of what it could have
been had the mask not been worn. Since there was no visual
evidence that tidal volume or respiratory rate were appreciably
influenced by the presence of the mask, respiratory moisture
loss must also have been reduced by 55%. It follows that when
a mask equipped with inlet and outlet valves is applied to an
animal, it must inevitably reduce the respiratory moisture
loss unless the dead space is kept very small. It would be
difficult to design an efficient mask suitable for use with
cattle in which the dead space was less than, say, one quarter
of the tidal volume; even this would result, according to
Fig. 27, in a reduction of respiratory evaporation by 24%.
Under conditions of very severe heat stress when tidal volume
falls to much lower values the problem would become more acute.
The results suggest that over a wide range of ambient temperatures
and humidities, the humidity of air expired by cattle corresponds
to approximately 90% of saturation at body temperature. Kibler
& Brody (1950, 1952) have reported that the moisture content
of air expired by cattle rises as air temperature increases
from -15 to 40°C, and is far below that corresponding to
saturation at body temperature. Taneja (1958) has reported
that the vapour pressure of air expired by cattle rose from
37 mm Hg at 30°C to 44 mm Hg at 42·5°C with fixed ambient vapour
pressure of 30 mm Hg. Taneja and also Knapp & Robinson (1954)
used modified forms of the mask method of Kibler & Brody (1950)
for measuring respiratory moisture loss. All of these workers
measured the humidity of the air expired from the mask rather
than that directly expired by the animal. If the results of

all these workers are examined it is found that the observed
respiratory moisture loss at high air temperatures is in nearly
every instance between 40 and 60% of what it would have been had
the air expired from the mask been saturated at body temperature.
It seems likely that respiratory moisture loss was in all
instances affected by mask dead space in the same way as has
been discussed on pp. 90 - 92 for the observations reported here.

At low air temperatures it is probable that the moisture
content of air expired by the animal is no longer maintained at
the level corresponding to 90% saturation at body temperature.
Fig. 26 shows that the humidity of air expired from the mask
was less at 15°C than at higher air temperatures, but this
could have been due partially to the accumulation of condensed
water in the mask itself. The results of Kibler & Brody
(1952) also show that below 20°C the observed respiratory
vaporization rate continued to decline although the rate calculated
by assuming expiration from the mask of air saturated at body
temperature remained virtually unchanged. The results of Taneja
(1958) however suggest that the moisture content of expired air
started to decline at an air temperature between 32·5 and 30°C.

The reasoning that has been applied to the effect of the
mask on respiratory evaporation must also hold for carbon dioxide
exchange and for respiratory convection. The presence of the
mask must have resulted in the animal inspiring air with a
carbon dioxide concentration of 0·5 to 1·5% instead of 0·08% as
was normal in room air.

The Regional Distribution of Cutaneous Evaporation

The rate of cutaneous evaporation clearly differs between

different body regions and the results show a considerable
degree of uniformity in this respect between animals.   The
main area of high evaporation in warm environments was found
to be the neck and forequarters of the trunk.   In general
evaporation tended to be greater on the fore and upper regions
than on the rear and lower regions of the trunk, although another
area of high evaporation was observed around the rear haunch.
Evaporation rate was relatively low on the head and least on
the underside of the trunk.   Evaporation rates were not measured
on the distal portions of the limbs or on the tail.   This
ranking of the regions is in broad agreement with those reported
for Holstein-Syrian crossbred cows (Volcani & Schindler, 1954:
Berman, 1957), Sindhi-Jersey crossbred cows (McDowell, McMullan,
Wodzika & Fohrman, 1955) and Brahman and Santa Gertrudis cows
(Kibler & Yeck, 1959).   It therefore appears that the regional
distribution of cutaneous evaporative heat loss is similar for
all breeds of cattle.   The results quoted earlier from the
findings of McDowell et al. (1954) do not, however, conform
with this pattern.   The order of decreasing evaporation for
the various skin regions studied shows no clear correlation
with the order of decreasing sweat gland density in any of the
ways in which this was expressed by Findlay & Yang (1950) for
Ayrshire cows.

The Responses to Different Thermal Environments
(Experiment D)

Heat production

Heat production did not vary significantly over the

temperature range 15 to 40°C.   This was expected in view of
the feeding routine whereby the animals were provided with a
constant diet of concentrates with additional hay.   The food
was offered each day, only after the completion of the climatic
room exposure, when the appetite of the animal was no longer
likely to be limited by heat stress;   also the food was all
consumed at least 16 hr before the start of the next exposure.
For the environments 35L, 35M and 35H the mean level of heat
production was 207, 224 and 245 kcal/hr respectively, the
difference in heat production being significant $(0 \cdot 01 > P)$
between the two extreme humidities but not significant $(P > 0 \cdot 05)$
between the intermediate and either of the extremes.   Since
body temperature was $0 \cdot 6°C$ higher at 35H than at the two lower
levels of humidity an increase in heat production of approximately
$4 \cdot 2\%$ or $8 \cdot 5$ kcal/hr (for $Q_{10} = 2 \cdot 0$) may be expected from the
Van't Hoff effect.   This partially explains the observed rise.
It is probable, however, that the increased work of respiration
was also involved;   respiratory rate was much higher at 35H
than at any other environmental condition.

The fixed level in the calculated value of heat production
over a wide temperature range results from the fact that the
measured values of both carbon dioxide output and respiratory
quotient remained virtually unchanged.   Although pulmonary
ventilation rate rose with increasing air temperature the
concentration of carbon dioxide in expired air fell, so that
the total output of carbon dioxide was unaffected.   With an
increase in air humidity at 35°C, however, when pulmonary
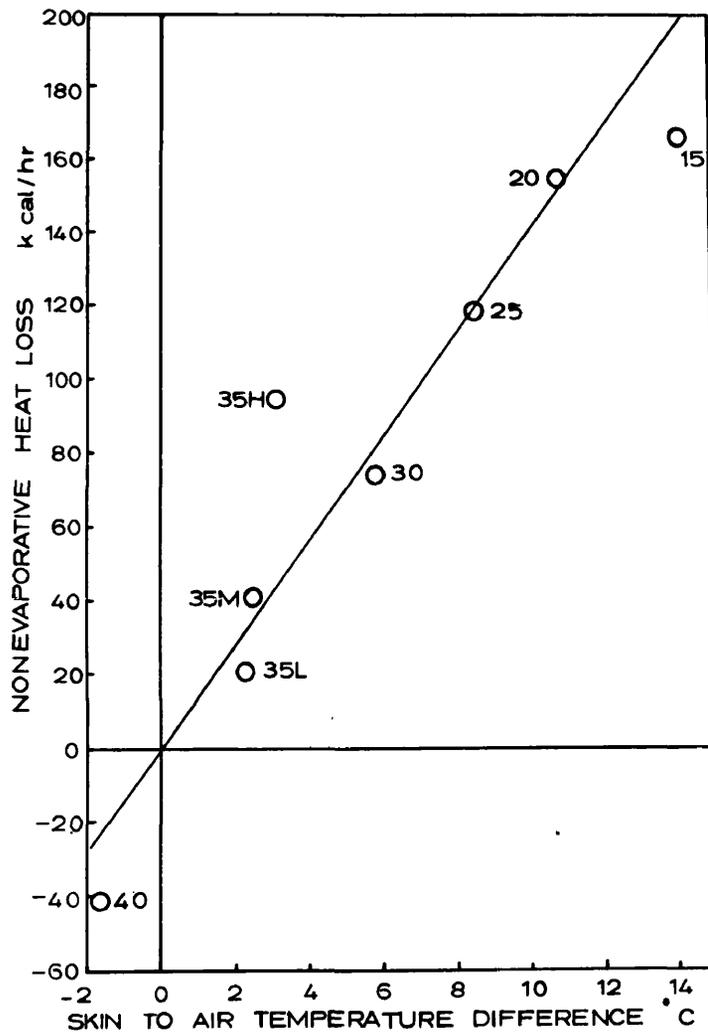
Fig. 28. The relationship between non-evaporative heat loss
and the temperature difference between skin and
air, at the various indicated environmental
conditions. The solid line represents a skin to
air thermal conductance of 14 kcal/hr.°C (Experiment
D).

ventilation rose considerably the fall in concentration was
not sufficient to prevent the total output of carbon dioxide
from rising. It might be argued that due to hyperventilation
the increase in carbon dioxide output occurred at the expense
of a lowering of carbon dioxide concentration in the body
fluids, and that the heat production was not in reality greater
than at other environmental conditions. This explanation,
seems unlikely in view of the fact that Bianca & Findlay (1961)
found no substantial change in the acid-base status of the
blood when they exposed calves to mild heat stress that resulted
in slightly more elevated respiratory rates than the condition
35H used here.

Non-evaporative heat loss

The non-evaporative heat loss was zero when air temperature
was approximately 37°C, and varied approximately linearly with
air temperature at a rate of -10·5 kcal/hr.°C over the range
25 to 40°C. At air temperatures below 25°C the linear relation-
ship was not maintained. According to physical laws non-
evaporative heat loss would be expected to vary linearly, not
with air temperature itself, but with the difference between
air and skin temperatures. Fig. 28 presents the data for all
environments in this way. The line drawn in the figure is not
a calculated 'best fit' for the points. It has been made to
pass through the origin and it represents a skin surface to air
thermal conductance of 14 kcal/hr.°C. The plotted points, with
the exception of those referring to the environmental conditions
15 and 35H, all lie within ±20 kcal/hr of the line. This
scatter is consistent with the combined errors of the estimates

of heat production and evaporative heat loss, the two

quantities from which non-evaporative heat loss was calculated

by difference.   At 15°C the mean level of non-evaporative heat

loss was 13% lower than that predicted by the line and at the

highest humidity level at 35°C it was more than 100% higher.

The difference between skin and air temperatures was

computed from the only skin temperature measurements made,

that is on the sacral region of the back.   Skin-to-air thermal

conductance should properly be based on the mean surface

temperature for the whole animal.   Although Beakley & Findlay

(1955b) have shown that skin temperature is nearly uniform

over the trunk, Whittow (1961) has found that at air temper-

atures of 15°C and below, but not at 20°C and above, skin

temperatures on the distal portions of the limbs of calves

are near to air temperature and much less than skin temperature

on the trunk.   It appears that at these low temperatures the

lower limbs and certain appendages such as ears and tail are

effectively 'shut off' as radiators of heat.   The point on

Fig. 28 corresponding to an air temperature of 15°C may thus

be expected to lie below any line of constant conductance

passing through the other points.

The exceptionally high rate of non-evaporative heat loss

per °C of skin to air temperature gradient observed at the

highest humidity level at 35°C is not so readily explicable.

The only obvious reason for an increase in skin-to-air

conductance at this environmental level is the extra flank

movement brought about by the greatly increased respiratory

rate that was observed at this environmental condition only.

Non-evaporative heat loss as calculated for the purpose
of plotting Fig. 28 included the heat loss due to forced
convection in the respiratory tract, which should properly
be excluded from the computation of skin-to-air conductance.
Respiratory convective loss could not be calculated since the
temperatures of inspired and expired air were not measured;
but even if it be assumed that respired air was heated from
room to body temperature it may be shown that respiratory
convection could only have represented less than 10% of the
total non-evaporative heat loss at every environmental
condition.   The presence of the mask is likely to have
nearly halved even this maximum possible level of respiratory
convective loss.

Taken as a whole, the estimates of non-evaporative heat
loss suggest that, under the conditions of air movement
pertaining in the climatic chamber, the skin-to-air conductance
of the animals was approximately 14 kcal/°C.hr.   The
reciprocal of this quantity, 0·071 hr.°C/kcal, represents
the thermal resistance or insulation of the skin-to-air
barrier.

Despite the large changes that occurred in the temperature
difference between deep body and skin, the total quantity of
heat lost from the surface (both evaporative and non-evaporative)
was of the same order of magnitude at all environmental
conditions.   These quantities and the ratio of one to the
other, which is a measure of the thermal resistance or
insulation of the tissues, are given in Table 16.   Tissue

Table 16. The total heat loss from the skin (H_s), the difference between rectal and skin temperatures $(T_r - T_s)$ and the tissue insulation $(T_r - T_s)/H_s$ for different environments (Experiment D).

Environment	H_s kcal/hr	$T_r - T_s$ °C	Tissue insulation hr.°C/kcal
15	183	8·53	0·047
20	177	6·88	0·039
25	158	4·47	0·028
30	167	2·49	0·015
35L	168	1·42	0·008
40	161	0·28	0·002
35M	186	1·21	0·007
35H	201	1·26	0·006

insulation, like skin-to-air insulation, should be based on
mean values of skin temperature over the whole surface, and
not just on a single estimate from one region. No great
accuracy can therefore be claimed for the insulation values
given in Table 16, but their relative values show an
unquestionable change with air temperature. Tissue insulation
increased from a value of approximately $0 \cdot 002$ hr.$^\circ$C/kcal at
40°C up to $0 \cdot 046$ hr.$^\circ$C/kcal at 15°C, i.e. by a factor of 23.
This remarkable change in tissue conductance would at first
sight be expected to influence both the non-evaporative and
the evaporative heat loss. Since body temperature did not
vary greatly the plot of non-evaporative heat loss against
air temperature (Fig. 17, p. 71) also effectively represents
non-evaporative heat loss plotted against the temperature
gradient from deep body to air. The reason why this relation-
ship is so nearly linear, despite the change in tissue
conductance, lies in the fact that at high air temperatures
tissue insulation is so much smaller than skin-to-air
insulation ($0 \cdot 071$ hr.$^\circ$C/kcal) that the former exerts negligible
influence on the non-evaporative heat loss. It is only at
relatively low air temperatures, when the resistance to heat
flow offered by the tissues becomes comparable with that
offered by the skin-to-air boundary, that non-evaporative heat
loss is effectively influenced by blood flow changes within
the body. This is evidenced by the changing slope at 20 to
15°C of the curve relating non-evaporative heat loss to air
temperature and by the apparent change in skin-to-air
conductance at 15°C, which as discussed earlier results from

blood flow changes in the distal portions of the limbs.

The changes in local surface temperatures that can occur near environmental temperatures of 15°C have been described for the ears by Beakley & Findlay (1955c) and for the limbs by Whittow (1961). The effects on both ears and limbs, which appear to result from dramatic alterations of blood flow in these organs and which occur within a limited range of air temperature, cannot explain the large change in tissue insulation that was observed over the air temperature range 20 to 40°C. The change may result from generalised cutaneous vasoconstriction-dilation over the trunk, which occurs more gradually than do the effects on the limbs and ears at lower air temperatures, or it may reflect blood flow changes at a deeper level. Blaxter, Graham, Wainman & Armstrong (1959) found correspondingly large changes in tissue insulation for shorn sheep at air temperatures above 25°C. Their measure- ments did not distinguish between respiratory and cutaneous evaporative heat losses and their estimates of tissue insulation were based on total heat losses from both respiratory tract and skin. They attributed the apparent large change in tissue insulation over this temperature range partly to the inclusion of respiratory moisture loss in their computation. The present results, however, show that for cattle the change in tissue insulation is still marked even if allowance is made for respiratory evaporation.

In the same and in a later paper (Armstrong, Blaxter, Clapperton, Graham & Wainman, 1960) these authors concluded that in sheep generalised cutaneous vasoconstriction and

vasodilation 'border on all or none effects' and that
vasodilation occurs at environmental temperatures which are
only slightly above the critical temperature.   Their
conclusions are based on comparisons of a quantity 'total
conductance', defined as the non-evaporative heat loss
divided by the temperature gradient from the rectum to the
environment.   Whereas this quantity is useful as a concept
for consideration of heat losses at low environmental
temperatures, where evaporative heat loss is small, its
application to conditions where vasoconstriction-dilation
occurs is open to question.   'Total conductance' relates one
form of heat flow (non-evaporative) to a temperature gradient
across part of which another form of heat flow (evaporative)
occurs simultaneously.   Changes in the rate of cutaneous
evaporation, which are considerable over the range of
environmental temperatures between which the comparison is
made (8 and 32°C) must affect 'total conductance'.

The present results and those of Beakley & Findlay
(1955b, c) and Whittow (1961) appear to suggest that thermo-
regulatory blood flow changes in cattle occur in two phases.
First, local variations of blood flow in the limbs, ears and
other appendages occur rapidly at air temperatures below
20°C.   These local variations are dramatic in their occurrence
which is not necessarily simultaneous on all areas and they
are effective in limiting the amount of non-evaporative heat
loss in cold environments.   Secondly, generalised cutaneous
vasoconstriction-dilation, particularly on the trunk, or blood
flow changes at a deeper level, operate gradually at air

temperatures above 20°C.   This second phase of thermo-regulatory blood flow change has little influence on non-evaporative heat loss because at air temperatures above 20°C the thermal resistance of the tissues to heat flow becomes negligible compared with that of the skin-to-air barrier. The reduction in thermal resistance of the tissues above 20°C is, however, necessary in order to allow an increasing amount of heat transport to the surface for dissipation in the form of cutaneous evaporation.

At very low air temperatures non-evaporative heat loss may be further influenced by physiological means such as pilar erection.   At air temperatures above 20°C, however, the only factors which effectively determine the quantity of non-evaporative heat loss are the nature and thickness of the coat and the physical properties of the environment.

Evaporative heat loss

Evaporative heat loss increased linearly with rising air temperature from 25°C at a rate of 11·9 kcal/hr.°C. From air temperatures of 25° down to 15°C evaporative heat loss declined less rapidly.   The rise in evaporative heat loss over the whole temperature range thus very nearly compensated for the fall in non-evaporative heat loss, the amount by which it failed to do so being represented by the amount of heat storage.   The storage of heat could obviously not continue indefinitely if the animals were to survive. It is probable that, if the waiting period of 2 hr before the measurements were begun had been extended, then evaporative heat loss would have been increased and heat storage eliminated.

The quantity of water evaporated from the respiratory tract (as estimated by the difference method at low air temperatures and by the direct method at high air temperatures) rose steadily over the temperature range studied at a rate of 1·5 g/hr.°C. Since the mean surface area of the animals was approximately 2·24 m², the rate of rise of respiratory evaporation may be represented as 0·67 g/m².hr.°C.

The quantity of moisture evaporated from the surface was similar to that from the respiratory tract at 15° and at 20°C, but as air temperature increased from 25° to 40°C surface evaporation rose steadily at a rate of 7·8 g/m².hr.°C.

As described earlier the presence of the mask is believed to have limited respiratory evaporation to only 55% of the level that it would have attained had the mask not been worn. It is interesting to speculate as to what effect the removal of the mask might have had on the overall heat balance. It is possible that the extra heat loss would have prevented body temperature from rising during the experimental period, i.e. it would have eliminated heat storage; in fact the quantity of extra heat dissipation involved is more than sufficient to have done this. Alternatively it is possible that there would have been a corresponding reduction in cutaneous evaporation. If this is accepted then the rates of increase of moisture evaporation per unit surface area at high air temperatures would have been 1·2 g/m².hr.°C. for respiratory evaporation and 7·3 g/m².hr.°C for cutaneous evaporation. Even under these circumstances the contribution from the surface, to the total evaporative heat loss at high air

temperatures, would still have been two to three times as great as that from the respiratory tract.

If, as is believed, the animal expires air nearly saturated with moisture at body temperature, the only way in which respiratory evaporation may be increased with rising air temperature, is by an increase in pulmonary ventilation. Moreover, for any given environmental level of absolute humidity, respiratory evaporative heat loss must vary directly with the rate of pulmonary ventilation. An increase in respiratory rate with rising air temperature, is therefore of no thermoregulatory value unless pulmonary ventilation also increases. In fact an increase in respiratory rate is usually associated with some increase in pulmonary ventilation, but the latter increase is normally limited by a coincident reduction in tidal volume (Findlay, 1957). Panting as a means of increasing heat loss in hot dry climates may, therefore, not be so efficient as might at first sight be supposed.

At an air temperature of 35°C increasing humidity resulted in a gradual decline in respiratory evaporative heat loss despite the doubling of respiratory rate without decline in tidal volume. Although respiratory evaporation would undoubtedly have fallen further had the increase in pulmonary ventilation not occurred, it is doubtful if the advantage gained by the increase was great enough to offset the extra heat production associated with the work of breathing. On the other hand if the apparent increase in skin-to-air conductance observed at the high level of humidity was consequent on increased flank movement, then the increase in

respiratory activity must have been of net advantage to the
animal as a means of cooling.

The observed rate of cutaneous evaporation was greater
(although the difference is not statistically significant)
at 35M than at 35L. The preliminary experiments (Table 6,
p. 33) and those of Taneja (1958) also provide evidence that
increasing humidity up to moderate levels does not result
in reduced cutaneous evaporation. A further increase in
environmental humidity to 35H did however result in a marked
reduction in cutaneous evaporation. At this environmental
condition, the humidity of outlet air from capsules placed
on some regions rose to within 90% of saturation at air
temperature; the proportional increase in outlet air humidity
necessary to maintain cutaneous evaporation at the same level
as at lower air humidities would have been physically
impossible. It appears, therefore, that it is only when air
humidity rises beyond a certain level that cutaneous evapor-
ation is limited by the environment. For the particular
animals studied and at an environmental temperature of 35°C
the air humidity level in question was not less than 20 mm Hg
(46% relative humidity).

When short term as opposed to day-to-day variations in
environmental humidity were applied, rectal temperature was
unaffected and respiratory rate not greatly affected. This
suggests that the short term variations did not appreciably
alter the overall thermal balance. Cutaneous evaporation,
however, was reduced by increasing environmental humidity
over the full range when the variations were of short duration.

Under these conditions cutaneous evaporation followed the
trends that would be expected of evaporation from an inanimate
surface under the laws of physics.   This occurred during a
short time interval in which the overall state of thermal
balance of the animal was not disturbed and physiological
control of evaporation had not, as it were, had time to act.
The response of skin temperature was almost identical both
to short term and day-to-day humidity variations.   At low
humidities the higher rate of evaporative cooling of the skin,
in the short term as opposed to the day-to-day variations, was
apparently counterbalanced by the higher level of deep body
temperature so that skin temperature was the same in both.
The reverse effects in the responses to high humidities also
resulted in the same skin temperatures for both the long and
the short term variations.

The overall heat balance of an animal as stated in Chapter
I may be expressed by the equation:

$$H_p = H_n + H_e + H_s$$

For an animal in a steady thermal state the heat storage
term H_s is zero.   In the experiments described, heat production
H_p was unaffected by air temperature or humidity except at the
condition 35H, presumably as a result of a steady level of food
intake.   Non-evaporative heat loss H_n was determined through-
out most of the temperature range solely by the thickness of
the coat and the physical properties of the environment.   The
remaining term in the equation, evaporative heat loss H_e, was
thus fixed near to a predetermined level equal to the difference
between H_p and H_n.   The observed value of H_s is a measure of

the extent to which H_e failed to be adjusted to this level.
The value H_e consists of two components, respiratory and
cutaneous evaporative heat losses.   Of these the former has
only minor influence on the total, and thus cutaneous
evaporation is the major channel of heat loss through which
regulation of body temperature may be maintained in the air
temperature range under consideration.

Evaporation being a physical process is subject to physical
laws.   Thus, for example, if the air humidity over the skin
is suddenly lowered an increase in cutaneous evaporation must
occur.   This was observed during the experiments when short
term humidity changes were applied.   However, after some hours
of exposure the rate of evaporation was approximately the same
for both the environments 35L and 35M.   In the steady thermal
state cutaneous evaporation thus becomes adjusted, regardless
(within limits) of the physical properties of the environment,
to the level determined by the requirements of homoeothermy.
Similarly, in the preliminary series of experiments it was
found that evaporation rates measured by capsules placed on
small finely clipped areas of skin were greater than those
from unclipped areas.   It was found also that if the entire
coat of an animal was clipped the rate of cutaneous evaporation
was reduced for exposures to 20°C; but not for exposures to
40°C where non-evaporative heat loss is zero for both shorn
and unshorn animals.   Reductions, as a result of shearing
the coats of animals, have also been reported in the insensible
weight loss of cattle (Kriss, 1930a; Mitchell & Hamilton,
1936) and sheep (Lefèvre & Auguet, 1930) and in the total

evaporative weight loss of sheep (Blaxter, Graham & Wainman, 1959). Also, increasing the rate of ventilation through a capsule results in increased evaporation from the area under test, but increasing wind velocity to which the animal is exposed results in a reduction in cutaneous evaporation (Thompson, Yeck, Worstell & Brody, 1954). These are all examples of instances in which the physical properties of the environment are changed so as to enhance evaporation from any surface or fixed vapour pressure. When the changes are applied suddenly or locally cutaneous evaporation increases; but when they are applied to the entire animal, resulting through increased non-evaporative heat loss in an overall diminution in the need for evaporative cooling, then cutaneous evaporation decreases.

Once a steady thermal state is attained physiological control thus results in the output of moisture from the body to the peripheral layer from which outward physical diffusion of vapour takes place, being quantitatively adjusted to the level of cutaneous evaporation required for the maintenance of homoeothermy. If this happens the physical conditions, necessary for the rate of evaporation being equal to the rate of supply of moisture from the body, occur automatically and independently of the environment. Thus if ambient humidity suddenly increases, then the temporarily reduced evaporation, due to the decreased diffusion gradient, results in a build-up in moisture concentration that automatically re-establishes the gradient at its previous level.

The above explanation has the same practical significance

as the theory involving wetted area (Gagge, 1937) and that involving relative humidity of the skin (Mole, 1948) both proposed in relation to cutaneous evaporation in man. The concept of wetted area as a physiological variable is however unnecessary to the argument. Wetted area, or relative humidity of the skin, or whatever it may be called, is merely a measure of the moisture concentration that exists at the peripheral layer from which outward diffusion takes place. The anatomical definition of this peripheral layer and the physiological means of controlling the supply of moisture to it are discussed in a later section.

In nearly all the studies on cattle reported from the University of Missouri (Kibler & Brody, 1950, 1952; Kibler & Yeck, 1959), evaporative heat loss, and in particular cutaneous evaporative heat loss, rose at first with increasing air temperature, but reached a limiting value at temperatures (depending on breeds and states of growth or lactation) of 27°C and upwards. For the same animals, heat production decreased from previously steady values when the air temperature was raised above approximately the same temperature levels. These animals were subjected to prolonged (up to 2 weeks) climatic room exposures to each environmental temperature, and other reactions to thermal stress included reductions in food consumption and milk production. Kibler (1960) exposed a group of animals, which had previously reacted to prolonged exposures in the manner just described, to temperatures of 40 to 43°C for periods of 6 hr. He found that the rates of heat production rose during the exposure. In the present studies

where the animals were also subjected to relatively short
exposures, evaporative heat loss rose steadily as air
temperature increased up to the highest level applied; mean-
while heat production showed no change, and the intake of
food (which was consumed each day after the animals had been
removed from the climatic room) was presumably the same
throughout.   Kibler & Brody (1952) describing their observations
stated that all breeds attained maximal sustained outer surface
evaporative rates of 150 g/m^2.hr and also that as non-evaporative
heat loss fell with rising air temperature an unlimited rise
of body temperature was prevented by a reduction in heat
production (also in food consumption and milk production).
This might have been expressed with different emphasis as
follows: due to the reduced food consumption at high air tem-
peratures heat production declined and so the need for incresed
evaporation to maintain a steady body temperature was obviated.

The question, as to whether heat production declined
because evaporative heat loss was incapable of further increase
or whether evaporative heat loss ceased to rise because heat
production declined, cannot be answered with certainty from
the data.   It is probable that the correct explanation lies
somewhere between the two extreme possibilities.   If an
animal is subjected to a hot environment, a steady level of
body temperature (disregarding diurnal fluctuations) is attained
after a few hours.   This steady level, despite increased
evaporative heat loss, is elevated above that normally main-
tained in a thermoneutral environment.   If the elevated body
temperature results in a voluntary reduction in food intake,
then prolonged exposure to the hot environment will eventually

result in reduced heat production and consequently a reduced
thermoregulatory requirement for evaporative heat loss.
Such an argument could explain why the evaporative heat loss
from animals subjected to prolonged high temperature exposures
does not rise beyond a certain limit with further increase in
air temperature.   Beef steers fed on fixed diets and subjected
by Blaxter & Wainman (1961) to exposures lasting 4 days, showed
no change in heat production between air temperatures of 15 and
25°C but a 3·5 to 7% increase at 35°C.   Heat production in
this instance was not depressed even after 4 days because the
food intake level was kept constant, and evaporative heat loss
was still sufficient to maintain a steady body temperature.
Neither the steers of Blaxter and Wainman, however, nor the
calves used in the present studies attained the maximal cutaneous
vaporization rate quoted by Kibler and Brody (150 g/m^2.hr), even
at the highest air temperatures to which they were exposed.   It
is therefore still uncertain whether or not this maximal rate
represents an absolute physiological upper limit of the
evaporative capacity of the skin.

The Reactions to Heat Stress at Different Ages
(Experiment E)

The rate of cutaneous evaporation from three animals
exposed to an air temperature of 38°C rose continuously as
they aged from 10 to 34 weeks, except that one animal showed
a decrease in evaporation during the first 'month' and another
did so in the last 'month'.   The increase in evaporation
occured from all body regions examined and the ranking of the

different regions in order of increasing evaporation was not appreciably altered as the animals grew older. Two of the calves used in Experiment D had approximately constant rates of cutaneous evaporation between the ages of 24 and 37 weeks but cutaneous evaporation from the third animal decreased over the age period 39 to 44 weeks. This general pattern of changing cutaneous evaporation with age conforms with that found for Shorthorn heifers permanently housed in a room maintained at 27°C (Kibler & Yeck, 1959), i.e. cutaneous evaporation rate rising with age to a maximum and then declining. The maximum rates from the Shorthorns, however, did not occur until an age of 10 to 11 months. Brahman and Santa Gertrudis heifers exposed to the same conditions as the Shorthorns evaporated decreasing amounts of moisture per unit area of skin over the entire period for which results were given, that is from 4 to 16 months of age. Taneja (1958) found higher rates of cutaneous evaporation at 8 and 12 months than at 4 months for both a Shorthorn and a Zebu-Shorthorn crossbreed. Klemm & Robinson (1955) measured total moisture loss and respiratory rate from Zebu-Hereford crossbreeds and from Australian-Illawara Shorthorns; from their data they concluded that the A-I. Shorthorns must have increased their rates of cutaneous evaporation between experiments conducted at 1 to 3 months and at 6 to 8 months, but they found no further increase in total evaporation per unit area at 12 to 13 months. Their crossbred animals maintained a steady total evaporative loss per unit area throughout.

The time of year, during which the present study on the

effects of age was carried out, was unfortunately chosen.
The observed increasing rates of cutaneous evaporation all
took place during the period over which outside air temperature
normally increases and the only two decreasing rates at about
the times when the trends in outside air temperature are also
reversed.   The results from Experiment D did not appear to
vary so consistantly with the weather; but on the other hand
relatively low cutaneous evaporation rates were also observed
in Experiment C, from calves subjected to hot room exposures
during November and December.   From the present results it is
therefore impossible to conclude that the variations in
cutaneous evaporation did not result at least in part, from
responses to varying weather conditions or to some related
factor such as the length of hair coat.   The relatively thinner
coat of an animal in summer, by allowing increased non-evaporative
heat loss, would be expected to result in decreased evaporative
heat loss for exposure to the same thermal environment.   This,
however, is the reverse of the observed trend.   Any variation
associated with time of year would not be expected to have so
much influence on the observations at Missouri where the animals
were permanently housed in the controlled atmosphere of the
climatic room, although the peak rate of cutaneous evaporation
for the Shorthorns again appears to have coincided with mid-
summer.   It is, however, unlikely that the large variations
observed in Experiment E in cutaneous evaporation rate,
respiratory rate and body temperature may all be attributed
entirely to seasonal effects.   Unfortunately, an experiment
that would distinguish conclusively between the effects of age

and season would, for obvious reasons, take a very long

time.   One other factor which must have a bearing on the

variation of cutaneous evaporation with age is the level of

heat production.   For the animals at Missouri heat production

increased throughout the ageing period but heat production

per unit area of surface (Kibler, 1957), which is the proper

variable for comparison with heat loss per unit area, increased

to a maximum at 6 to 7 months of age and then declined.   This

pattern was, however, observed with all three breeds (Shorthorn,

Santa Gertrudis and Brahman) and cannot therefore be the sole

factor accounting for the responses of cutaneous evaporation,

which, for the Shorthorns only, rose to a maximum and then

declined.

Whatever the reason for the changes in cutaneous evaporation

the negative correlations between cutaneous evaporation on the

one hand and skin and rectal temperatures and respiratory rate

on the other are most striking, especially for calves 219 and

220 (Fig. 24, p. 78).   The elevated skin and rectal temperatures

of these animals when young and in a hot environment suggests

that any physiological mechanism for increasing heat loss must

have been stimulated;   this apparently resulted in very great

respiratory activity and yet cutaneous evaporation remained

low.   As the animals grew older the skin and body temperatures

were lower and the stimulus presumably reduced, as evidenced

by the decrease in respiratory activity, and yet cutaneous

evaporation increased.   It appears that as the animals grew

older the physiological mechanisms that control cutaneous

evaporation or that make moisture available for evaporation

were undergoing development. The very fact that they were undergoing development and providing increasing evaporation from the skin, resulted in increased cooling and a progressive decrease in the stimulus for respiratory activity. If these effects are due to ageing, and it is hard to believe that they are purely seasonal, then there appears to be a case for providing cooled living quarters for young European stock being reared in tropical environments. In the experiments at Missouri the Shorthorn calves raised in an environment of 27°C had lower rates of live weight gain than a similar group raised at 10°C, but the Brahmans put on weight more rapidly at the higher temperature (Ragsdale, Chu Shan Cheng & Johnson, 1957). On the other hand it is possible that the need for evaporative cooling may provide a stimulus to the development of the physiological means of providing it.

Evaporation and Heat Tolerance

The results of Experiment E suggest that the heat tolerance of an animal subjected to a hot environment improves as the animal's capacity for cutaneous evaporative cooling increases; this observed trend is, however, associated either with age or with season. The combined results of Experiments C, D and E further suggest that heat tolerance, between different animals of the same breed and comparable age, is greatest for the animals with the highest rates of cutaneous evaporation (Table 14, p. 79); the evidence for this is not so conclusive and is also obscured by the possible influence of season. In each of these comparisons between exposures to similar thermal
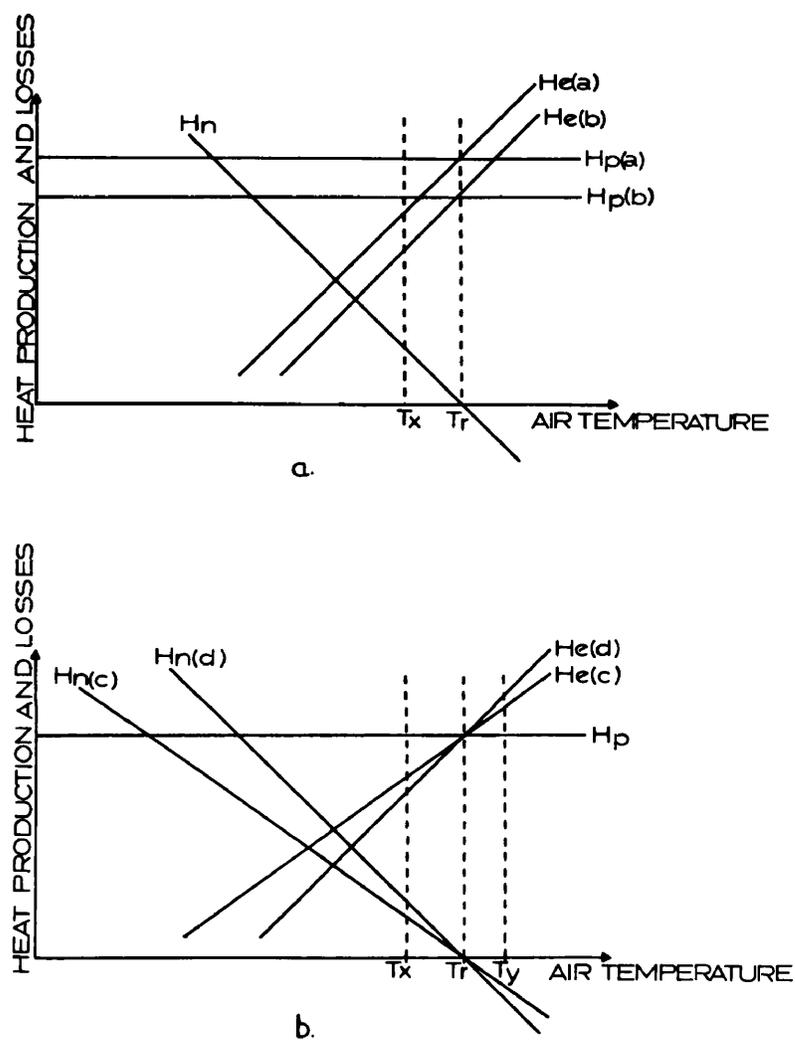
__Fig. 29.__   Theoretical inter-relationships between heat
        production (H_p), and evaporative (H_e) and non-
        evaporative (H_n) heat losses per unit surface
        area at different air temperatures.

    a. for two animals (a & b) with the same coat
        insulation but different levels of heat
        production.
    b. for two animals (c & d) with different coat
        insulations but the same level of heat
        production.

environments increasing rates of cutaneous evaporation are associated with decreasing levels of rectal temperature. These findings are not, as might at first sight appear, contradictory to the evidence of Kibler & Yeck (1959). They found that for animals of different breeds all exposed to the same warm environment (27°C) those of the most heat tolerant breed (Brahman), that is those with the lowest level of rectal temperature, were also the ones with the lowest rate of evaporation per unit area from the skin. They concluded:- 'Evaporative cooling per se is not the determining factor in the heat tolerance of different breeds of cattle'.

The distinction lies in the difference between evaporative capacity on the one hand and the thermoregulatory requirement for evaporative cooling into a given environment on the other. The possession of a high evaporative capacity does not imply that the capacity must be utilised. Other factors, notably heat production per unit area and thermal insulation of the coat, are often of greater practical significance than evaporative capacity in determining heat tolerance. This is illustrated by Fig. 29. Suppose that two animals A and B (Fig. 29a) have heat production levels per unit surface area $H_p(a)$ and $H_p(b)$ over the range of physical thermoregulation, and that the insulation of the coat is the same for both animals; then non-evaporative heat loss for both animals will vary with air temperature according to the line H_n which passes through zero when air temperature is approximately equal to body temperature, and the slope of which, as discussed earlier, is nearly constant and primarily determined by skin-to-air

insulation.   In order to maintain body temperature constant,
evaporative heat loss must be held at all air temperatures
equal to the difference between heat production and non-
evaporative heat loss.   This is represented by the lines
$H_e(a)$ for animal A and $H_e(b)$ for animal B.   At any moderately
high air temperature, T_x, evaporative heat loss must be greater
for A, which has the higher level of heat production, than for
B.   This rate of evaporation must be maintained regardless of
the animal's evaporative capacity.   Similarly Fig. 29b represents
the corresponding heat losses for two animals C and D which have
the same level of heat production per unit area H_p, but different
amounts of coat insulation and therefore different non-evaporative
heat losses $H_n(c)$ and $H_n(d)$.   Evaporative heat loss must be
held at levels $H_e(c)$ for animal C and $H_e(d)$ for animal D.   At
air temperature T_x, C with the greater coat insulation must
lose more heat by evaporation than D.   At an air temperature
T_y, above body temperature, the superior coat insulation of C
protects him against non-evaporative heat gain and he does not
require to lose as much heat by evaporation as does D.   At
such very high air temperatures the ultimate ability of the
animal to maintain the necessary sustained high level of
cutaneous evaporation may be reached.   The theoretical curves
of Fig. 29 relating heat production and non-evaporative and
evaporative heat losses to air temperature have been demonstrated
in practice by Blaxter, Graham, Wainman & Armstrong (1959) and
Blaxter, Graham & Wainman (1959) for sheep.   Their data on
shorn sheep fed at different levels of nutrition and on sheep
with varying fleece lengths are beautiful illustrations of

Figs. 29a and 29b respectively. For any two animals with the
same heat production per unit area and the same coat insulation
the evaporative requirement is the same, and the animal with
the greatest cutaneous evaporative capacity will presumably
maintain the required rate with least increase in body temper-
ature and respiratory activity.

This reasoning may be applied to the three series of
practical observations summarised at the beginning of this
section (p. 117). The higher cutaneous evaporation rates
associated with lower rectal temperatures as the animals grew
older (Experiment E) suggest that, in the special case of
young European calves, evaporative capacity is a limiting factor
in determining heat tolerance; although changes in the rate of
heat production per unit surface area may also influence
evaporative requirement. For the comparison between nine
animals all of the same breed, all within a relatively limited
age group, all fed on the same rations and therefore presumably
all with similar rates of heat production per unit area and
similar amounts of coat insulation, again evaporative capacity
appears to have influenced heat tolerance though not so greatly.
Finally, for the comparison between breeds (Kibler & Yeck, 1959),
heat production per unit area and coat insulation were evidently
the over-riding factors. The different rates of evaporation at
the same air temperature give little information on the relative
evaporative capacities of the three breeds since they were
evidently stressed to different degrees by the same environment.

Physiological Control and Origin of Cutaneous Evaporation

In man the layer from which outward diffusion of moisture takes place is commonly accepted to be the skin surface. The supply of moisture from the body to the surface is accomplished both by sweating and by diffusion. The latter is a reversible process (Buettner, 1953) and is quantitatively small in comparison to the potential output of the sweat glands. By contrast cattle have been frequently described in the past as 'non-sweating', 'slightly sweating' or 'panting' animals. In recent years an increasing amount of evidence, suggesting that the sweat glands of cattle have a thermoregulatory function, has been published. Ferguson & Dowling (1955) have observed through a microscope the formation of droplets at the openings of the sweat gland ducts during exposure of Zebu-Jersey cross-bred and Ayrshire heifers in a hot environment; and they have obtained prints showing the location of the droplets on bromothymol blue papers pressed onto the skin surface. Visual observation of thermally induced sweat on cattle has been reported also by Taneja (1958). The stepwise increase in the rate of cutaneous evaporation during the initial rise on exposure to heat is suggestive of secretory activity. Similar fluctuations have also been induced artificially in relatively cool environments by local heating of the hypothalamus (Ingram, McLean & Whittow, 1961) which also induced panting and vaso-dilation. Finally the quantitative dependence of cutaneous evaporation on environmental temperature and humidity reported here and by many other workers already cited cannot be explained by simple diffusion.

The only evidence advanced for the belief that cattle do
not sweat in inconclusive; this belief probably arose from
the fact that 'streams of sweat' may never be observed on cattle
as on horses.   It has been suggested that the very poor blood
supply to the sweat glands of cattle by comparison with man may
account for the inability of the glands to secrete.   On the
other hand the number of sweat glands per unit area of cattle
skin is greater than that of man, and a rough calculation shows
that the mean output per gland in cattle would only have to be
about one-fiftieth of that in man to produce the quantities of
evaporated moisture that have been observed; the size of sweat
droplets on cattle would therefore not be expected to be nearly
so great as on man.   This, together with the difficulty of
observation caused by the coat, may well be the reason why
thermal sweating is never obviously visible in cattle.   It can
only be stated with certainty that the overall secretion rate
of cattle is never great enough for the formation of streams
of sweat.   One other reason for concluding that cattle do not
sweat has been raised by Freeborn et al. quoted by Findlay
(1950) and by Regan & Richardson (1938).   These workers washed
down cattle that had been subjected to thermal stress and found
a negative result when they tested the wash water for chlorides;
this only suggests that the sweat secreted by cattle, if there
is any at all, does not contain chlorides.   Villares & Berthet
(1952), however, have reported a positive result from a
similar experiment.

The weight of evidence thus seems overwhelmingly in
favour of the sweat glands of cattle having some thermoregulatory

function.   If this is accepted then it is probable that the region from which outward diffusion of moisture takes place is, as on man, the skin surface.

The physiological mechanism that stimulates sweating in cattle is not known, and that in man is still subject to controversy.   Benzinger (1959) has reported evidence suggesting that in the range of physical regulation, sweating and thermo-regulatory changes of blood flow in man are solely and minutely determined by internal temperature.   This conclusion was drawn from experiments on one subject only and with fixed levels of humidity and air movement.   In a later paper Benzinger (1960) reported that the critical level of internal temperature above which sweating takes place and the rate of increase of evaporation with increasing internal temperature differs between subjects. Benzinger assumes that, with the low level of humidity that was maintained in the calorimeter, the rate of evaporation was equal to the rate of sweat secretion.   It is likely that this assumption is valid as an approximation, although the experiments of Buettner (1959a, b) and of Buettner & Holmes (1959) show that backward diffusion of sweat through the skin of man can result in the rate of evaporation being considerably less than the rate of secretion.   Had Benzinger's experiments been extended to include observations at other levels of humidity and air movement it is probable that different rates of evaporation would have been obtained at any fixed level of rectal temperature.   This is, however, only a minor reservation and it does not invalidate Benzinger's conclusion that the rate of sweat secretion is determined solely by internal temperature.   If this is true for
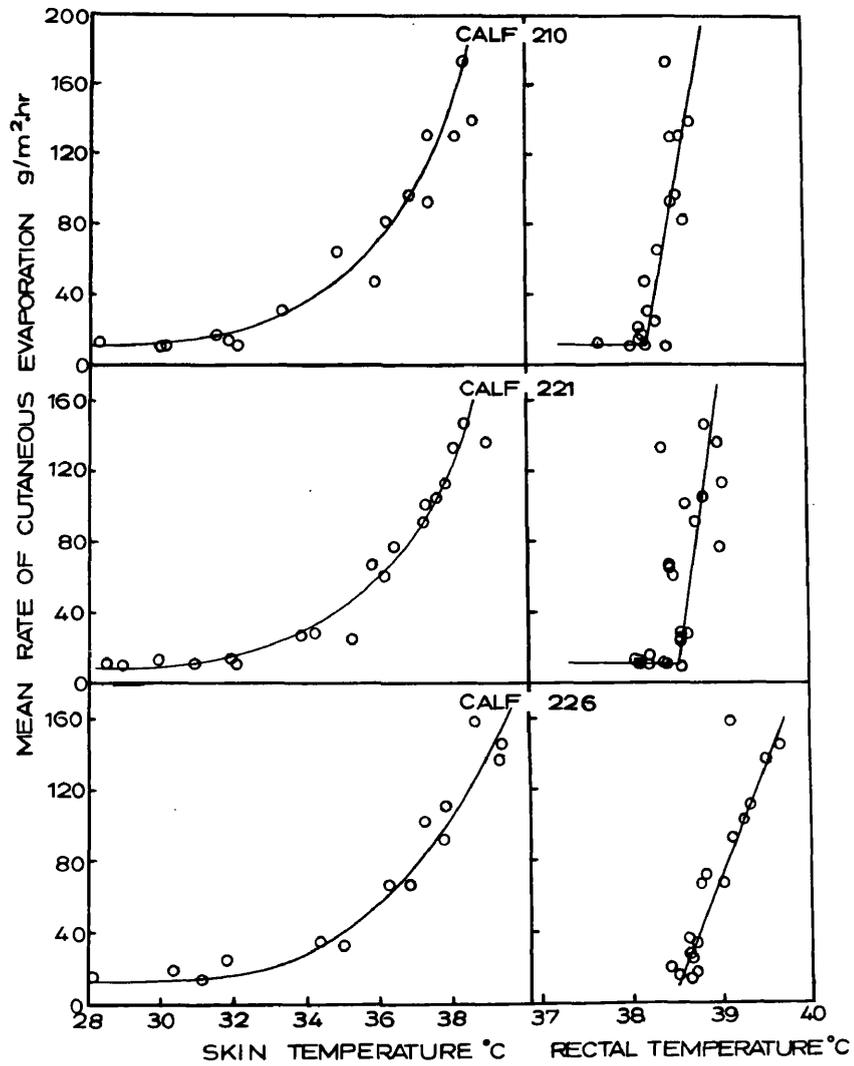
Fig. 30. Mean rates of cutaneous evaporation plotted against
skin and rectal temperatures for individual
exposures of three calves (Experiment D).

man, is it also true for cattle?

The mean rates of cutaneous evaporation observed in Experiment D are plotted in Fig. 30 for each animal against both skin and rectal temperatures. Each point represents the mean of the observations during a single exposure of an animal at a fixed low level of humidity; measurements at the conditions 35M and 35H are not included. If secretion rate is determined solely by internal temperature then any scatter about a fixed line, of the points relating evaporation rate and rectal temperature, must be due to errors of approximation or measurement. The standard deviation of a measurement of mean evaporation rate is estimated at $\pm6\cdot5$ g/m^2.hr; this in itself is clearly insufficient to account for the scatter. The accuracy of the thermocouple system ($\pm0\cdot1^\circ$C) is also too small to be a significant cause. The use of rectal temperature as a measure of the internal temperature that stimulates the thermoregulatory mechanisms is, however, open to question (Benzinger, 1961). Bligh (1957) has shown that the rectal temperature of calves differs from the temperature of the blood in the carotid artery by a constant amount in steady state conditions. It is, however, frequently found, when the rectal thermometer is re-inserted following defaecation, that the observed temperature has altered from its previous level by up to $0\cdot3^\circ$C; but the effects of such variations should be reduced by the process of averaging over six to eight quarter-hourly readings. The lines on the graphs of Fig. 30 have been drawn by eye. The scatter of the points about the lines relating evaporation to rectal temperature could be due to the

combined effects of the errors just discussed for calves 210

and 226, with one exception in each instance; for calf 221

the scatter is greater.   Similarly the scatter of the points

about the lines relating evaporation to skin temperature could

be due to errors of measurement, especially since skin temper-

ature was measured on only two body regions.   Taken as a

whole these results do not provide any conclusive proof that

sweating activity in cattle is initiated solely by either

peripheral or central afferent stimulus.

If sweat gland activity is determined solely by internal

temperature then the graphs of Fig. 30 suggest that both the

internal threshold temperature for the activation of the sweat

glands and the rate of increase of evaporation with increasing

rectal temperature differ between individuals.   Thus a higher

level of rectal temperature was required in order to provide

the stimulus necessary for a given rate of evaporation from

calf 226 than from the other two animals.   This is suggestive

of differing evaporative capacities between the animals.   The

results of Experiment E also suggest widely differing evaporative

capacities between young animals at different ages.   In that

experiment the relationship between evaporation rate and rectal

temperature was altogether different; increasing rates of

evaporation being associated with decreasing levels of rectal

temperature.   It is clear that any close correlation between

evaporation rate and internal temperature presupposes both a

fixed threshold temperature for sweat gland activity and a fixed

evaporative capacity for any one animal.   It is by no means

certain that these conditions were satisfied in Experiment D

which was conducted on growing animals and with the measurements on each animal spread over 8 to 14 weeks.

If the points corresponding to the condition 35H are inserted in Fig. 30 it is found in all instances that they lie well to the right of the rising lines drawn through the plotted points. The points corresponding to 35M also tend to fall to the right of the lines but do not depart from them greatly. If secretion rate is determined by internal temperature it is necessary to assume that at the higher humidity levels much of the secreted moisture, since it did not visibly accumulate on the skin, must have diffused backwards through the skin. This explanation is also necessary to account for the local effects due to varying hair coat length and ventilation rate within capsules.

The fact that the overall mean rate of cutaneous evaporation is always adjusted to maintain a constant or near constant level of body temperature is of itself suggestive of internal control of evaporation rate. It is difficult to visualise how any thermoregulatory system can effectively maintain internal temperature within such close limits if the stimulus for thermoregulatory processes is primarily dependent on surface temperature. Conversely if the stimulus is primarily or solely derived from internal temperature, then the evaporation rate and degree of vasomotor activity so determined will influence the skin temperature level attained. It would therefore be expected that skin temperature should be correlated with evaporation rate; but skin temperature in this instance would be the effect rather than the cause.

The stepwise increases in the rate of cutaneous evaporation and the coincident transient rises in skin temperature that were observed following the start of climatic room exposures may be analogous to the more marked effects that have been described for sheep (Bligh, 1961).   Bligh observed occasional spontaneous increases in skin temperature and in the humidity of air passing through a 'sweat cup' that was attached to the skin of the animal.   He attributed these effects to spontaneous discharges of moisture from apocrine sweat glands and to the heat evolved in the exothermic reaction that occurs when wool is wetted.   The transient rises in the skin temperature of the calves were only observed during the initial period of each exposure and were of a lower order of magnitude than those reported for sheep.   This could be due to the hair of cattle having a lower 'heat of wetting' than that of wool or it could be due to the quantity of sweat secreted by cattle being smaller than that secreted by sheep.

SUMMARY

1.   The ventilated capsule method for measuring cutaneous evaporation has been critically analysed. A technique has been developed for eliminating the effect, due to the presence of the capsule, on the rate of cutaneous evaporation. Wet and dry bulb thermocouples have been used with ventilated capsules to provide continuous instantaneous records of cutaneous evaporation from calves.

2.   A mask method has been used to determine respiratory evaporative and metabolic weight losses and heat production of calves.

3.   Insensible weight loss determinations and simultaneous measurements by the capsules and the mask have been used to provide an independent quantitative check on the accuracy of both methods.

4.   The regional distribution of cutaneous evaporation from Ayrshire calves subjected to heat stress has been investigated. Evaporation was greatest on the neck and forequarters of the trunk and also on the rear haunch; evaporation was less on the remaining upper portions of the trunk, still less on the flanks and head and least on the under side of the trunk. This distribution is in broad agreement with those previously reported for a number of other breeds.

5.   A partition has been made of the heat losses from Ayrshire calves exposed to air temperatures between 15 and 40°C. The following conclusions have been drawn:

a)   Heat production is uniform over the entire air

temperature range, except at high temperature high

humidity conditions where it is elevated; this increase

is attributed to the metabolic cost of increased

respiratory movement and to the Van't Hoff effect.

b) The thermal insulation of the tissues is small

compared with that of the skin to air boundary except

at low air temperatures. Blood flow changes therefore

exert little influence on non-evaporative heat loss at

air temperatures above 20°C. At air temperatures below

20°C non-evaporative heat loss is limited by vasocon-

striction in the limbs and in severe heat stress it may

be enhanced by increased flank movement due to respiratory

activity. Between these extremes non-evaporative heat

loss is primarily determined by the insulation of the coat

and the physical conditions of the environment.

c) Respiratory evaporation contributes only a small

proportion to the total evaporative heat loss under

conditions of heat stress. There is some evidence that

expired air, except at the lowest air temperature employed,

is always 90 to 100% saturated with moisture at body

temperature. The presence of the mask is, however,

believed to have limited respiratory evaporation to nearly

one half of the normal amount. It is suggested that mask

methods of respiratory analysis must seriously affect

respiratory gaseous exchange unless the dead space is

kept extremely small.

d) Cutaneous evaporation is the major means of heat loss

under conditions of heat stress. It is quantitatively

controlled by physiological means to such a level that
it always makes up the difference between heat production
and the other forms of heat loss.   Physiological control
of cutaneous evaporation is thus effective in overcoming
the physical limitation of evaporation by the environment,
except at conditions combining high temperature and high
humidity.

6.   The effects of short term (duration 20 min) alterations
in ambient humidity on body temperature, respiratory rate
and on cutaneous evaporation have been compared with the
effects of day-to-day humidity alterations of similar
magnitude.   Rectal temperature was unaffected by the short
term variations in humidity, and cutaneous evaporation fell
with increasing humidity as would be expected of evapor-
ation from an inanimate surface.   These results, together
with other cutaneous evaporation measurements obtained with
capsules ventilated at different rates and placed over
clipped and unclipped skin regions, point to the following
conclusion:-   Except under extreme conditions, the
physical properties of the environment can directly affect
the rate of cutaneous evaporation only from local skin
areas or for relatively short periods.

7.   Measurements of cutaneous evaporation, respiratory
rate and body temperatures have been made on Ayrshire
calves exposed to hot dry environments at ages of 10 to
34 weeks.   Cutaneous evaporation rose for most of this
ageing period but there was some evidence of a maximum
rate being attained at approximately 30 weeks old.

Cutaneous evaporation under these conditions was negatively correlated with respiratory rate and with skin and rectal temperatures. The increasing heat tolerance of calves as they grew older was due partly to a rising capacity for cutaneous evaporation. The results, however, do not of themselves distinguish as to whether the observed changes are attributable to increasing age alone or whether seasonal effects are also involved.

8.   The results of cutaneous evaporation measurements on nine Ayrshire calves have been compared and some evidence has been found that a high level of heat tolerance is associated with high evaporative capacity. Reasons are suggested as to how this finding may be reconciled with the converse statement which has been reported for comparisons between different breeds.

9.   From the quantitative measurements of cutaneous evaporation, from the fluctuating nature of cutaneous evaporation under certain circumstances and from evidence in the literature it has been concluded that the sweat glands of cattle are functional.

10.   The results have been briefly discussed in relation to the possible sites of the thermal receptors that provide afferent stimulus for the physiological control of cutaneous evaporation.

APPENDIX I

Detailed Results of Experiment C.

Animal	196						197				199				
Date	13/11	16/11	11/11	4/11	9/11	20/11	17/11	11/12	14/12	4/12	23/11	27/11	18/12	30/11	7/12
Air temp. D.B. °C	20.5	25.3	30.5	34.4	40.6	15.9	25.5	30.0	35.0	39.9	15.7	25.2	29.7	34.9	41.2
Air temp. W.B. °C	16.1	17.7	23.7	24.6	26.7	10.2	17.8	23.3	24.7	26.6	10.2	17.6	23.2	25.5	26.9
Rectal temp. °C	38.4	38.4	38.6	38.7	39.9	39.7	38.8	39.1	39.3	40.5	38.3	38.6	39.2	39.8	40.4

Evaporation rates from right hand side regions ($g/m^2.hr.$).

Region	13/11	16/11	11/11	4/11	9/11	20/11	17/11	11/12	14/12	4/12	23/11	27/11	18/12	30/11	7/12
Dewlap	15	56	114	139	175	5	53	130	170	193	3	18	98	150	155
Fore haunch	13	52	131	125	197	3	19	86	124	122	7	17	92	114	127
Shoulder	8	47	89	123	154	5	12	74	131	216	9	14	86	69	83
Neck	9	51	100	98	146	7	13	60	117	134	6	9	63	63	63
Back thoracic	8	49	127	114	147	6	7	27	56	107	10	8	22	18	54
Fore flank	12	36	88	-	154	6	7	26	57	67	8	15	55	49	51
Rear haunch	14	42	79	98	128	6	11	39	59	69	6	9	45	22	45
Rear mid flank	10	26	80	-	131	10	10	36	46	87	9	8	21	9	34
Back lumbar	6	27	53	78	127	5	7	25	44	87	7	7	20	15	37
Back sacral	5	15	49	71	117	4	6	33	61	101	3	3	15	12	25
Mid flank	8	24	88	75	103	6	7	20	29	75	7	4	18	11	39
Rear lower flank	12	36	65	-	95	8	-	17	24	27	10	9	33	39	53
Cheek	10	23	39	-	-	6	10	16	42	85	7	10	8	16	19
Rear leg	17	30	42	21	44	10	18	43	53	54	7	9	37	18	34
Forehead	11	10	24	37	27	7	24	41	53	48	9	26	28	26	43
Mid lower flank	8	20	60	36	87	7	11	13	8	17	4	6	5	7	16
Rear belly	18	18	15	15	21	7	-	11	11	25	7	9	15	7	25
Mid belly	13	11	14	11	21	8	14	10	12	16	6	7	6	11	-10
Left mid flank	7	20	74	87	100	5	4	17	38	72	4	4	15	10	35

APPENDIX II

Detailed Results of Experiment D

Results are given for the following quantities:

Env.   Nominal environmental conditions.

An.   Animal.

No.   Exposure number.

D.B.   Room dry bulb temperature, °C.

W.B.   Room wet bulb temperature, °C.

V.P.   Room vapour pressure, mm Hg.

T_r Rectal temperature, °C.

T_s Skin temperature, °C.

R   Respirations per minute.

V_t Tidal volume, litres.

V   Volume of dry air expired, l./hr at s.t.p.

y_o Percentage of carbon dioxide in dry expired air
         (by volume).

B Th   Back thoracic   )

M F   Mid flank   )   Rate of cutaneous

R L   Rear leg   )   evaporation from

M B   Mid belly   )   each region and

D   Dewlap   )   mean rate from

Sh   Shoulder   )   all six regions $(g/m^2 .hr)$.

Mean   )

W   Body weight, kg.

A   Body surface area, m^2.

E_s Weight loss by cutaneous evaporation, g/hr.

E_r Weight loss by respiratory evaporation, g/hr.

W_m Metabolic weight loss, g/hr.

Sum	$E_s + E_r + W_m$, g/hr.
W_t	Total insensible weight loss, g/hr.
H_p	Heat production, kcal/hr.
H_e	Total evaporative heat loss, kcal/hr.
H_s	Heat storage, kcal/hr.
H_n	Non-evaporative heat loss, kcal/hr.

The values quoted for weight loss by respiratory evaporation are all calculated by the direct method. The values quoted for total evaporative heat loss at environments 30, 35L, 35M and 40 are based on respiratory evaporation calculated by the direct method. The mean values quoted for total evaporative heat loss at environments 15, 20, 25 and 35H are based on respiratory evaporation calculated by the difference method; these values are each marked by an asterisk. The double asterisks indicate exposures for which the data are incomplete; the results for these exposures are excluded from average values of all heat losses, weight losses, body temperatures and respiratory quantities.

Appendix II (cont.)

Env.	An.	No.	Details of environment			Body temps.		Respiratory quantities			
			D.B.	W.B.	V.P.	T_r	T_s	R	V_t	V	y_o
	210	1	15·2	11·4	8·2	38·43	30·16	29	0·94	1500	2·94
		2	15·6	11·6	8·2	38·03	30·02	24	1·23	1550	2·99
		3	15·5	11·7	8·4	37·66	28·31	20	1·22	1350	3·12
		Av	15·4	11·6	8·3	38·04	29·50	24	1·13	1460	3·02
	221	1	16·1	11·8	8·2	38·57	-	22	-	-	2·82**
15		2	15·9	11·8	8·3	38·40	28·93	23	0·98	1220	2·74
		3	15·6	11·8	8·5	38·09	-	17	1·36	1260	2·93
		4	15·6	11·6	8·2	38·09	28·52	16	1·40	1240	3·04
		Av	15·7	11·7	8·3	38·19	28·72	19	1·25	1240	2·90
	226	1	15·7	11·7	8·3	38·61	31·10	23	0·65	830	2·94
		2	15·6	11·7	8·4	38·72	-	22	1·22	1440	3·12
		3	15·5	11·7	8·4	38·52	28·11	14	1·06	820	3·35**
		Av	15·6	11·7	8·4	38·66	31·10	22	0·94	1140	3·03
	Average		15·6	11·7	8·3	38·30	29·77	22	1·10	1280	2·98
	210	1	20·4	13·5	8·2	38·20	32·11	30	0·97	1560	2·60
		2	21·2	13·9	8·3	38·13	31·88	26	1·20	1640	2·72
		3	20·5	13·7	8·4	38·17	31·53	24	1·45	1880	2·96
		Av	20·7	13·7	8·3	38·17	31·84	27	1·21	1700	2·76
	221	1	21·4	14·1	8·4	38·20	32·07	26	-	-	2·50**
20		2	21·0	13·9	8·4	38·20	31·92	29	0·87	1350	2·45
		3	20·3	13·6	8·3	38·06	29·93	22	1·09	1300	2·56**
		4	20·3	13·6	8·3	38·37	30·96	22	1·17	1340	2·84
		Av	20·6	13·8	8·4	38·28	31·44	25	1·02	1350	2·64
	226	1	20·6	13·7	8·3	38·61	-	32	0·87	1500	2·56**
		2	20·3	13·6	8·3	38·64	31·80	23	0·95	1180	2·92
		3	20·4	13·6	8·3	38·42	30·35	20	1·15	1240	2·97
		Av	20·4	13·6	8·3	38·53	31·08	22	1·05	1210	2·94
	Average		20·6	13·7	8·3	38·33	31·45	25	1·09	1420	2·78

Appendix II (cont.)

Env.	An.	No.	Details of environment D.B.	W.B.	V.P.	Body temps. T_r	T_s	Respiratory quantities R	V_t	V	y_o
	210	1	26·0	15·6	8·1	38·32	–	33	0·93	1640	2·35
		2	26·2	15·9	8·4	38·23	33·35	29	1·04	1580	2·53
		3	25·2	15·3	8·1	38·13	–	24	1·27	1570	2·76
		Av	25·8	15·6	8·2	38·23	33·35	29	1·08	1600	2·55
	221	1	25·7	15·5	8·1	38·56	35·25	33	–	–	2·26**
		2	26·1	15·8	8·3	38·63	33·89	30	0·74	1190	2·42
25		3	25·3	15·3	8·0	38·56	34·24	32	0·98	1630	2·54
		4	25·2	15·3	8·1	38·55	–	26	0·99	1360	2·68
		Av	25·5	15·5	8·1	38·58	34·06	30	0·90	1390	2·55
	226	1	25·2	15·3	8·1	38·73	35·00	40	0·76	1570	2·19
		2	25·4	15·3	8·0	38·76	34·40	29	0·93	1390	2·52**
		3	25·3	15·4	8·2	38·61	34·31	25	0·94	1210	2·71
		Av	25·2	15·4	8·2	38·67	34·66	32	0·85	1390	2·45
	Average		25·5	15·5	8·2	38·49	34·02	30	0·94	1460	2·52
	210	1	30·0	17·1	8·2	38·63	36·25	36	1·09	2040	2·34
		2	30·9	17·4	8·2	38·37	34·88	40	1·14	2310	2·24
		3	30·3	17·0	7·9	38·20	35·91	34	1·08	1840	2·22
		Av	30·4	17·2	8·1	38·40	35·68	36	1·10	2060	2·27
	221	1	30·2	17·1	8·1	38·47	36·17	40	0·67	1370	2·08
		2	30·8	17·4	8·2	39·00	36·44	36	0·79	1480	2·24
30		3	30·4	17·3	8·3	38·43	35·81	33	1·00	1700	2·29
		4	30·3	17·1	8·0	38·44	–	34	1·01	1740	2·25
		Av	30·4	17·2	8·2	38·58	36·14	36	0·87	1570	2·22
	226	1	30·2	17·0	7·9	39·00	36·81	42	0·73	1570	2·04
		2	30·3	17·2	8·2	38·77	36·26	45	0·84	1920	1·94
		3	30·1	17·0	8·0	38·80	–	48	0·87	2130	1·95
		Av	30·2	17·1	8·0	38·86	36·54	45	0·81	1870	1·98
	Average		30·3	17·2	8·1	38·61	36·12	39	0·93	1840	2·16

Appendix II (cont.)

Env.	An.	No.	D.B.	W.B.	V.P.	T_r	T_s	R	V_t	V	$\dot{y}_o$
	210	1	35·5	18·9	8·1	38·60	37·40	41	1·12	2370	2·34
		2	35·0	18·8	8·2	38·57	36·92	42	1·03	2190	2·12
		3	35·1	18·6	7·8	38·51	37·42	35	1·09	1920	2·25
		Av	35·2	18·8	8·0	38·56	37·25	39	1·08	2160	2·24
	221	1	35·3	18·8	8·0	39·08	37·89	65	0·64	2110	1·88
		2	35·4	18·9	8·1	38·63	37·30	37	-	-	2·11**
35L		3	35·3	19·6	9·3	38·74	37·26	34	0·93	1610	2·22
		4	35·0	18·7	8·0	38·82	37·62	41	0·98	2030	2·13
		Av	35·2	19·0	8·4	38·88	37·59	47	0·85	1920	2·08
	226	1	35·4	18·7	7·8	39·31	37·80	70	0·67	2330	1·78
		2	35·5	19·3	8·7	39·23	37·21	55	0·80	2230	1·90
		3	34·9	18·7	8·1	39·14	37·67	51	0·76	1930	1·85
		Av	35·3	18·9	8·2	39·23	37·56	58	0·74	2170	1·84
	Average		35·2	18·9	8·2	38·89	37·47	48	0·89	2080	2·05
	210	1	40·4	20·3	7·8	38·46	38·47	31	-	-	2·29**
		2	40·3	20·4	8·0	38·75	38·74	78	0·98	3860	1·48
		3	40·3	20·4	8·0	38·50	38·20	33	1·17	1920	2·24
		Av	40·3	20·4	8·0	38·62	38·47	55	1·08	2890	1·86
	221	1	-	-	-	-	-	-	-	-	1·81**
		2	40·0	19·9	7·4	38·36	38·10	46	0·67	1550	1·99
40		3	40·3	20·8	8·7	38·84	38·40	50	0·88	2220	1·88
		4	40·2	20·3	7·9	39·00	39·00	55	0·83	2250	1·84**
		Av	40·2	20·4	8·0	38·60	38·25	48	0·78	1880	1·94
	226	1	40·3	20·4	8·0	39·54	39·32	84	0·65	2680	1·33
		2	40·4	20·9	8·8	39·11	38·64	64	0·64	2030	1·46
		3	40·5	20·3	7·8	39·68	39·40	89	0·74	3260	1·39
		Av	40·4	20·5	8·2	39·44	39·12	79	0·68	2660	1·39
	Average		40·3	20·4	8·1	38·89	38·61	61	0·85	2480	1·73

Appendix II (cont.)

Env.	An.	No.	Details of environment			Body temps.		Respiratory quantities			
			D.B.	W.B.	V.P.	T_r	T_s	R	V_t	V	$\dot{y}_o$
35M	210	1	35·1	25·3	19·3	38·81	37·46	42	1·09	2300	2·16**
		2	35·0	25·2	19·1	38·52	37·34	47	1·14	2720	1·91
		3	35·5	25·5	19·5	38·53	37·18	38	1·40	2600	2·40
		Av	35·2	25·4	19·3	38·52	37·26	42	1·27	2660	2·16
	221	1	35·4	25·3	19·1	39·00	37·82	68	0·71	2460	1·52
		2	35·1	25·4	19·5	38·80	37·53	57	0·76	2180	1·84
		3	34·6	25·3	19·5	38·78	37·85	58	0·99	2880	1·78
		4	35·3	25·5	19·6	38·79	37·46	49	0·94	2300	1·74
		Av	35·1	25·4	19·4	38·84	37·66	58	0·85	2450	1·72
	226	1	35·3	25·6	19·8	39·26	37·99	61	0·68	-	- **
		2	35·2	25·5	19·6	38·95	37·65	55	0·75	2090	1·70
		3	35·0	25·4	19·5	39·13	38·08	75	0·69	2590	1·27
		Av	35·1	25·4	19·6	39·04	37·86	65	0·72	2340	1·48
	Average		35·1	25·4	19·4	38·80	37·59	55	0·95	2490	1·79
35H	210	1	35·5	32·3	34·7	39·26	38·27	101	0·96	4840	1·11
		2	35·4	32·7	35·8	39·22	38·35	85	1·11	4760	1·37
		3	34·5	32·3	35·2	38·75	38·01	70	1·18	4090	1·51
		Av	35·1	32·4	35·2	39·08	38·21	85	1·08	4560	1·33
	221	1	35·5	32·3	34·7	39·50	38·15	114	0·67	3800	1·07
		2	35·2	32·6	35·6	39·82	38·74	125	0·86	5400	1·00
		3	34·8	32·0	34·3	39·16	38·40	62	0·82	2520	1·49
		4	35·4	32·1	34·2	39·77	37·62	119	0·88	5180	1·02
		Av	35·2	32·2	34·7	39·56	38·23	105	0·81	4230	1·14
	226	1	34·7	32·2	34·8	39·95	38·47	142	0·72	5110	0·94
		2	34·9	31·9	34·0	39·74	38·00	89	0·80	3510	1·27
		3	35·4	32·1	34·2	39·61	38·13	104	0·80	4100	1·16
		Av	35·0	32·1	34·3	39·77	38·20	112	0·77	4240	1·12
	Average		35·1	32·2	34·7	39·47	38·21	101	0·89	4340	1·20

Appendix II (cont.)

Env.	An.	No.	B Th	M F	R L	M B	D	Sh	Mean	W	A
	210	1	9	10	12	10	11	12	10·8	123	2·22
		2	9	10	15	9	11	9	10·4	135	2·34
		3	9	12	17	17	12	13	13·4	149	2·47
		Av	9	11	15	12	11	11	11·5		
	221	1	6	10	12	10	10	8	9·2	97	1·94
		2	6	12	13	13	10	8	10·4	104	2·03
15		3	8	12	13	11	8	10	10·3	126	2·25
		4	12	16	9	8	13	13	11·8	136	2·35
		Av	8	12	12	10	10	10	10·4		
	226	1	12	14	18	9	16	13	13·7	96	1·93
		2	22	18	15	12	15	23	17·6	111	2·09
		3	16	16	11	12	13	21	15·0	114	2·13
		Av	17	16	15	11	15	19	15·4		
	Average		11	13	14	11	12	13	12·4		
	210	1	8	9	17	15	11	10	11·7	128	2·27
		2	12	12	11	13	11	13	12·0	138	2·37
		3	12	18	34	13	13	14	17·3	153	2·51
		Av	10	13	21	14	12	12	13·7		
	221	1	7	12	19	6	10	8	10·2	94	1·91
		2	10	12	29	13	12	10	14·3	106	2·04
20		3	9	14	21	13	8	14	13·2	123	2·22
		4	14	14	15	0	12	12	11·2	139	2·38
		Av	10	13	21	8	10	11	12·2		
	226	1	26	25	34	13	27	33	26·2	97	1·95
		2	37	29	21	11	15	31	24·0	107	2·06
		3	28	23	19	10	15	19	19·1	116	2·15
		Av	30	26	25	11	19	28	23·1		
	Average		17	17	22	11	14	17	16·3		

Appendix II (cont,)

Env.	An.	No.	Rates of cutaneous evaporation							Body weight and area	
			B Th	M F	R L	M B	D	Sh	Mean	W	A
	210	1	24	14	56	26	14	17	25·2	132	2·31
		2	30	14	46	25	35	33	30·5	141	2·40
		3	22	14	42	9	12	25	20·8	152	2·50
		Av	25	14	48	20	20	25	25·5		
	221	1	14	24	45	13	27	32	25·9	95	1·92
		2	16	17	65	28	17	21	27·3	104	2·02
25		3	21	21	42	19	25	38	27·7	127	2·26
		4	35	35	20	0	18	41	24·8	135	2·34
		Av	22	24	43	15	22	34	26·4		
	226	1	32	32	40	15	40	38	32·9	96	1·93
		2	42	32	-	13	-	40	-	107	2·05
		3	31	30	72	14	33	35	35·9	116	2·14
		Av	35	32	56	14	36	38	34·4		
	Average		27	23	49	16	26	32	28·8		
	210	1	68	46	185	49	80	66	82·4	133	2·32
		2	44	50	127	37	71	60	64·8	147	2·46
		3	26	26	78	17	55	84	47·8	151	2·49
		Av	46	41	130	34	69	70	65·0		
	221	1	46	54	108	28	61	66	60·5	97	1·94
		2	77	56	146	49	53	89	78·3	114	2·13
30		3	84	76	72	19	46	102	66·6	125	2·24
		4	120	70	46	0	53	104	65·6	137	2·36
		Av	82	64	93	24	53	90	67·8		
	226	1	98	64	70	19	61	86	66·5	98	1·95
		2	70	74	113	15	73	52	66·0	107	2·05
		3	77	52	79	13	116	93	71·8	115	2·14
		Av	82	64	87	16	83	77	68·1		
	Average		70	56	103	25	68	79	67·0		

Appendix II (cont.)

Env.	An.	No.	Rates of cutaneous evaporation							Body weight and area	
			B Th	M F	R L	M B	D	Sh	Mean	W	A
	210	1	134	90	215	68	127	158	131·9	133	2·32
		2	76	87	130	78	96	120	97·8	146	2·44
		3	58	90	165	15	121	109	92·9	148	2·47
		Av	89	89	170	54	115	129	107·5		
	221	1	113	120	165	39	127	120	113·9	102	2·00
		2	109	89	139	74	76	122	101·5	108	2·07
35 L		3	144	98	61	31	78	137	91·4	128	2·27
		4	196	108	53	18	101	154	105·1	136	2·35
		Av	141	104	104	40	96	133	103·0		
	226	1	144	118	122	27	101	150	110·3	99	1·97
		2	108	90	140	24	120	131	102·2	111	2·10
		3	142	97	52	19	110	135	92·4	120	2·19
		Av	131	102	105	23	110	139	101·6		
	Average		120	98	126	39	107	134	104·0		
	210	1	206	144	205	125	141	218	173·1	132	2·31
		2	154	140	106	52	213	172	139·4	149	2·47
		3	111	124	169	23	190	163	130·1	152	2·50
		Av	157	136	160	67	181	184	147·5		
	221	1	157	167	–	–	–	–	–	100	1·98
		2	170	129	169	65	110	160	133·8	110	2·08
40		3	211	168	123	26	150	205	147·2	131	2·30
		4	231	158	70	15	147	199	136·7	138	2·37
		Av	192	156	121	35	136	188	139·2		
	226	1	180	139	162	31	151	162	137·4	96	1·93
		2	195	148	188	30	201	192	158·9	108	2·06
		3	203	162	95	22	193	197	145·2	123	2·22
		Av	192	149	148	28	182	184	147·2		
	Average		180	147	143	43	166	185	144·6		

Appendix II (cont.)

Env.	An.	No.	Rates of cutaneous evaporation							Body weight and area	
			B Th	M F	R L	M B	D	Sh	Mean	W	A
	210	1	117	84	–	69	–	147	–	135	2·34
		2	106	100	66	61	184	134	108·4	146	2·45
		3	132	90	118	17	125	129	101·7	155	2·53
		Av	118	91	92	49	154	137	105·0		
	221	1	119	116	149	59	107	115	110·8	97	1·95
		2	130	96	100	40	75	115	92·7	111	2·09
35M		3	172	142	106	16	136	144	119·3	135	2·34
		4	154	122	66	6	119	157	104·0	133	2·32
		Av	144	119	105	30	109	134	106·7		
	226	1	113	89	104	18	94	109	87·8	103	2·01
		2	149	118	122	19	151	118	112·9	110	2·08
		3	130	91	70	10	146	164	101·8	117	2·16
		Av	131	100	99	16	130	130	100·8		
	Average		131	103	99	32	131	134	104·2		
	210	1	116	78	118	61	118	103	98·9	134	2·33
		2	88	70	76	21	92	94	73·6	147	2·46
		3	90	82	77	23	93	82	74·3	154	2·52
		Av	98	77	90	35	101	93	82·3		
	221	1	82	86	98	52	136	85	89·8	96	1·93
		2	93	80	92	42	103	88	82·9	115	2·14
35H		3	95	75	62	14	94	88	71·3	130	2·29
		4	106	77	59	15	105	106	78·1	141	2·40
		Av	94	79	78	31	110	92	80·5		
	226	1	86	74	91	28	91	87	76·1	101	1·99
		2	111	81	106	27	103	102	88·3	113	2·12
		3	110	82	51	23	90	125	80·1	123	2·22
		Av	102	79	83	26	95	105	81·5		
	Average		98	78	84	31	102	97	81·4		

Appendix II (cont.)

Env.	An.	No.	Weight losses					Heat exchange			
			E_s	E_r	W_m	Sum	W_t	H_p	H_e	H_s	H_n
	210	1	24	7	15	46	57	239		12	
		2	24	8	26	57	62	224		-10	
		3	33	6	22	61	82	207		0	
		Av	27	7	21	55	67	223		1	
	221	1	18	-	-	-	44	-		- 9	**
		2	21	6	17	45	44	164		3	
15		3	23	6	11	40	60	202		- 7	
		4	28	6	18	52	67	188		-15	
		Av	24	6	16	46	57	185		- 6	
	226	1	26	4	11	41	65	126		0	
		2	37	6	24	67	81	222		6	
		3	32	4	13	49	-	139		- 3	**
		Av	32	5	17	54	73	174		3	
	Average		28	6	18	52	66	194	29*	- 1	166*
	210	1	27	16	20	63	87	201		6	
		2	28	17	22	67	78	223		1	
		3	43	18	30	92	118	270		-13	
		Av	33	17	24	74	94	231		- 2	
	221	1	20	-	-	-	52	-		1	**
		2	29	14	16	59	75	164		-19	
20		3	30	12	12	53	-	178		-17	**
		4	27	13	21	60	104	185		25	
		Av	28	13	18	60	90	175		3	
	226	1	51	14	14	80	-	204		0	**
		2	49	10	13	73	81	182		3	
		3	41	12	17	70	78	188		1	
		Av	45	11	15	71	80	185		2	
	Average		35	14	19	68	88	197	41*	1	155*

Appendix II (cont.)

Env.	An.	No.	Weight losses					Heat exchange			
			E_s	E_r	W_m	Sum	W_t	H_p	H_e	H_s	H_n
	210	1	58	28	19	104	117	191		14	
		2	73	28	19	120	111	200		- 1	
		3	52	25	18	95	132	223		0	
		Av	61	27	19	106	120	205		4	
	221	1	50	-	-	-	111	-		-13	**
		2	55	20	11	87	96	150		19	
25		3	63	26	18	107	140	211		- 7	
		4	58	22	15	96	89	188		0	
		Av	59	23	15	96	108	183		4	
	226	1	64	25	16	105	110	172		2	
		2	-	22	14	-	120	181		27	**
		3	77	20	19	116	130	156		14	
		Av	70	23	17	110	120	164		8	
	Average		63	24	17	104	116	184	60*	5	118*
	210	1	191	47	27	265	272	226	148	9	70
		2	159	51	28	239	274	248	130	0	118
		3	119	42	11	173	175	226	100	2	124
		Av	156	47	22	226	240	234	126	4	104
	221	1	117	30	14	162	194	140	91	2	46
		2	167	32	18	217	204	159	124	8	27
30		3	149	37	13	199	213	209	115	5	89
		4	155	39	24	217	221	181	120	0	61
		Av	147	34	17	198	208	172	112	4	56
	226	1	130	37	12	179	174	167	103	7	57
		2	135	44	12	191	237	200	111	11	79
		3	154	49	27	230	194	186	125	12	48
		Av	140	43	17	200	202	184	113	10	61
	Average		148	42	19	208	217	197	117	6	74

Appendix II (cont.)

Env.	An.	No.	Weight losses					Heat exchange				
			E_s	E_r	W_m	Sum	W_t	H_p	H_e	H_s	H_n	
	210	1	306	58	33	397	417	258	228	1	29	
		2	239	49	22	310	305	230	180	29	21	
		3	229	48	18	296	291	220	173	12	35	
		Av	258	52	25	334	338	236	194	14	28	
	221	1	228	49	19	296	300	194	173	0	21	
		2	210	-	-	-	249	-	-	-	-	**
35L		3	207	36	18	261	261	176	152	10	14	
		4	247	47	21	314	315	213	184	12	17	
		Av	228	44	19	290	292	195	170	7	17	
	226	1	217	56	22	296	308	196	170	9	17	
		2	214	51	24	289	284	199	166	13	20	
		3	202	47	17	266	273	177	156	10	11	
		Av	211	51	21	284	288	191	164	11	16	
	Average		232	49	22	303	306	207	176	11	21	
	210	1	399	-	-	-	400	-	-	8	-	**
		2	344	90	29	463	538	272	272	-1	1	
		3	325	50	19	394	418	216	237	5	-26	
		Av	335	70	24	429	478	244	255	2	-12	
	221	1	-	-	-	-	224	-	-	-	-	**
		2	279	35	16	329	358	149	199	-5	-45	
40		3	338	49	20	407	414	206	245	-10	-29	
		4	324	53	21	398	-	200	238	33	-71	**
		Av	308	42	18	368	386	178	222	-7	-37	
	226	1	265	70	14	349	346	179	210	10	-41	
		2	328	47	16	391	376	137	237	15	-115	
		3	322	78	28	428	397	201	251	19	-70	
		Av	305	65	20	389	373	172	233	15	-75	
	Average		316	59	20	395	412	198	236	3	-42	

Appendix II (cont.)

Env.	An.	No.	E_s	E_r	W_m	Sum	W_t	H_p	H_e	H_s	H_n	
			Weight losses					Heat exchange				
	210	1	–	42	26	–	340	240	–	–	–	**
		2	265	48	24	337	386	259	188	28	43	
		3	257	51	27	336	393	319	185	3	131	
		Av	261	50	26	336	390	289	186	15	87	
	221	1	216	42	15	273	255	190	155	– 9	44	
		2	194	37	19	250	278	195	139	0	57	
35M		3	280	50	26	356	368	249	198	11	39	
		4	242	42	18	301	296	200	170	2	27	
		Av	233	43	20	295	299	208	165	1	42	
	226	1	177	36	–	–	232	–	128	10	–	**
		2	235	36	13	284	250	185	163	17	4	
		3	220	47	14	280	275	162	160	22	-20	
		Av	228	41	14	282	262	174	161	20	– 8	
	Average		240	45	20	304	317	224	171	12	40	
	210	1	230	45	21	297	288	266		24		
		2	181	37	36	253	295	302		38		
		3	187	27	21	235	297	323		6		
		Av	200	36	26	262	293	297		23		
	221	1	173	34	15	222	191	204		17		
		2	178	42	28	247	246	248		-3		
35H		3	163	20	13	196	211	196		16		
		4	188	50	31	269	248	231		24		
		Av	175	37	22	234	224	220		14		
	226	1	151	34	19	204	174	232		21		
		2	187	28	22	237	257	211		27		
		3	178	40	29	247	214	210		40		
		Av	172	34	24	229	215	218		29		
	Average		182	36	24	242	244	245	129*	22	94*	

APPENDIX III

Detailed Results of Experiment E

Calf 219

'Month'	Day	B S	B Th	R H	M B	M F	N	Ch	D	Av	T_r	T_s	Respirations per min.
					Rates of cutaneous evaporation (g/m².hr)						Temp. °C		
1	1	19	33	21	14	17	27	18	37	23·2	40·09	39·4	182
	2	27	28	39	38	17	23	16	45	29·1	40·50	40·1	213
	3	19	26	23	24	18	25	18	21	21·8	40·68	40·0	-
	Av	22	29	28	25	17	25	17	34	24·7	40·42	39·8	198
2	1	39	80	104	3	41	95	65	50	59·6	40·08	39·6	182
	2	55	88	83	5	60	110	57	66	65·5	39·70	39·2	172
	3	69	124	113	11	56	98	54	37	70·2	39·67	39·2	169
	Av	54	97	100	6	52	101	59	51	65·1	39·82	39·3	174
3	1	86	116	130	6	65	128	46	64	80·1	39·37	38·7	122
	2	84	95	147	11	58	154	54	103	88·2	39·25	38·7	117
	3	103	82	131	0	62	136	58	71	80·4	38·84	38·5	102
	Av	91	98	136	6	62	139	53	79	82·9	39·15	38·6	114
4	1	99	105	150	12	51	120	38	79	81·8	39·28	38·7	117
	2	113	94	151	11	60	148	41	120	92·2	38·96	38·6	110
	3	116	114	153	10	65	142	32	110	92·8	39·10	38·4	88
	Av	109	104	151	11	59	137	37	103	88·9	39·11	38·6	105
5	1	99	103	144	28	73	108	36	89	85·0	38·92	38·0	115
	2	117	101	143	33	90	138	44	114	97·5	38·98	38·2	98
	3	117	113	137	26	88	109	35	110	91·9	38·64	38·0	69
	Av	111	106	141	29	84	118	38	104	91·5	38·85	38·1	94
6	1	131	121	151	17	107	164	80	147	114·8	39·05	38·2	98
	2	115	143	141	21	129	149	68	83	106·1	39·10	38·0	84
	3	129	175	142	22	106	156	62	110	112·8	38·68	38·1	62
	Av	125	146	145	20	114	156	70	113	111·2	38·94	38·1	81
7	1	138	137	133	25	131	174	76	126	117·5	38·97	37·8	63
	2	136	141	147	25	84	179	85	125	115·2	38·96	38·1	52
	3	154	155	154	22	130	161	63	131	121·2	38·70	37·8	52
	Av	143	144	145	24	115	171	75	127	118·0	38·88	37·9	56

Appendix III (cont.)

Calf 220

'Month'	Day	Rates of cutaneous evaporation (g/m².hr)									Temp. °C		Respirations
		B S	B Th	R H	M B	M F	N	Ch	D	Av	T_r	T_s	per min.
1	1	3	27	29	12	14	45	25	82	29·6	39·50	38·9	—
	2	11	49	57	18	45	61	46	60	43·4	39·76	39·2	187
	3	9	40	42	21	30	62	47	44	36·9	39·98	39·4	133
	Av	8	39	43	17	30	56	39	62	36·6	39·75	39·2	160
2	1	10	15	38	9	5	9	13	64	20·4	40·00	39·4	176
	2	13	25	15	11	12	50	32	48	25·8	40·23	39·6	220
	3	17	62	60	10	25	60	36	62	41·5	40·32	39·8	215
	Av	13	34	38	10	14	40	27	58	29·2	40·18	39·6	204
3	1	42	49	78	12	16	30	15	53	36·9	40·08	39·6	205
	2	23	51	99	8	17	48	34	97	47·1	39·72	39·2	184
	3	12	36	65	11	22	40	27	88	37·6	39·90	39·4	161
	Av	26	45	81	10	18	39	25	79	40·5	39·90	39·4	183
4	1	50	65	68	24	37	39	31	93	50·9	39·95	39·0	165
	2	67	62	97	25	50	75	39	88	62·9	39·46	38·8	164
	3	42	50	88	17	46	90	50	92	59·4	39·58	38·8	123
	Av	53	59	84	22	44	68	40	91	57·7	39·66	38·9	151
5	1	72	73	132	22	74	81	65	104	77·9	39·92	38·6	160
	2	73	109	151	24	69	95	57	84	82·8	39·42	38·6	135
	3	96	118	148	23	77	123	68	110	95·4	39·60	38·7	116
	Av	80	100	144	23	73	100	63	99	85·3	39·65	38·6	137
6	1	111	139	127	25	131	144	96	142	114·4	39·22	38·0	73
	2	104	140	132	27	82	145	103	147	110·0	39·10	38·0	88
	3	103	132	144	28	94	135	94	122	106·5	39·38	38·4	72
	Av	106	137	134	27	102	141	98	137	110·3	39·23	38·1	78
7	1	124	168	126	19	139	146	95	106	115·4	38·72	37·8	58
	2	120	147	150	22	146	154	98	147	123·0	39·02	37·8	67
	3	122	128	151	24	103	148	105	126	113·4	39·05	38·2	60
	Av	122	148	142	22	129	149	99	126	117·2	38·93	37·9	62

Appendix III (cont.)

Calf 222

'Month'	Day	Rates of cutaneous evaporation (g/m².hr)									Temp.°C		Respirations per min.
		B S	B Th	R H	M B	M F	N	Ch	D	Av	T_r	T_s	
1	1	85	86	116	7	91	91	50	103	78·6	39·70	38·6	135
	2	89	125	117	12	88	112	59	105	88·4	39·12	38·4	105
	3	62	139	154	11	88	120	72	94	92·5	39·08	38·5	106
	Av	79	117	129	10	89	108	60	101	86·5	39·30	38·5	115
2	1	57	120	146	22	55	101	79	75	81·9	39·10	38·3	77
	2	88	122	152	21	77	101	83	110	94·2	38·57	37·8	55
	3	75	113	142	14	86	125	89	110	94·2	38·53	37·9	66
	Av	73	118	147	19	73	109	84	98	90·1	38·73	38·0	66
3	1	108	94	124	47	65	91	73	113	89·4	38·70	37·6	77
	2	119	105	127	44	74	90	68	126	94·1	38·46	37·5	65
	3	123	123	169	45	102	130	100	147	117·4	38·48	37·7	78
	Av	117	107	140	45	80	104	80	129	100·3	38·55	37·6	73
4	1	115	119	152	33	85	118	104	124	106·2	38·68	37·9	67
	2	140	125	147	41	98	117	105	132	113·1	38·40	37·4	41
	3	148	169	180	53	132	151	115	156	138·0	39·12	38·3	80
	Av	134	138	160	42	105	129	108	137	119·1	38·73	37·9	63
5	1	137	137	182	27	124	145	98	131	122·6	39·02	38·2	49
	2	158	162	164	34	118	149	111	141	129·6	38·77	37·9	70
	3	142	148	171	34	119	157	105	162	129·8	38·72	37·8	45
	Av	146	149	172	32	120	150	105	145	127·3	38·84	38·0	55
6	1	159	168	171	16	123	171	133	119	132·5	39·57	38·4	74
	2	140	168	144	17	126	193	134	116	129·8	39·18	38·4	81
	3	145	169	171	16	129	174	146	140	136·2	39·03	38·3	82
	Av	148	168	162	16	126	179	138	125	132·8	39·26	38·4	79
7	1	104	142	138	10	81	147	92	76	98·8	39·80	38·8	89
	2	129	159	151	12	93	143	91	84	107·8	39·22	38·6	79
	3	116	161	148	14	83	115	87	109	104·1	39·10	38·7	89
	Av	116	154	146	12	86	135	90	90	103·5	39·37	38·7	86
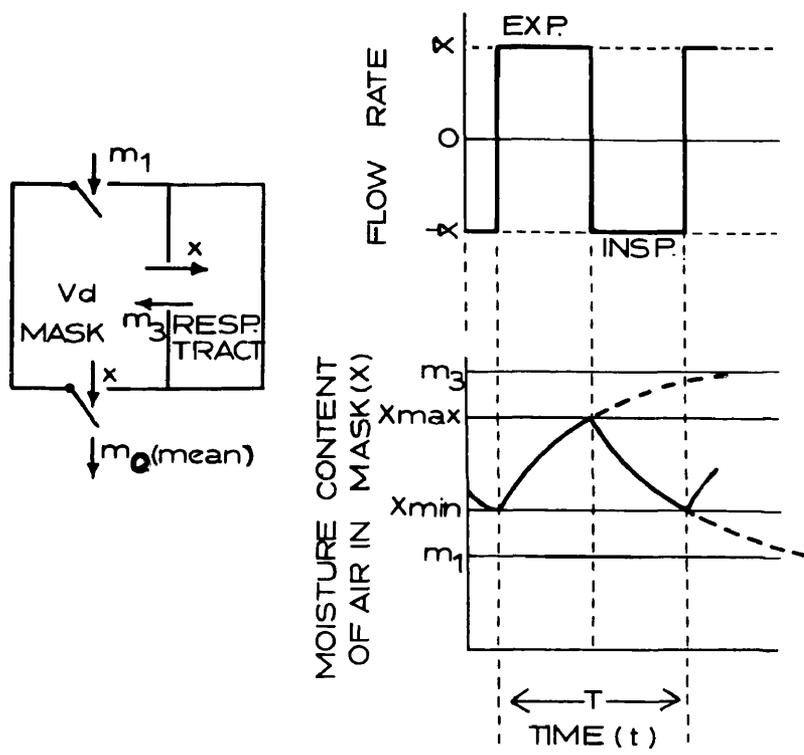
Fig. 31. Theoretical instantaneous inter-relationships between ventilation rate, respiratory volumes and moisture concentrations (see p. 150)

APPENDIX IV

The Humidity Relationships of Expired Air

The following assumptions and approximations are made:-

1. That instantaneous mixing of gas takes place within the mask.

2. That the volumes of inspired and expired air are equal.

3. That the instantaneous rate of gas flow is constant throughout each inspiration and each expiration (i.e. 'square wave' breathing).

Definitions (see Fig. 31):-

α is the instantaneous rate of air flow.

V_t is the tidal volume.

V_d is the ventilated dead space of the mask.

T is the respiratory period (reciprocal of respiratory rate).

m_1 is the moisture content of air entering the mask through the inspiratory valve (constant).

m_o is the mean moisture content of air leaving the mask through the expiratory valve (i.e. after mixing in the flexible tubing).

m_3 is the moisture content of air expired into the mask by the animal (constant).

x is the instantaneous moisture content of the air in the mask.

x_{max} and x_{min} are the limiting values of x attained at the end of each expiration and inspiration respectively.

t is time measured from the beginning of an inspiration or expiration.

$$K = V_t/V_d.$$

$$\text{then } V_t = \frac{\propto T}{2}$$

The basic equations are similar to those used to derive theoretical rates of nitrogen elimination from two lung compartments ventilated in series (Robertson, Siri & Jones, 1950).

For an expiration:-

$$\frac{dx}{dt} = \frac{\propto (m_3 - x)}{V_d} \qquad - - - - - - - - - - - \quad (1)$$

$$\int_0^{T/2} \frac{\propto x dt}{V_t} = m_o \qquad - - - - - - - - - - - \quad (2)$$

From (1), $- \log_e (m_3 - x) = \propto t/V_d + \text{constant}$

The value of the constant can be found by substituting the limiting condition: $x = x_{max}$ at $t = T/2$, hence:

$$x = m_3 - (m_3 - x_{max}) e^{-\propto (t - T/2)/V_d}$$

Substituting this value of x in (2) and integrating:

$$m_o = m_3 + (m_3 - x_{max})(1 - e^K)/K \qquad - - - - - \quad (3)$$

For an inspiration:-

$$\frac{dx}{dt} = \frac{\propto (m_1 - x)}{V_d} \qquad - - - - - - - - - - - \quad (4)$$

$$\int_0^{T/2} \frac{\propto x dt}{V_t} = m_1 + m_3 - m_o \qquad - - - - - - - - - - - \quad (5)$$

From (4), $- \log_e (m_1 - x) = \propto t/V_d + \text{constant}$

The limiting condition is $x = x_{max}$ at $t = o,$

hence $x = m_1 + (x_{max} - m_1) e^{-\alpha t/V_d}$

Substituting this value of x in (4) and integrating:

$$m_o = m_3 - (x_{max} - m_1)(1 - e^{-K})/K \qquad - - - - - - - \quad (6)$$

Eliminating x_{max} from equations (3) and (6) gives:

$$m_o = m_1 + (m_3 - m_1) \left[1 - \frac{1}{K} \frac{(e^K - 1)}{(e^K + 1)}\right]$$

REFERENCES

Albert, R.E. & Palmes, E.D. (1951).   Evaporative rate patterns
from small skin areas as measured by an infrared gas
analyzer.   J. appl. Physiol. 4, 208-214.

Allan, F.E. & Wishart, J. (1930).   A method of estimating the
yield of a missing plot in field experimental work.
J. agric. Sci. 20, 399-406.

Armstrong, D.G., Blaxter, K.L., Clapperton, J.L., Graham, N.McC.
& Wainman, F.W. (1960).   Heat production and heat
emmision of two breeds of sheep.   J. agric. Sci. 55,
395-401.

Beakley, W.R. (1952).   Studies in the Interchange of Heat
between the Bovine and its Environment.   Ph.D. Thesis,
Univ. Glasgow.

Beakley, W.R. & Findlay, J.D. (1955a).   The effect of
environmental temperature and humidity on the rectal
temperature of calves.   J. agric. Sci. 45, 339-352.

Beakley, W.R. & Findlay, J.D. (1955b).   The effect of
environmental temperature and humidity on the skin
temperature of Ayrshire calves.   J. agric. Sci. 45,
353-364.

Beakley, W.R. & Findlay, J.D. (1955c).   The effect of
environmental temperature and humidity on the ear
temperatures of Ayrshire calves.   J. agric. Sci. 45,
373-379.

Benzinger, T.H. (1959).   On physical heat regulation and the
sense of temperature in man.   Proc. nat. Acad. Sci.
Wash. 45, 645-659.

Benzinger, T.H. (1960).   The sensory receptor organ and

quantitative mechanism of human temperature control

in warm environment.   Fed. Proc. 19, 32-41.

Benzinger, T.H. (1961).   The human thermostat.   Sci. Amer.

204, 134-147.

Berman, A. (1957).   Influence of some factors on the relative

evaporation rate from the skin of cattle.   Nature,

Lond. 179, 1256.

Bianca, W. & Findlay, J.D. (1961).   The effect of thermally

induced hyperpnea on the acid-base status of the blood

of calves.   Res. vet. Sci. (In the Press).

Blaxter, K.L., Graham, N.McC., Wainman, F.W. & Armstrong, D.G.

(1959).   Environmental Temperature, Energy Metabolism

and Heat Regulation in Sheep.   II.   The partition of

heat losses in closely clipped sheep.   J. agric. Sci.

52, 25-40.

Blaxter, K.L., Graham, N.McC. & Wainman, F.W. (1959).

Environmental Temperature, Energy Metabolism and Heat

Regulation in Sheep.   III.   The metabolism and

thermal exchanges of sheep with fleeces.   J. agric.

Sci. 52, 41-49.

Blaxter, K.L. & Wainman, F.W. (1961).   Environmental

temperature and the energy metabolism and heat

emission of steers.   J. agric. Sci. 56, 81-90.

Bligh, J. (1957).   The relationship between the temperature

in the rectum and of the blood in the bicarotid trunk

of the calf during exposure to heat stress.   J.

Physiol. 136, 393-403.

Bligh, J. (1961). The synchronous discharge of aprocrine sweat glands of the Welsh mountain sheep. Nature, Lond. 189, 582-583.

Brody, S. (1945). Bioenergetics and Growth. New York: Reinhold Publ. Corp.

Brouwer, E. (1958). Symposium on Energy Metabolism. p. 182-191. Rome: European Ass. Anim. Production.

Buettner, K. (1953). Diffusion of water and water vapor through human skin. J. appl. Physiol. 6, 229-242.

Buettner, K.J.K. (1959a). Diffusion of liquid water through human skin. J. appl. Physiol. 14, 261-268.

Buettner, K.J.K. (1959b). Diffusion of water vapor through small areas of human skin in normal environment. J. appl. Physiol. 14, 269-275.

Buettner, K.J.K. & Hommes, F.F. (1959). Diffusion of water vapor through human skin in a hot environment and with application of atropine. J. appl. Physiol. 14, 276-278.

Ferguson, K.A. & Dowling, D.F. (1955). The function of cattle sweat glands. Aust. J. agric. Res. 6, 640-644.

Findlay, J.D. (1950). The effects of temperature, humidity, air movement and solar radiation on the behaviour and physiology of cattle and other farm animals. Hannah Dairy Res. Inst. Bull. No. 9.

Findlay, J.D. (1957). The respiratory activity of calves subjected to thermal stress. J. Physiol. 136, 300-309.

Findlay, J.D. & Beakley, W.R. (1954). Environmental physiology of farm mammals. In Progress in the Physiology of

<u>Farm Animals</u>, vol. I, p. 252, ed. Hammond, J.
London: Butterworths sci. Publ.

Findlay, J.D. & Yang, S.H. (1950). The sweat glands of
Ayrshire cattle. <u>J. agric. Sci.</u> 40, 126-133.

Findlay, J.D., McLean, J.A. & Bennet, R.D. (1959). A
climatic laboratory for farm animals. <u>Heat Vent.</u>
<u>Engr.</u> 33, 95-100.

Gregory, H.S. & Rourke, E. (1957). <u>Hygrometry.</u> London:
Crosby Lockwood and Son, Ltd.

Gagge, A.P. (1937). A new physiological variable associated
with sensible and insensible perspiration. <u>Amer.</u>
<u>J. Physiol.</u> 120, 277-287.

Hardy, J.D. (1949). Heat transfer. In <u>Physiology of Heat</u>
<u>Regulation and The Science of Clothing</u>, p. 78, ed.
Newburgh, L.H. Philadelphia: W.B. Saunders Co.

Hardy, J.D. & DuBois, E.F. (1938). Basal metabolism, radiation,
convection and vaporization at temperatures of 22 to
35°C. <u>J. Nutr.</u> 15, 477-497.

Hellman, G. (1955). <u>Aspirations - Psychrometer - Tafeln</u>,
3rd ed. Braunschweig: Friedr. Vieweg & Sohn.

Hodgman, C.D. (1939). <u>Handbook of Chemistry and Physics</u>,
23rd ed. Cleveland, Ohio: Chemical Rubber Publishing
Co.

Ingram, D.L., McLean, J.A. & Whittow, G.C. (1961). Increase
of evaporative water-loss from the skin of the ox
in response to local heating of the hypothalamus.
<u>Nature, Lond.</u> (In the Press).

Kibler, H.H. (1957). Energy metabolism and cardiorespiratory

activities in Shorthorn, Santa Gertrudis and Brahman heifers, during growth at 50 and 80°F temperatures. <u>Univ. Mo. agric. Exp. Sta. Res. Bull</u>. No. 643.

Kibler, H.H. (1960). Oxygen comsumption in cattle in relation to rate of increase in environmental temperature. <u>Nature, Lond.</u> <u>186</u>, 972-973.

Kibler, H.H. & Brody, S. (1950). Influence of temperature, 5° to 95°F, on evaporative cooling from the respiratory and exterior body surfaces in Jersey and Holstein cows. <u>Univ. Mo. agric. Exp. Sta. Res. Bull</u>. No. 461.

Kibler, H.H. & Brody, S. (1952). Relative efficiency of surface evaporative, respiratory evaporative, and non-evaporative cooling in relation to heat production in Jersey, Holstein, Brown Swiss and Brahman cattle, 5° to 105°F. <u>Univ. Mo. agric. Exp. Sta. Res. Bull</u>. No. 497.

Kibler, H.H. & Yeck, R.G. (1959). Vaporization rates and heat tolerance in growing Shorthorn, Brahman and Santa Gertrudis calves raised at constant 50° and 80°F temperatures. <u>Univ. Mo. agric. Exp. Sta. Res. Bull</u>. No. 701.

Klemm, G.H. & Robinson, K.W. (1955). The heat tolerance of two breeds of calves from 1 to 12 months of age. <u>Aust. J. agric. Res.</u> <u>6</u>, 350-364.

Knapp, B.J. & Robinson, K.W. (1954). The role of water for heat dissipation by a Jersey cow and a Corriedale

ewe. _Aust. J. agric. Res._ 5, 568-577.

Kriss, M. (1930a). The insensible loss in body weight of
cattle. _J. agric. Res._ 40, 271-281.

Kriss, M. (1930b). Quantitative relations of the dry matter
of the food consumed, the heat production, the
gaseous outgo, and the insensible loss in body
weight of cattle. _J. agric. Res._ 40, 283-295.

Lefèvre, J. & Auguet, A. (1930). Rapports sur le
foncionment des laboratoires de la Station
Central de Recherches sur l'alimentation. I.
Laboratoire de Bioenergétique. _Bull. Soc. Sci._
Hyg. Aliment. 18, 328-339.

List, R.J. (1951). _Smithsonian Meteorological Tables_,
6th ed. Washington: Smithsonian Institution.

Mitchell, H.H. & Hamilton, T.S. (1936). The estimation
of the heat production of cattle from the
insensible loss in body weight. _J. agric. Res._
52, 837-854.

McDowell, R.E., Lee, D.H.K. & Fohrman, M.H. (1954). The
measurement of water evaporation from limited
areas of a normal body surface. _J. Anim. Sci._
13, 405-416.

McDowell, R.E., McMullan, H.F., Wodzika, M., Lee, D.H.K.
& Fohrman, M.H. (1955). Rate of water evaporation
from various areas of a normal body surface and
with sweat glands inactivated under hot conditions.
J. Anim. Sci. 14, 1250.

Mole, R.H. (1948). The relative humidity of the skin.
J. Physiol. 107, 399-411.

Nisbet, W. (1956).   An instrument for measuring respiratory
        rates and volumes.   J. sci. Instrum. 33, 154-158.

Nisbet, W. (1958).   A simple electric respiration counter.
        J. Physiol. 144, 4-5P.

Ragsdale, A.C., Chu Shan Cheng & Johnson, H.D. (1957).
        Effects of constant environmental temperatures of
        50°F and 80°F on the growth responses of Brahman,
        Santa Gertrudis, and Shorthorn calves.   Univ. Mo.
        agric. Exp. Sta. Res. Bull. No. 642.

Randall, W.C., Peiss, C.N. & Hertzman, A.B. (1953).   An
        analysis of the desiccating capsule technique in
        the measurement of regional water losses from the
        skin.   U.S.A.F. Tech. Rep. 6680, Part 14.

Regan, W.M. & Richardson, G.A. (1938).   Reactions of the
        dairy cow to changes in environmental temperature.
        J. Dairy Sci. 21, 73-79.

Rhoad, A.O. (1944).   The Iberia heat tolerance test for
        cattle.   Trop. Agriculture, Trin. 21, 162-164.

Riek, R.F. & Lee, D.H.K. (1948a).   Reactions to hot
        atmospheres of Jersey cows in milk.   J. Dairy Res.
        15, 219-226.

Riek, R.F. & Lee, D.H.K. (1948b).   Reactions of Jersey
        calves to hot atmospheres.   J. Dairy Res. 15,
        227-232.

Robertson, J.S., Siri, W.E. & Jones, H.B. (1950).   Lung
        ventilation patterns determined by analysis of
        nitrogen elimination rates;   use of the mass
        spectrometer as a continuous gas analyzer.   J. clin.

Invest. 22, 577-590.

Robinson, K.W. & Klemm, G.H. (1953). A study of heat
        tolerance of grade Australian Illawarra Shorthorn
        cows during early lactation. Aust. J. agric.
        Res. 4, 224-234.

Scholander, P.F., Hock, R., Walters, V., Johnson, F. &
        Irving, L. (1950). Heat regulation in some artic
        and tropical mammals and birds. Biol. Bull.,
        Wood's Hole. 99, 237-258.

Taneja, G.C. (1958). Cutaneous evaporative losses in calves
        and its relationship with respiratory evaporative
        loss and skin and rectal temperatures. J. agric.
        Sci. 50, 73-81.

Taneja, G.C. (1959). Cutaneous evaporative loss measured
        from limited areas and its relationship with skin,
        rectal, and air temperatures. J. agric. Sci.
        52, 50-61.

Thompson, H.J., Yeck, R.G., Worstell, D.M. & Brody, S. (1954).
        The effect of wind on evaporative cooling and
        surface temperature in dairy cattle. Univ. Mo.
        agric. Exp. Sta. Res. Bull. No. 548.

Villares, J.B. & Berthet, L.A. (1952). Contribuição para
        a demonstração do funcionamento das glândulas
        sudoriparas nos Bos Taurus e Bos Indicus. Bol.
        Industr. anim. 13, 25-36.

Volcani, R. & Schindler, H. (1954). Physiological reactions
        of dairy cows in various seasons and in different
        regions of Israel. Refuah. vet. 11, 174-177.

Whittow, G.C. (1961). The significance of the extremities
of the ox (Bos taurus) in thermoregulation. (In
preparation for submission to J. agric. Sci.)

Winslow, C-E.A., Herrington, L.P. & Gagge, A.P. (1937).
Physiological reactions of the human body to
varying environmental temperatures. Amer. J.
Physiol. 120, 1-22.

Yeck, R.G. & Kibler, H.H. (1956). Moisture vaporization
by Jersey and Holstein cows during diurnal
temperature cycles as measured with a hygrometric
tent. Univ. Mo. agric. Exp. Sta. Res. Bull. No.
600.

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Synopsis

A quantitative analysis has been made of the heat losses from Ayrshire calves subjected in climatic chambers to different environmental conditions. The results have been used to compare the relative influence of the physical and physiological barriers to heat flow. By this means an attempt has been made to assess the limits of effectiveness of the various physiological adjustments to heat stress.

Cutaneous evaporation was measured by means of ventilated capsules. This method was critically analysed and a technique was developed for eliminating the effect, due to the presence of the capsule, on the rate of cutaneous evaporation. Respiratory evaporation and heat production were estimated by means of an open circuit mask method. Simultaneous measurements by the capsule and mask methods were used to assess the total insensible weight loss, which was also estimated by direct weighing, thereby providing an independent check on the accuracy of the methods used. Non-evaporative heat loss was calculated by difference from the other heat exchange measurements.

The heat production of calves was found to be uniform over the air temperature range 15 to 40°C except at conditions combining high temperature and high humidity, where it was slightly elevated. The thermal insulation of the tissues was found to be small compared with that of the skin-to-air boundary except at low temperatures. It was concluded that, at air temperatures above 20°C, the quantity of non-evaporative heat loss from cattle is not appreciably influenced by blood flow changes and is primarily determined by the coat insulation and by the physical properties of the environment. Respiratory evaporation contributed only a small proportion to the total evaporative heat loss even at the highest air temperatures

employed.   There was evidence that, at air temperatures of
20°C and above, the air expired by the animals was always 90 to
100% saturated with moisture at body temperature.   The
presence of the mask, however, is believed to have reduced
respiratory evaporative heat loss to nearly half of the normal
amount.   Cutaneous evaporation was the major means of heat
loss under conditions of heat stress.   It appeared to be
quantitatively controlled by physiological means so that it
tended to a level that made up the difference between heat
production and the other forms of heat loss.   Physiological
control was thus effective in overcoming the physical limitation
of evaporation by the environment.   The physical properties
of the environment appeared to exert direct influence on the
rate of cutaneous evaporation from the animal as a whole only
under extreme conditions or during initial adjustments to sudden
changes in environmental conditions.

The regional distribution of cutaneous evaporation from
Ayrshire calves subjected to heat stress was found to be in
broad agreement with results previously reported for different
breeds by other workers.   Cutaneous evaporation was found to
increase and respiratory rate to decrease from calves subjected
to heat stress as they aged from 10 to 34 weeks.   This was
partially attributed to a developing capacity for cutaneous
evaporation.   The results, however, did not of themselves
distinguish as to whether these observed changes were attributable
to increasing age alone or whether seasonal effects were also
involved.

The results have been discussed in relation to the
importance of cutaneous evaporation as a determinant of heat
tolerance, the functional ability of bovine sweat glands and the
possible sites of the thermal receptors that provide afferent
stimulus for the physiological control of cutaneous evaporation.