NORMAL RESPONSES OF SHEEP TO ACUTE THERMAL STRESS

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
DAVID R. AMES
1968

This is to certify that the

thesis entitled

NORMAL RESPONSES OF SHEEP TO
ACUTE THERMAL STRESS

presented by

David R. Ames

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Animal Husbandry and Physiology

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Date Nov 22, 1968

O-169

ABSTRACT

NORMAL RESPONSES OF SHEEP TO ACUTE THERMAL STRESS

by David Robert Ames

Biothermal responses of sheep to a wide range of thermal environments were studied to: (1) evaluate the influence of the environment on the efficiency of animal production; (2) establish standards of environmental control for semi or completely closed animal management; and (3) extend the study of basic environmental physiology. This study describes physiological responses of defined sheep (i.e., in terms of diet, fleece, size, age, breed and geographic location) exposed to ambient temperatures ranging from 10 to 45° C. Rectal temperature, skin temperatures (ear, face, forelimb, trunk, stifle), metabolic heat production, respiratory rate, respiratory evaporative water loss and cutaneous evaporative water loss were determined. The "normal limits" of rectal temperature in sheep were relatively wide resulting in a substantial Q_{10} effect on physiological reactions. Thermal circulatory indices and changes in skin surface temperatures indicated that the ears, forelimbs and face (characterized by freedom from fleece, high surface area to mass ratio, and overlying areas of little fat or muscle tissue) were capable

of vasomotion and were able to modify sensible heat exchange. Conversely, on these same basis the trunk and stifle areas (characterized by the presence of fleece, low surface area to mass ratio and overlying subcutaneous fat and muscle tissue) were probably incapable of altering skin blood flow and consequently unable to modify sensible heat exchange. Respiratory rate increased logarithmically from critical temperature II (hyperthermal rise) until when ambient temperature equalled rectal temperature. These data suggested that changes in respiratory rate were valid indicators of thermoregulatory mechanisms. Evaluation of panting indices suggested that at rates exceeding 240 breaths per minute, panting became a thermal liability. Comparison of obligatory and observed cutaneous evaporative water loss indicated the presence of active sweating in sheep. It was hypothesized that cutaneous and respiratory evaporative water loss were both important avenues of heat loss in shorn sheep during heat stress. It appeared that respiratory evaporative water loss was relatively more important during mild heat stress (35° C.) but that sweating was relatively more important during severe heat stress (40 and 45° C.). Increases of heat production during cold stress was due to shivering. Increases during heat stress were attributed to respiratory activity of panting but more importantly to the Q_{10} effect. The 5° C. intervals of ambient temperature used did not allow for the accurate determination of critical temperatures. The data suggest that critical temperature I is equal to or greater than 20° C. and that critical temperature II is equal to or less than 30° C. On the basis of physiological responses indicative of heat and cold stress, the lower limit of the thermoneutral zone for sheep (as defined in this experiment) is equal to or greater than 20° C. while the upper limit is equal to or less than 30° C. The use of skin surface temperature to estimate the thermoneutral zone is questioned.

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By

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A Thesis

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Departments of Animal Husbandry and Physiology

1968

ACKNOWLEDGMENTS

The author wishes to express his appreciation to the members of the Departments of Animal Husbandry and Physiology for their contributions leading to the completion of this study. In particular I would like to express my gratitude to Dr. John E. Nellor and Dr. Thomas Adams, my academic and research advisors, respectively, for their assistance throughout the author's doctorate program. Appreciation is extended to Dr. Gail Riegle, Dr. Hugh Henderson, Dr. Harold Henneman, and Dr. Elwin Miller for their counsel.

The author wishes to thank the staff of the Endocrine Research Unit for their cooperation throughout the experimental studies.

The writer is grateful to his wife, Marsha, for her continual support.

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I. INTRODUCTION

Homeotherms are those animals which through complex physiological mechanisms maintain body temperature within narrow limits, even when exposed to varying and stressing thermal environments. Previous investigations describing thermoregulatory mechanisms primarily focused upon man and conventional laboratory animals. A growing interest is developing in the biothermal responses of large domesticated animals. This impetus is attributed to: (1) the importance of the environmental influences on the efficiency of animal production; (2) the impending increase in semi or completely closed animal management that will require standards for environmental control; and (3) the logical extension of basic environmental physiological studies to a greater range of animals.

This study describes the normal biothermal responses of sheep acutely exposed to a range of thermal environments. The sheep was chosen as an experimental animal because: it is (1) an economically important animal; (2) well suited to experimental procedures; (3) exhibits unusual thermal balance problems in the fleeced and shorn condition; and

(4) mechanisms of thermal control in sheep are inadequately described. The experiments in this study were designed to determine the biothermal responses of sheep exposed to a range of ambient temperatures, to establish thermoneutral zones, and critical temperatures for a "well-defined" (i.e., size, breed, sex, fleece, diet, and geographic location) animal exposed to controlled environmental conditions.

II. LITERATURE REVIEW

Mechanisms of thermal control in homeotherms have been widely reviewed (Strom, 1960; vonEuler, 1961; Hardy, 1961; Hammel, 1968). It is tacitly assumed that basic biothermal control in sheep is qualitatively similar to that described for other mammals, although the relative importance of specific avenues of heat exchange and the manner by which body temperature is controlled in sheep is unique to the species.

2.A. Basic Thermoregulation in the Sheep

2.A.1 Thermoneutral Zone

The thermoneutral zone has been defined as the ambient temperature below which heat production and above which heat loss must be increased if a constant internal body temperature is to prevail (Graham *et al*., 1959). Dukes (1956) described the thermoneutral zone for domestic animals (swine, cattle), excluding the sheep because of complexities inherent with the fleece. Diet (Graham *et al*., 1959), tissue insulation (Slee, 1966) and other variables also have been shown to alter the thermoneutral zone in sheep. These

changes have not been qualitatively related to specific environmental conditions.

Thermoneutral temperature for shorn, adult, Down Cross wethers (Blaxter et al., 1959a and Armstrong et al., 1960), adult, Scottish Blackface sheep (Slee and Sykes, 1968) and young lambs (Alexander and Brook, 1960) is reportedly 30° C. (86° F.). Hemingway and Hemingway (1966), using water immersed sheep, suggested 33 to 35° C. (91.4 to 95° F.) as the thermoneutral zone of fasted adult sheep.

2.A.2 Critical Temperatures

The environmental temperature below which an animal must increase its metabolic heat production to avoid hypothermia has been defined as critical temperature (Graham et al., 1959). Blaxter (1962) considers this temperature to be coincident with the environmental temperature where vasoconstriction in response to cold is complete. Graham et al. (1959) reported that critical temperatures of closely clipped sheep on a "medium energy level ration" (1200 gm. dried grass cubes) was 33° C. (86° F.). Further investigation by Graham revealed that the critical temperature changes with diet; rising to 39 to 40° C. (100.2 to 104° F.) with low energy rations (600 gm. dried grass cubes) and falling to 24 to 27° C. (75.2 to 80.6° F.) with high level

rations (1800 gm. dried grass cubes).

The effect of fleece length on the critical temperature of sheep was reported by Armstrong et al. (1960). The critical temperature in shorn adult sheep was 30° C. (86° F.), but values as low as 0° C. (32° F.) were observed in sheep with 10 cm. of fleece. Blaxter (1962) implied that tissue insulation also effects critical temperature, although, specific critical temperatures relating to explicit degrees of insulation were not disclosed. Slee and Sykes (1968) reported that the critical temperature was reduced in cold acclimatized adult sheep.

2.A.3 Rectal Temperature

Numerous mean rectal temperatures have been reported for sheep: Brody (1945), 100 to 103° F. (37.9 to 39.5° C.); Kammlade (1947), 100.9 to 103.8° F. (38.2 to 39.8° C.); Lee (1950), 101.5 to 103.0° F. (38.5 to 39.5° C.); MacFarlane (1964), 37 to 39° C. (98.6 to 102.2° F.). Differences in these values may be due to individual and breed variability; variations in fleece; the ability to produce and conserve heat in cold environments; the efficiency of heat loss in warm environments; and existing environmental conditions.

Rectal temperature is reported to be positively correlated with ambient temperature. Experiments by Knapp and Robinson (1954) showed that the rectal temperature of a Corriedale ewe

increased from 102 to 106° F. (38.9 to 40.2° C.) as ambient temperature rose from 86 to 104° F. (30 to 40° C.). Similarly, Webster (1966) reported a decline in the rectal temperature of sheep when ambient temperature fell below the thermoneutral zone. Webster (1966) reported that rectal temperature rose above thermoneutral zone levels when ambient temperature changed from 5 to 8° C. (41 to 46.4° F.). He explained this as an "overshoot" of metabolic response to cold. Rectal temperature of Cheviot wethers with six weeks growth of wool declined when the ambient temperature decreased from 20 to -11° C. (68 to 12.2° F.) (Bailey, 1964). This supports the findings of Webster (1966) as an "overshoot" of rectal temperature in response to thermal stress.

A characteristic rise in rectal temperature following initial cold exposure has been observed in adult sheep (Joyce and Blaxter, 1964 and Slee, 1966) and in lambs (Alexander, 1961). Slee (1966) suggested that this increase results from an overcompensating rise of metabolic rate coupled with vasomotor changes. Slee and Sykes (1967) noted that rectal temperatures of sheep previously acclimatized at sub-critical temperatures of 8° C. (46.6° F.) were higher than non-cold acclimatized sheep at a thermoneutral temperature (30° C.) (86° F.). Variations in physiological responses were observed among sheep of the same sex, breed, age, and weight

to acute cold exposure. Eyal (1963a) compared rectal temperatures of shorn and unshorn Awassi sheep in the shade versus direct sunlight. When ambient temperature was less than 30° C. (86° F.), deep body temperature was lower in shorn than in unshorn animals. Rectal temperatures rose at a greater rate in fleeced sheep. The deep body temperature of shorn sheep was equal to or greater than fleeced sheep when ambient temperatures were above 30° C. (86° F.). Webster (1966) reported that when environmental temperature was above the critical temperature, rectal temperature of Cheviot and Suffolk sheep increased by 0.5° C./cm. of fleece depth. Blaxter et al. (1959b) stated that fleece length influenced body heat content of sheep.

The effect of relative humidity on rectal temperatures of Awassi sheep was described by Eyal (1963d). The least variation in rectal temperatures between shorn and fleeced individuals occurred at lower humidities.

Blaxter et al. (1965) reported that increased air velocity lowered the insulatory properties of the fleece. Eyal (1963d) reported that wind increases the differences (shorn lower than fleeced) in rectal temperature when ambient temperature is between 24° C. (75.2° F.) and 29° C. (84.2° F.). In direct sunlight, increased wind velocity decreased the effect of direct radiation on the shorn sheep.

2.A.4 Skin Temperature

Skin temperatures in adult sheep vary with the measurement site and depend on the rate of cutaneous blood flow (Webster and Johnson, 1964). Webster and Blaxter (1966) reported that the trunk surface temperature decreased when ambient temperature was reduced from 5 to -10° C. (41 to 14° F.) in Suffolk and Cheviot sheep with varying amounts of fleece. A greater decrease was apparent when ambient temperature was reduced from 30 to 0 to 5° C. (86 to 32 to 41° F.) in shorn sheep, shank surface temperature decreased at a greater rate than did trunk surface temperature (Suffolk and Cheviot sheep do not have wool on the forelimb, ears, or face). The rate of shank surface temperature decline was reduced at sub-freezing temperature; surface temperatures did not fall below 0° C. (32° F.).

Cold induced vasodilation, defined as fluctuating skin temperatures during severe cold stress, has been reported to occur in the limbs of sheep by Webster and Blaxter (1966). The ear exhibited greater cold induced vasodilation than the shank or trunk. The ear had the "hunting reaction" described by Lewis (1930). Temperature changes were so large that a mean ear skin temperature in the cold (below 0° C.) (32° F.) was misleading in view of the wide range of temperatures. The importance of this phenomenon in preventing tissue injury

in cold environments is not clear in sheep.

Blaxter et al. (1959a) related skin surface temperatures to ambient temperatures above 22° C. (69.8° F.). Skin temperatures increased as ambient temperatures increased from 22 to 38° C. (69.8 to 100.4° F.). These workers emphasized the differences between skin temperature responses of areas with insignificant muscle layer (i.e., legs and ears) as compared with the trunk. Ear temperatures remained about 1 to 2° C. (1.8 to 3.6° F.) above environmental temperature until 25 to 27° C. (77 to 80.6° F.). When environmental temperature rose above 25 to 27° C. (77 to 80.6° F.), ear skin temperature increased to 36 to 38° C. (96.8 to 100.4° F.). Further increases in environmental temperature resulted in smaller increases in ear skin temperature. This reportedly reflected opening of artero-venous anastomoses in the ears, and to increased blood flow. These workers concluded that there is increased blood supply to areas without fasical tissue above the thermoneutral zone. Eyal (1963c) reported that as ambient temperatures ranged between 10 to 42° C. (50 to 105.8° F.), skin temperatures varied from 10 to 40° C. (50 to 104° F.) in shorn and from 29 to 40° C. (82.4 to 104° F.) in unshorn adult sheep. During exposure to the sun, skin surface temperatures of shorn sheep reached 47° C. (116.6° F.).

2.A.5 Other Temperature Measurements

Rectal temperature is commonly used as an index of "deep" body temperature. Various temperature measurements in the sheep have been utilized to establish more reliable estimates of "deep" body temperature. Mendal and Raghaven (1964) compared rumen, rectal, skin (at various locations), jugular and subcutaneous tissue temperatures to that of the internal carotid artery. Jugular temperature was more positively correlated with carotid blood temperature than was rectal temperature. Rectal temperature used as an index of mean deep body temperature was criticized since it did not reflect rapid fluctuation in blood temperature. However, since "deep" body temperature is not the same measurement as carotid blood temperatures, it may be a reliable indicator of mean "deep" body temperature, in that it "sums" the effects of minor regional temperature changes in the main body mass.

2.A.6 Respiratory Frequency

Numerous authors (Lee and Robinson, 1941; Miller and Monge, 1946; Riek _et_ _al_., 1950; Lee, 1950; Knapp and Robinson, 1954; and others) have reported marked increases in respiratory rate in heat exposed sheep. Values of 200 breaths per minute were reported (Lee, 1950; Blaxter _et_ _al_., 1959a; and Hales and Webster, 1967).

Hales and Webster (1967) defined two phases of respiratory response in sheep. The first phase is characterized by an increased respiratory minute volume due to a rise in respiratory rate even though a decrease in tidal volume. Following prolonged heat exposure (90 min.), a second phase is characterized by increased respiratory minute volume resulting from increased tidal volume; respiratory rate is lower than in the first phase but above that observed at thermoneutral values. Respiratory frequency in sheep subjected to ambient temperatures below the thermoneutral zone is relatively constant until the ambient temperature falls below 0° C. (32° F.), according to Slee and Sykes (1968). Below this temperature the increase in respiratory frequency was attributed to increased oxygen demands of the cold stressed animal.

Blaxter *et al.*, (1959a) reported that diet, fleece and exercise are related to changes in respiratory frequency at given ambient temperatures, but asserted that these variables shift the thermoneutral zone and do not directly influence respiratory rate.

2.B. Heat Exposure

2.B.1 Sensible Heat Exchange

Heat exchange by radiation, conduction and convection is

termed sensible heat exchange. The initial response of homeotherms exposed to heat stress is an increased sensible heat loss by vasodilation (Hardy, 1961; Adams, 1968; and Hammel, 1968). MacFarlane (1964) noted that regions of the body surface are characterized by different degrees of vasomotion. This infers that variations occur in the rates of sensible heat loss.

The insulating properties of the fleece were investigated by Scholander <u>et al</u>. (1950), who reported that the pelt of Dall sheep had an insulating value of 2.7 clo [one clo is defined by Adams, 1960, as the amount of insulative clothing required to maintain a resting-sitting man with a metabolic rate of one met indefinitely comfortable at an environmental temperature of 21° C. (70° F.)]. Scholander's data were obtained on the pelt and may not be applicable to the fleece of the living animal. Blaxter <u>et al</u>. (1959a) reported that within a narrow range above the thermoneutral zone sensible heat loss from the skin of shorn sheep could be increased three-fold by increasing blood flow through the peripheral layers of the extremities. In fleeced sheep, Blaxter <u>et al</u>. (1959b) reported that the rate of sensible heat loss is inversely related to fleece length. Armstrong <u>et al</u>. (1960) supported these findings by stating that sensible heat loss divided by skin conductance of fleece covered areas is

linearly related to the logarithm of the fleece length.

Studies by Eyal (1963b) and by Riek _et al_. (1950) indicated that pulse rate is positively correlated with ambient temperature above the thermoneutral zone (30° C.) (86° F.). Riek proposed that high ambient temperatures and humidity resulted in increased pulse rates in sheep. Neither Eyal nor Riek attributed changes of pulse rate entirely to vasomotor changes but suggested that such a relationship may exist.

2.B.2 Evaporative Water Loss

Heat losses in sheep exposed to heat stresses are primarily a function of increased skin and respiratory evaporative water loss (Brockway _et al_., 1965; Brook and Short, 1960; Alexander and Brook, 1960; Wodzicka, 1959; Knapp and Robinson, 1954; and Riek _et al_., 1950).

2.B.3 Sweating in Sheep

The question of the sheep's ability to sweat is debatable. Early workers did not find moisture in the fleece following a period of high climatic temperature or excessive exercise (Lennox, 1938, and Freney, 1940) and concluded that sheep probably do not sweat. Ironically, the description of an apocrine gland in close association with each primary wool follicle (Duerden and Ritchie, 1924) was published at approximately the same time when experiments suggested that

sheep apparently didn't sweat. Carter and Clarke (1957) later determined, in a wide variety of breeds of sheep, that the mean number of sweat glands in the sheep is 2.9/mm^2 of skin. More recent reports using desiccating capsules and calorimetric chambers (Cragg and Davies, 1947; Riek _et_ _al_., 1950; Wodzicka, 1959; and Brook and Short, 1960) proposed that sheep do sweat in response to a heat stress. Disagreement emerges, however, as to sweating rates of sheep at different environmental temperatures. Values ranging from 3 gm./m^2/hr. (Brockway _et_ _al_., 1965) to 210 gm./m^2/hr. (Wodzicka, 1959) have been reported.

Variables other than temperature which may alter sweating rate in sheep have been reported. Fleece does not appreciably affect sweating rate according to Blaxter _et_ _al_. (1959b). They compared cutaneous evaporative heat loss at various ambient temperatures to fleece lengths and concluded that fleece does not affect cutaneous water loss. Eyal (1963d) stated that the sweating rates at high ambient temperatures may be the same in shorn and fleeced sheep but that efficiency of heat loss may favor the shorn animal since the heat of vaporization at the fleece surface may be influenced more by the environment than the animal. Dukes (1956) and Eyal (1963d) reported that the rate of sweating in sheep was inversely related to relative humidity. Dukes supported this by citing one example of a sheep able to withstand ambient temperatures of 100° F. (37.1° C.) but only when the relative humidity was less than 65%.

The relative importance of cutaneous (sweating) and respiratory water loss in sheep is not clear. Riek _et_ _al_. (1950) concluded that at ambient temperatures from 30 to 40° C. (86 to 104° F.), cutaneous evaporative water loss is greater than respiratory water loss. Knapp and Robinson (1954) supported this contention by concluding that two-thirds of the total water loss of the sheep is cutaneous water. Conversely, Brook and Short (1960), in the adult sheep, and Alexander and Williams (1962), in the lamb, reported that respiration is responsible for the major portion of evaporative water loss when ambient temperature is above 30° C. (86° F.).

Brockway _et_ _al_. (1965) specifically studied the basis for a controversy between the relative importance of respiratory and cutaneous water loss. Only respiratory evaporative water loss varied with ambient temperature and they concluded that sheep rely primarily upon this avenue of heat loss to maintain thermal balance during heat stress. This study was conducted at ambient temperatures of 12, 20, and 30° C. (53.6, 68, and 86° F.) and did not include temperatures above the thermoneutral zone where evaporative water loss mechanisms are most important. Conversely, Brook and Short (1960) found increases in sweating rates of sheep when ambient temperatures increased from 20 to 40° C. (68 to 104° F.). Knapp and Robinson (1954) reported sweating rates of 76 $gm./m^2/hr.$, an amount which represented two-thirds of total evaporative water loss during heat stress. It remains that the relative importance of respiratory and cutaneous evaporative water loss in the sheep has not been determined.

2.C. Cold Exposure

2.C.1 Behavioral Adjustments

Behavioral adjustments to severe cold exposure in sheep consist of postural changes such as tucking the legs and burying the nose in the shoulder of the fleece, seeking shelter, and huddling. The importance of these voluntary adjustments in reducing heat loss under natural conditions is difficult to assess. Munro (1962) stated that increased wind velocity induces sheep to seek shelter, whereas Powell (1963) reported that sheltering is related to the chill index of the environment. Brockway *et al.* (1965) observed a reduction in oxygen consumption in sheep when lying as opposed to standing, however, they did not relate these findings to thermoregulation.

2.C.2 Sensible Heat Loss

Vasoconstriction at environmental temperatures below the thermoneutral zone in sheep reduces sensible heat loss by increasing tissue insulation. Blaxter (1964) indicated that following this initial adjustment to cold, additional cooling has little effect on tissue insulation, concluding that vasoconstriction is an all-or-none phenomenon, and that tissue insulation cannot be increased by a further reduction in ambient temperature. Webster and Blaxter (1966) found that tissue insulation at -10° C. (14° F.) was less than at either 5° C. (41° F.) or 0° C. (32° F.). Increased sensible heat loss below thermoneutral zone temperatures occurs regardless of vasoconstriction. Blaxter et al. (1959b) calculated that at subcritical temperatures, a constant value of 85 cal./m^2/24 hr./°C. will be lost via sensible heat loss.

External insulation affects the conservation of heat by reducing sensible heat loss. The sheep is of particular interest compared to bare skinned mammals because of the external insulation of the fleece. Armstrong et al. (1960) reported a three-fold increase in insulation due to fleece when compared to shorn animals. Webster and Blaxter (1966) suggested that fleece type has little effect on the insulation provided by a given thickness of fleece in still air.

The effect of wind on sensible heat loss was described by Joyce and Blaxter (1964). These studies indicated that wind does not affect tissue insulation regardless of the amound of fleece. Differences in tissue insulation existed between breeds of sheep. Joyce and Blaxter (1964) originally reported that this difference was due to blood vessel patterns observed previously by Ryder (1955). However, Blaxter (1959a, 1959b) in more recent articles discounts this hypothesis stating that "the amount of fat present in different breeds permits increased tissue insulation". Conversely, Armstrong _et al_. (1960) suggested that breeds do not differ in the insulation provided by the skin and subcutaneous tissue.

The effect of wind on external insulation was investigated by Joyce and Blaxter (1964). These workers found that at a wind speed of 0.6 mph, the external insulation was 0.46 units per mm. fleece length, whereas, when wind speed was 9.6 mph. the insulation was only 0.27 units/mm.

Webster and Blaxter (1966) reported that sensible heat loss from the extremities is low when skin surface temperature is near that of air, but as air temperature falls below 0° C. (32° F.) sensible heat loss increases markedly.

Webster and Blaxter (1966) reported that at air temperatures below 0° C. (32° F.), cold induced vasodilation (CIVD) occurred frequently in the ears but rarely in the shanks. At air temperatures above 0° C. (32° F.), CIVD was rarely seen.

2.C.3 Evaporative Water Loss

Evaporative water loss is reduced at temperatures below the thermoneutral zone (Knapp and Robinson, 1954; Blaxter *et al.*, 1959a, 1959b; Alexander, 1962; and Brockway *et al.*, 1965. Blaxter *et al.* (1959b) suggested that total evaporative water loss during cold stressing temperature is constant at approximately 310 cal./m^2/24 hr. in adult sheep, providing that temperatures do not fall to values which alter respiration rates. When increases in metabolic rate are necessary to increase heat production, increased respiratory frequency lead to increased evaporative water loss (Blaxter *et al.*, 1959b). Brockway *et al.* (1965) maintained, as mentioned previously, that sweating is constant in sheep; however, the majority of authors (Brook and Short, 1960; Eyal, 1963d; and others) report reduction of sweating at ambient temperatures below thermoneutral temperatures.

2.C.4 Metabolic Rate

Sheep exposed to temperatures below the critical temperature continue to lose heat regardless of increased tissue insulation. To increase heat production, the sheep must increase metabolic rate.

The basal metabolism of sheep in a thermoneutral environment was measured by Blaxter (1962) under the following conditions:

fasting	850 kcal./m^2/24 hrs.
maintenance	1250 kcal./m^2/24 hrs.
full feed	1600 kcal./m^2/24 hrs.

These data emphasize the role of plane of nutrition in basal metabolic heat production.

During cold stress sheep must increase heat production to maintain a constant body temperature. Kleiber (1961) compared the rate of increase of metabolic rate in sheep with varying amounts of fleece at environmental temperatures below critical temperatures, and reported that the greater the length of fleece the slower the rate of increase of metabolic rate. Similarly, Webster (1966) noted that sheep with less than 15 mm. of fleece length exhibited oxygen consumption increases of 71% of final equilibrium value in 10 minutes during sudden exposure to -8.9° C. (15.8° F.). Sheep with 15 to 25 mm. fleece length only increased to 13% of the final equilibrium value in 10 minutes. Graham et al. (1959) reported that heat production in shorn sheep increased at a constant rate ($\Delta H_m/t/m^2/^{\circ}C.$) irrespective of the level of feeding, and that heat production at 8° C. (46.4° F.) was more than double the minimal metabolism determined at the medium level of feeding. The rate of increase was, in this case, 115 cal./m^2/24 hrs./°C. ambient temperature.

The immediate increase in metabolic heat production in sheep exposed to cold temperatures [23° C. (71.6° F.) in shorn sheep] results from shivering (Blaxter, 1962). Hardy

(1961) indicated that shivering is capable of increasing energy expenditure by a factor of about four. Alexander (1962) reported that lambs are capable of increasing heat production by a factor of five by shivering.

Although non-shivering thermogenesis in adult sheep exposed to cold has not been reported, Alexander (1961) stated that heat production in the newborn lamb can be increased two to three times by increased oxidation of fats. Dawes and Mott (1959) also observed non-shivering increases in oxygen consumption in lambs at birth.

III. MATERIALS AND METHODS

3.1 Animals

Three yearling, non-pregnant, purebred Suffolk ewes (77.5 to 88.0 kg. in body weight) were utilized in this study. Animals were selected with similar genetic background in order to reduce intersubject variability (Blaxter *et al.*, 1966 and Miller and Mange, 1946). Suffolk sheep were selected since they readily adapt to new environments (Webster and Blaxter, 1966) and this reduced the training periods. Each animal was maintained shorn (less than 0.3 cm. of fleece) by weekly trimming, and the sheep were group housed in a 6 x 6 meter pen. The diet contained 1500 kcal./day and water was fed *ad libitum*.

3.2 Training

The effect of training on the responses of sheep in climate chambers has been reported (Webster and Blaxter, 1966; and Slee and Halliday, 1968). The sheep were trained for three weeks before the beginning of trials in the environmental chamber.

3.3 Annex Room

Sheep were housed in a heated, insulated annex adjacent to the laboratory containing the environmental chamber. The temperature of the annex was maintained between 17 and 27° C.

3.4 Environmental Chamber

A temperature and humidity controlled chamber (Figure 1) was constructed of plywood with 3.75 cm. of fiber glass insulation and had an effective range of 5 to 50° C. ± 5° C. The heating system consisted of a three gallon insulated water bath containing two immersible heating coils (Chill Chaser Co. Matheson Cat. No. 28420) which maintained the bath at 80 to 90° C. The cooling system was a 15 gallon insulated bath which contained 50% methanol solution cooled by an immersed coil. A thermistor temperature controller (Yellow Springs, Model 71) regulated the pumping of either heated or cooled liquid through convective heat exchangers inside the chamber. Fans were positioned behind each to increase air flow across the heat exchangers.

Chamber humidity was controlled within 5 percent relative humidity at a given temperature by a humidifier (Kenmore Model No. 758.72912) and a dehumidifier (Coldspot Model 106.637140) cycled by a humidity controller (Humistat Model 15-3205, Hygrodynamics Inc.). Both systems were located outside the chamber and connected to the unit by 10 inch diameter flexible air ducts.

Air was circulated inside the chamber by an oscillating,

20 cm. fan. Two plexiglass sliding windows (66 x 91 cm.) allowed observation of the animal and adjustment of apparatus during the experiment.

3.5 Respiration Rate

Respiratory rate was measured with a mercury in rubber strain gauge transducer matched to a Model 270 plethysmograph and monitored on one channel of a dual strip chart recorder, (Sanborn Model 322 Dual Channel DC Amphifer-recorder). The strain gauge was attached to an elastic band (2.5 cm. wide) placed around the animal's trunk posterior to the last rib.

3.6 Heat Production

Heat production was calculated by open circuit, indirect calorimetry techniques (Figure 3). A ventilated cylindrical hood 45 cm. in diameter and 61 cm. long was placed over the head (including ears of the animal). Air was drawn through the hood at a rate of 60 liters/min. Oxygen consumption (Oxford Instrument Co.) was recorded (STPD) and converted to kcal./kg.$^{3/4}$ as suggested by Kleiber (1961). For temperatures above the thermoneutral zone (25° C. and above) metabolic heat production was calculated by the following equation (Joyce and Blaxter, 1964):

$$Hm = k(0_2 \text{ consumed})$$

where: Hm = heat production (kcal.)

O_2 consumed = oxygen consumption (liters/hr.)

$k = 5$, no. of kilocalories per liter of oxygen utilized.

The following equation was used for temperatures below the thermoneutral zone (Joyce and Blaxter, 1964):

$$Hm = H_{m25} + k\ (A_1 - A_2)$$

where: Hm = heat production at ambient temperatures below TNZ (kcal.)

H_{m25} = heat production at 25° C. (kcal.)

A_1 = oxygen consumption at temperature below TNZ (liter/hr.)

A_2 = oxygen consumption at 25° C. (liters/hr.)

$k = 4.68$, no. of kilocalories per liter of oxygen utilized.

The different values of the constant, k, compensates for the difference in R.Q.'s. This difference is due to increased fat catabolism at subcritical temperatures (Graham et al., 1959).

3.7 Temperature Measurements

Temperatures were measured using copper constantan thermocouples referenced to an ice water bath with EMF's monitored on an adjustable range, adjustable zero, strip chart recorder, (Mosley Model 7100B) with a full scale sensitivity of 0 to 50° C. The temperature recording system was calibrated daily to the nearest 0.1° C. against a

National Bureau of Standards thermometer. An automatic stepping relay allowed sequential monitoring of nine temperatures on one recording channel.

Rectal temperature was measured with a thermocouple mounted in a flexible catheter inserted 10 cm. into the lower colon.

Skin temperatures were measured as follows:

a) Ear skin temperatures were obtained by locating the thermocouple on the dorsal side of the ear, anterior to the midline and approximately 5 cm. from the distal tip. Thermocouples were held in place by spraying the ear with an adhesive (Ace Spray Adhesive) and taping the thermocouple in place with porous adhesive tape (Figure 2). Thermocouple placement was adjusted so that there was less than a 2° C. difference between ears to eliminate placement directly over a large blood vessel. The mean skin temperature of the two ears was used for statistical analysis and other computations.

b) Face skin temperature was measured with a thermocouple, attached as described above, to the midline of the face approximately 5 cm. anterior to the eyes.

c) Forelimb skin temperature was measured midway between the knee and pastern joints on the left foreleg. The thermocouple was held in place by a 1 cm.^{2} area of nylon screening attached to a 1 inch elastic band (Figure 2) placed around the limb.

d) Stifle skin temperature was measured midway between the hock and stifle joints on the outside of the left rear leg. Procedures for thermocouple attachment were as described for the forelimb.

e) Trunk skin temperatures were measured approximately 10 cm. lateral to the dorsal midline and 10 cm. posterior to the scapula on the animal's left side. Procedures for thermocouple attachment were the same as described for the forelimb with the elastic band belting the trunk.

3.8 Evaporative Water Loss

Respiratory and skin evaporative water losses were measured by a relative humidity transducer (Hygrodynamics Model 15-7012) in a measured air flow system. Electric potentials of 0 to 5.4 v. output (corresponding to 0 to 100% relative humidity) were monitored on an adjustable range, adjustable zero strip chart recorder (Mosley Model 7100B). The adjustable air flow system serving the respiration hood (Figure 3) was operated at a rate of 60 liters/min. and that

of the skin capsule as shown in Figure 4 at 2.5 liters/min.

A vacuum pump withdrew air samples at the rate of 2.5 liters/min. from the respiratory hood and the ventilated skin capsule (Figure 4). A reference air sample was drawn from within the chamber at a rate of 2.5 liters/min. Water evaporation was calculated by:

$$H_2O \text{ loss} = A(RH_0 - RH_1)F_A$$

where: H_2O loss = water loss (gm.)

A = gram of water in one liter of saturated air (gm./liter)

RH_0 = relative humidity in chamber (%)

RH_1 = relative humidity of sampled air (%)

F_A = air flow (liters/min.)

Heat of vaporization was calculated by the formula described by Kleiber (1961):

$$Hvap = K_1 - K_2 T$$

where: Hvap = heat of vaporization (kcal./gm.H_2O)

K_1 = 0.5959 latent heat of vaporization at 0° C.

K_2 = correction constant for temperature

T = temperature in degrees centigrade

3.9 Whole Body Insulation

Whole body thermal insulation was calculated as described for sheep by Webster and Blaxter (1966) as follows:

$$I_t = \frac{T_r - T_{\bar{s}}}{H_m}$$

where: I_t = tissue insulation (°C./kcal.• m^2.hr.)

T_r = rectal temperature (°C.)

$T_{\bar{s}}$ = mean skin temperature (°C.)

H_m = heat production per unit body surface area per unit time (kcal./m^2 •hr.)

Surface area was calculated as 0.09 x wt. (kg.) 0.667 (correction factor for sheep) (Mitchell, 1927).

3.10 Thermal Circulatory Index

Thermal circulatory index was calculated for all skin surface temperatures according to the following formula (Burton and Edholm, 1955):

$$T.C.I. = \frac{T_S - T_A}{T_r - T_S}$$

where: TCI = thermal circulatory index

T_S = skin surface temperature (°C.)

T_A = ambient temperature (°C.)

T_r = rectal temperature (°C.)

3.11 Panting Index

Panting index was calculated according to the following equation (Adams, 1968):

$$\text{Panting index} = \frac{(Hl)p - (Hl)r}{(Hm)p - (Hm)r}$$

where: (Hl)p = heat loss during panting

(Hl)r = heat loss during rest

(Hm)p = heat production due to panting

(Hm)r = heat production during rest

3.12 Mean Body Temperature

The formula of Hardy and DuBois (1938) was used to calculate mean body temperature as follows:

$$T_{\bar{b}} = K_1 T_r + K_2 T_{\bar{s}}$$

where: $T_{\bar{b}}$ = mean body temperature

T_r = rectal temperature

$T_{\bar{s}}$ = mean skin temperature

K_1 = 0.80, portion of body mass represented by core

K_2 = 0.20, portion of body mass represented by shell

3.13 Body Heat Content

Body heat content was calculated as described for sheep by Blaxter _et al._, 1959 using the mean body temperature formulated by Hardy and DuBois (1938) and the specific heat (0.83) of body tissue reported by Schafer (1898). This value was calculated as follows:

$$BHC = (T_{\bar{b}})(K_1)(M)$$

where: BHC = body heat content (cal.)

$T_{\bar{b}}$ = mean body heat (K^o)

M = body mass (gm.)

K_1 = 0.83, specific heat of body tissue of sheep

3.14 Mean Skin Temperature

Mean skin surface temperature was obtained by proportioning trunk temperature and the mean of all extremity temperatures (ear, face and forelimb) in the ratio 9:1 as described for sheep by Webster and Blaxter (1966):

$$T_{\bar{s}} = K_1(T_t) + K_2 \frac{T_e + T_f + T_{fl}}{3}$$

where: $T_{\bar{s}}$ = mean skin temperature ($^oC.$)

K_1 = 0.9, portion of skin surface represented by the trunk

K_2 = 0.1, portion of skin surface represented by extremities

$\frac{T_e + T_f + T_{fl}}{3}$ = mean extremity skin temperature ($^oC.$)

where: T_e = mean ear skin temperature ($^oC.$)

T_f = face skin temperature ($^oC.$)

T_{fl} = forelimb skin temperature ($^oC.$)

3.15 Experimental Procedures

A total of 48 trials were conducted (replication of a series of 24 trials) on three sheep at eight ambient tempera-

tures (5° intervals ranging from 10 to 45° C.).

Following training, the animals were loosely haltered and led from the annex room (Sec. 3.3) to the environmental chamber (Sec. 3.4). A 20 min. preconditioning period at 25° C., considered to be thermoneutral on the basis of a series of pilot trials, preceeded each trial. Following preconditioning the temperature and humidity were adjusted to the appropriate treatment values. Due to the limits of the humidity control system humidity was controlled in three ranges as:

Treatment Temp. (°C.)	Relative Humidity (%)
10, 15, 20	35 ± 5
25, 30, 35	55 ± 5
40, 45	65 ± 5

With the attainment of the selected temperature, skin and rectal temperatures as well as oxygen consumption and respiratory rate were recorded at 5 min. intervals on previously prepared data sheets. Respiratory and cutaneous evaporative water loss were recorded at 10 min. intervals. Each trial was conducted for a minimum of one hour or until all parameters had reached a "steady state". This was defined as a stabilizing (or reversing) of all parameters for two consecutive 5 min. periods. Animals were not subjected to the experimental procedures more than once daily.

The sheep were fed daily at 4:00 a.m. Trials were conducted between 8:00 a.m. and 4:00 p.m. to insure that the animals were in a comparable post absorpative state.

Means calculated from values recorded during the last 20 min. of each trial were used for statistical analysis and other computations.

3.16 Statistical Analysis

Means, standard deviation, simple correlation and regression equations were calculated by the computer laboratory (3600 Computer). Duncan's new multiple range test was used to compare treatment means.

IV. RESULTS

4.1 Rectal Temperature

Mean rectal temperature responses are reported in Figure 5. Rectal temperature was correlated with ambient temperature ($r = 0.65$). Data reported in Table 1 indicate that a significant increase in rectal temperature ($P < .05$) was recorded at 45° C. as compared to all other ambient temperatures. A significant difference was not found among rectal temperatures recorded from 10 to 40° C. ambient temperature. The mean rectal temperature for all observations was $39.9 \pm 0.48^\circ$ C. Rectal temperature increased 0.03° C. per degree increase in ambient temperature. Linear regression analysis of rectal temperature (y) on ambient temperature (x) is shown in Appendix III. A significant difference ($P < .05$) in rectal temperature among sheep or between trials at a given temperature was not observed. The mean change in rectal temperature, defined as the absolute change from preconditioning to treatment, was $-0.42 \pm .42^\circ$ C. Change in rectal temperature was negatively correlated with ambient temperature ($r = -0.57$).

4.2 Skin Temperature

Mean skin surface temperatures are related to ambient temperatures (Figures 6 through 10). Correlation coefficients

relating skin surface temperatures to ambient temperatures ranged from r = .93 to r = .97 (Appendix II).

Although all skin surface temperatures increased as ambient temperature increased, Table 1 shows that the responses varied with the site of measurement. Ear and forelimb skin temperatures increased significantly ($P < .05$) with each 5° C. increase in ambient temperature. Face and stifle skin temperatures rose significantly from 10 to 30° C. and from 10 to 35° C., respectively. Trunk skin temperature was constant from 10 to 15° C. and from 35 to 40° C. with significant increases ($P < .05$) recorded at other temperatures.

At ambient temperatures of 35° C. or less, skin surface temperatures were always higher than the ambient temperature (Figure 11). Conversely, when ambient temperature was 40° C. or above, skin surface temperatures were always lower than ambient temperatures. Face, ear and trunk skin temperatures were higher than rectal temperature when the ambient temperature was 45° C. (Figure 11). Figure 11 shows that the means of various skin temperatures converge at 30° C.

The rates of skin temperature change per degree centigrade increase in ambient temperature are presented in Table 3. These data demonstrate that ear skin temperature is the most responsive to changes in ambient temperature while the stifle is the least responsive to changes in

ambient temperature.

The ambient temperature interval where skin surface temperatures changed the most varied with place of measurement (Table 3). The face, trunk and forelimb temperatures changed the most from 15 to 20° C., stifle temperature from 20 to 25° C. and ear temperature from 25 to 30° C. The weighted mean skin temperatures were positively correlated with ambient temperature ($r = .96$) and increased significantly ($P < .05$) with each increase in ambient temperature above 15° C. (Figure 12).

Statistical comparisons indicated that significant differences ($P < .05$) in mean skin temperatures did not occur among sheep at a given temperature.

4.3 Body Heat Content

A range of 21,179 to 21,429 kcal. was observed in body heat content (Figure 18). Whole body heat was positively correlated with ambient temperature ($r = .94$).

4.4 Whole Body Insulation

As noted in Figure 12, whole body insulation increases as ambient temperature decreases from 45 to 15° C. This relationship is represented by the regression equation $Y = .0046 + .000103X$.

There was not a significant decrease ($P < .05$) in

tissue insulation at 35, 40, and 45° C. ambient temperature when compared to ambient temperatures below 35° C. Figure 12 shows that low insulation values were recorded at 10° C. These values are significantly lower than the values at 15° C.

Whole body insulation is negatively correlated with ambient temperature ($r = -.83$) and skin temperature ($r < .60$) but inversely related to skin thermal circulatory indexes.

4.5 Thermal Circulatory Index

Thermal circulatory index (TCI) is positively related to ambient temperature in the skin areas measured. Table 4 lists the means and percentage change of each TCI. These data indicate relative low but highly variable TCI values in areas of the body characterized by a high surface area to mass ratio. Stifle and trunk areas which overlay muscle and subcutaneous fat have consistantly high TCI values with lower percentage change.

4.6 Respiratory Rate

Mean respiratory rates demonstrate that respiratory frequency was constant at ambient temperatures from 10 to 30° C. (Figure 19). Mean respiratory rate increased to a maximum of 179 breaths per min. at 45° C., with a minimum value of 19 breaths per min. at 15° C. Respiratory rates increased

significantly ($P < .05$) at each interval of ambient temperature above 30° C. (Table 2). Although significant differences in respiratory rate were not observed at temperatures below 30° C., there was an increase in mean respiratory rate at 10° C. when compared to 15, 20, and 25° C.

Respiratory frequency was more highly correlated with ambient temperature ($r = .83$) than with rectal temperature ($r = .68$). A linear response was observed from 10 to 30° C. Then an exponential increase as ambient temperatures increased above 30° C. Table 2 shows that water loss per breath decreases significantly ($P < .05$) at 40° C. Linear regression analysis of RR/Rewl (y) on ambient temperature (x) is given in Appendix III. A significant difference did not occur in respiratory rate between or among sheep.

4.7 Respiratory Water Loss

Respiratory evaporative water losses (Rewl) are plotted in Figure 21. Rewl was the lowest at 25° C. which coincides with low respiratory rates. Rewl values increase significantly ($P < .05$) at high ambient temperatures (35, 40, and 45° C.), increasing 63% between 30 and 35° C. Rewl was correlated ($r = .79$) with respiratory rate. When Rewl is plotted as a function of RR, a linear relationship exists at respiratory rates below 30° C. At temperatures above 30° C. the characteristic relationship between Rewl and RR was not

linear. A decrease in Rewl/RR is observed as ambient temperature increases (Figure 22). This relationship, as opposed to Rewl, was linearly related to ambient temperature and is represented by the regression equation $y = .045 + .00049X$ (Appendix III). Variations in Rewl/RR were observed at ambient temperatures below 40° C. However, consistant values were obtained among animals at 40 and 45° C. There were no significant differences ($P < .05$) among sheep in RR, Rewl or Rewl/RR responses at a given ambient temperature. Panting indexes are tabulated in Table 5 and plotted in Figure 23.

Rewl was correlated with skin water loss ($r = .70$), rectal temperature ($r = .52$) and with changes in rectal temperature ($r = .67$). The latter two were linearly related with Rewl.

4.8 Cutaneous Water Loss

Cutaneous evaporative water loss is plotted as a function of ambient temperature in Figure 24. This figure shows a nine-fold increase in cutaneous water loss was observed between 10 and 45° C., with values at 40 and 45° C. significantly higher ($P < .05$) than at ambient temperature less than 40° C. A 133% increase in cutaneous water loss occurred between 35 and 40° C. This increase was appreciably more than the significant increase in Rewl

observed between 30 and 35° C. The data in Table 2 also demonstrate that sweating at 35° C. was significantly higher ($P < .05$) than at ambient temperatures from 10 to 25° C. Cutaneous and respiratory evaporative water loss were correlated ($r = .74$) with trunk skin temperature. No significant difference ($P < .05$) in sweating at a given ambient temperature was found among sheep.

4.9 Heat Production

Changes in heat production are plotted in Figure 26. A minimum mean value of 65.1 kcal./kg.3/4/hr. was observed at 30° C. The relationship between heat production and ambient temperature is non-linear. A significant ($P < .05$) increase in heat production at 10° C. when compared to higher temperatures is noted in Table 2. There was no significant difference ($P < .05$) among temperatures from 15 to 35° C. or between 40 and 45° C., although there is a significant increase in heat production at 45° C. when compared to 35° C. The increase in heat production at 10° C. was the largest observed being 57% and 26% greater at 15 and 45° C., respectively (Figure 26). Heat production was not highly correlated with any other single variable (Appendix II).

V. DISCUSSION

The rectal temperature of homeotherms varies within "normal limits". The dimension of these limits is not universal; some homeotherms are more precise regulators of rectal temperature than others. Data reported here indicate that the "normal limits" of rectal temperature for the sheep are relatively wide with significant differences ($P < .05$) in rectal temperature observed over the range of ambient temperatures studied. Rectal temperature ranged from 38.8 to 41.1° C. and increased approximately 0.027° C./°C. change in ambient temperature over the range of 10 to 45° C. (Figure 5).

The relatively wide "normal limit" for internal temperature in sheep is also reported by others (Blaxter et al., 1959a; Brook and Short, 1960; Slee and Sykes, 1967; and Webster, 1968). This wide "normal" range of rectal temperature has important implications. Rectal temperature is a physiological measurement used as an indicator of health, disease and other physiological states. The influence of ambient temperature on the rectal temperature of sheep should therefore be considered when rectal temperature is used as an index of these states in sheep exposed to

different thermal environments. Chemical reactions are accelerated as temperature rises according to the Q_{10} law. An increase in "deep" body temperature would increase (or a decrease if body temperature would decrease) the rate of physiological reactions. When evaluating data recorded concurrently with changing "deep" body temperature, it is important to consider the Q_{10} effect on physiological reactions.

The rate of heat exchange between the skin surface and the external environment is dependent upon the thermal gradient. Control of cutaneous blood flow by vasomotion regulates the rate of heat flow from the core to the skin. Therefore, vasomotion is capable of modifying sensible heat loss. Vasomotor variability, termed "tissue insulation" or its reciprocal "tissue conductance" is a thermoregulatory response (Hammel, 1968), and is the only adjustable means of distributing internal heat to the skin. The present study demonstrates that the sheep has the ability to modify sensible heat loss by varying tissue insulation (Figure 12). Whole body tissue insulation was significantly higher ($P < .05$) at ambient temperatures above 30° C., when compared to values calculated from 15 to 30° C. (Table 3). These values are similar to those of Blaxter (1962) who reported 3.5 and 1.2° C. X 10^{-3}/kcal.m^2/24 hrs. for shorn sheep

exposed to cold and heat stress respectively.

Whole body insulation is inversely related to ambient temperature, from 15 to 45° C. (Figure 12). These findings are teleologically compatable with the maintenance of homeothermy. Conversely, a decrease in whole body insulation was observed at 10° C. Similar findings have been reported by Blaxter _et al_. (1959a). This phenomenon can be explained by the hypothesis that during shivering, which was observed at 10° C., the fascial muscles are supplied with blood. The opening of capillary beds within the muscles would result in decreased tissue insulation.

Skin surface temperatures are a function of cutaneous blood flow and environmental temperature. Changes in either of these determinates is reflected by changes in skin surface temperature. The difficulty in distinguishing the influence of vasomotion from that of changes due to environmental temperature can introduce erroneous conclusions regarding cutaneous blood flow, and consequently, the regulation of sensible heat loss.

The thermal circulatory index (TCI) (Burton and Edholm, 1955), used to distinguish vasomotor changes, indicated that vasomotor responses vary with the region of measurement (Figures 13 through 17). Wool free regions with high surface area to mass ratio (ears, face and forelimb) had relatively large changes in TCI values compared to regions of small surface area to mass ratio (Table 4). These areas, therefore, may play an active role in modifying sensible heat loss. Conversely, trunk and stifle regions, which are fleeced areas and are characterized by underlying subcutaneous fat and muscle respectively, varied less in cutaneous blood flow as reflected by relatively constant TCI values. The exception was noted in a substantially elevated TCI value of the trunk at 10° C. (Table 4). A concurrent decrease in tissue insulation at 10° C. (Figure 12) supports the contention that blood flow must increase in these areas. This occurrence is attributed to shivering which was observed at 10° C. With the increased TCI of the trunk value accounted for, it is concluded that on the basis of TCI values the skin of the trunk and stifle (Figures 16 and 17) do not respond to thermal changes (between 10 and 45° C. ambient temperature) by vasomotion.

The magnitude of skin surface temperature change can be used to identify vasomotion. Slee (1968) defined vasomotion in sheep as the point where the change in skin surface temperature exceeds 0.5° C./°C. change in ambient temperature. This relationship was based on the observation that when the change was less than this value, skin temperature variations were attributed to environmental temperature.

Using the criteria of Slee, data reported here indicate

that skin temperature changes of about 0.4° C./°C. change in ambient temperature can be attributed to environmental temperature. A similar ratio between skin surface temperature and environmental temperature was observed at all measurement sites above 30° C. which suggests that vasodilation was complete at 30° C. ambient temperature. It is concluded that when temperature changes of more than 0.4° C./°C. change in ambient temperature may be indicative of vasomotion.

Table 3 indicates large differences in the magnitude of change among the various skin regions. The change in skin temperatures of the trunk and stifle approximates 0.4° C./°C. change in ambient temperature which infers that these areas are without vasomotion. Conversely, changes in skin temperatures of the ear, face and forelimb areas were greater than 0.4° C./°C. change in ambient temperature and assumed to result from vasomotion in these regions. These findings parallel those of the thermal circulatory index. On the basis of thermal circulatory indices and the magnitudes of skin surface temperature change per degree change in ambient temperature, it is concluded that the ear, face and forelimb are capable of modifying sensible heat loss by vasomotion. Conversely, the trunk and stifle regions appear to lack this ability.

Table 3 demonstrates that the ambient temperature interval where the greatest change in skin temperature was

observed varies with the region of measurement. Ear skin temperature had the greatest change (0.8° C./$^{\circ}CT_A$) between 25 and 30° C. while the face and forelimb changed the most between 15 and 20° C., with changes of 0.6° C./$^{\circ}C.T_A$ and $0.6^{\circ}C./^{\circ}C.T_A$, respectively. These data question the value of surface temperature changes in the skin for defining thermoregulatory parameters in sheep, since these changes are largely dependent on the region of measurement. The use of ear skin temperature to determine the thermoneutral zone (Blaxter _et_ _al_., 1959a) in sheep appears to be a result of circumstance; large changes of ear skin temperature coinciding with feasible values for the thermoneutral zone. The use of skin surface temperatures to define the thermoneutral zone and critical temperatures in sheep is therefore not completely justified.

As ambient temperature rises above critical temperature II, (also termed hyperthermal rise and defined as the ambient temperature where heat stress begins) heat loss from the skin surface decreases until skin temperature equals rectal temperature, at which point there is no net sensible heat exchange. When ambient temperature surpasses rectal temperature, the thermal gradient is reversed and the skin surface gains heat; an added liability to the homeotherm. Vasodilation in these circumstances jeopardizes homeothermy because blood flow through cutaneous vessels increases the rate of

heat gain. The jackrabbit (Schmidt-Nielsen et al., 1965) and the ostrich (Crawford and Schmidt-Nielsen, 1965) vasodilate cutaneous vessels up to an ambient temperature near body temperature, and then to vasoconstrict these same vessels at still higher air temperatures. Vasoconstriction, and consequent increased tissue insulation, have been reported to reduce heat gain when ambient temperature is above rectal temperature. The data here do not suggest that this phenomenon is not operative in sheep.

Changes of body heat content have been reported as an important thermoregulatory mechanism (Bleakley and Findlay, 1955). Blaxter et al. (1959a) reported that below the critical temperature the body heat of sheep decreased by approximately 7 to 10 kcal./°C. decrease in ambient temperature. These workers also reported that body heat content varied approximately 300 kcal. at ambient temperatures from 10 to 40° C. The present data (Figure 18) recorded a 247 kcal. difference in total body heat between 10 and 45° C., this difference resulting from modifications of body core and shell. This mechanism could serve as an important biothermal control mechanism during acute thermal stress by buffering a rise (or fall) in deep body temperature. However, after shell and core temperatures reach an equilibrium (after 1 to 3 hrs.), body heat content does not change and

therefore cannot benefit homeothermy. Elevated respiratory rates which were observed below critical temperature I were attributed to the increased metabolic heat production which accompanies shivering (Figure 26). Slee and Sykes (1967) reported significant increases in respiratory rate of shorn sheep between thermoneutral (30° C.) and subzero temperatures. Subzero temperatures were not utilized in the present study.

Significant increases in respiratory rate (Table 2) were observed during heat stress. Respiratory frequency increased logarithmically above the critical temperature II until ambient temperature equalled rectal temperature (Figure 20). Respiratory rates can therefore be predicted within a defined range of ambient temperature. This relationship between respiration rate and ambient temperature could be useful in detecting respiratory insufficiencies resulting from administration of tranquilizers, anesthetics, etc. Respiratory rate response is frequently utilized in biothermal investigations to identify the onset of heat stress (critical temperature II). Comparison of the beginning of active heat loss (evaporative water loss) and of respiratory rate response (Table 2) justifies the utilization of respiratory rate increase to estimate the initiation of heat stress (critical temperature II). The use of respiratory rate, per se is not valid for this estimate since numerous studies have reported wide ranges of respiratory rate at identical ambient

temperatures.

Hales and Webster (1967) report two phases of respiratory pattern responses to heat in sheep. The first is characterized by increased frequency and a decrease in tidal volume. A second phase, characterized by decreased frequency and increased tidal volume, was observed by these authors after 70 minutes of heat exposure (40 to 60° C.). In the present study, sheep exposed to 45° C. for one hour did not obviously enter the second phase of respiratory responses described by Hales and Webster (1967).

Respiratory evaporative water loss increased exponentially at ambient temperature above 30° C. (Figure 21). The calculated theoretical maximum gross respiratory evaporative heat loss, using the size adjusted respiratory minute volume of Hales and Webster (1967), was approximately 2000 kcal./day. During heat stress, in the present study, slightly more than one-fourth of this potential was attained. Respiratory evaporative water loss was similar (r = .80), but not equivocal to respiratory frequency. This difference is explained by the changing RR/Rewl ratio (Figure 22).

Increased respiratory evaporative water loss by panting (defined for this study as a significant increase in respiratory rate above thermoneutral levels) is accompanied by the increased heat production due to the inherent in muscular activity. Therefore, the net efficiency of heat loss during

panting must be considered. Whittow and Findlay (1968) reported that only a portion of increased heat production during heat stress is attributable to the muscular activity of panting in cattle. Although many sources of increased heat production were present (increased heart rate, elevated catcholamines, sweat gland activity), these workers reported that the Q_{10} effect of increased rectal temperature on general metabolic reactions accounted for a major portion of increased heat production observed during heat stress. Values used to calculate the panting index, considering increased heat production according to the Q_{10} law, are shown in Table 5. Figure 23 plots panting index as a function of respiration rate. A non-linear response was expected because of the changing RR/Rewl ratio during heat stress. Extension of the panting index curve (Figure 23) suggests that when respiratory rate reaches approximately 240 breaths per minute, the panting index equals one; the limit of net respiratory evaporative heat loss.

Cutaneous evaporative water loss (Figure 24) increased significantly ($P < .05$) at 35° C. when compared to 25° C. (Table 2). A significant difference was not observed between 30° C. and either 25 or 35° C. The data suggest that active sweating begins at 40° C. ambient temperature. The data show a nonsignificant increase in sweating occurred at 45° C. when compared to 40° C., suggesting that the maximum rate had been

reached. A positive correlation (r = .74) between sweating rate and skin temperatures suggests that increased skin temperature may stimulate sweating. Data presented in Table 2 does not conclusively demonstrate the ability of sheep to sweat. Increases in obligatory cutaneous water loss due to increases in skin surface temperature could account for significant increases in cutaneous water loss. To investigate this possibility, Figure 25 compares vapor pressure increase (proportional to evaporative water loss from a wet surface) and cutaneous water loss as a function of trunk skin temperature. The difference in the shape of these curves indicates a limited ability for sheep to control actively skin water losses, probably involving the secretion of apocrine glands found in conjunction with wool follicles. Allen and Bligh (1968) reported phasic patterns of sweat discharge in sheep subjected to heat (40° C.), and attributed this to variations in sweat secretory patterns. The wide range of values obtained during heat stress, in conjunction with the absence of variations during cold stress, adds support to suggestions of the existence of thermally related sweat gland activity in the sheep.

Effective heat loss due to sweating is difficult to quantify since the heat of vaporization is in part from the environment and the rate of sweating is not consistent among

skin areas. The measurement of skin water loss on a known surface area of the trunk (as done in the present experiments) therefore, cannot be multiplied by total body surface to accurately determine total skin water loss. For these reasons the rate of cutaneous water loss in the present study should be interpreted as qualitative responses to heat stress. However, these data do suggest the existence of an active cutaneous evaporative water loss control mechanism.

These data shed new light on the controversy concerning the relative importance of respiratory and cutaneous evaporative water loss in sheep. Previous approaches to this question have eliminated one avenue of evaporative heat loss while measuring the other, or measured one avenue of evaporative heat loss and related it to total heat loss. These methods have been uniformly unsuccessful in explaining the relative importance of Rewl and Cewl. Brockway et al., (1965) measured both respiratory and cutaneous evaporative water loss simultaneously but only at temperatures below 30° C. Their conclusions cannot be considered applicable to heat stress. The present series of experiments suggest that both respiratory and cutaneous evaporative water loss are important avenues of heat loss in sheep and that each increases significantly during heat stress. This is in contrast with prior workers who have reported that sweating does not occur in sheep. In the present experiment, sweating increased

eight-fold while respiratory water loss increased only three-fold. With ambient temperatures of 40° C. and above, the primary avenue of heat loss is evaporative water loss. If the data are expanded to 24 hr. these data show that at 40° C. respiratory water loss accounted for 486 kcal./da. while heat production was 2,280 kcal./da. Therefore, cutaneous evaporative heat loss must have been responsible for a portion of total heat loss. Accordingly, Table 2 tabulated a significant increase in sweating at 40° C. and 45° C. when compared to lower temperatures. On the basis of these findings, both cutaneous and respiratory evaporative water loss are hypothesized as important avenues of heat loss in shorn sheep during heat stress. In addition, increased respiratory water loss precedes the onset of sweating and therefore is relatively more important during mild heat stress (35° C.). However, during severe heat stress (40 and 45° C.) heat loss by cutaneous evaporative water loss is relatively more important.

Metabolic heat production increased above thermoneutral values during both heat and cold stress (Figure 26). Significant ($P < .05$) increases in heat production above the critical temperature II are believed due to two factors. First, muscular activity associated with panting results in elevated heat production. Second, a rise in "deep" body temperature leads to increased heat production in accordance

with the Q_{10} law. Data presented in Table 5 indicate that the Q_{10} effect may be greater than the effect of panting. The importance of the Q_{10} effect on heat production in sheep suggests a need for further study.

Increased metabolic heat production during cold stress (Figure 26) is attributed to shivering. Slee and Sykes (1967) reported the onset of shivering in shorn sheep at 16° C., and moderate shivering at 5 to 10° C. Conclusive shivering was detected in the present experiment at 10° C. which coincided with a significant increase in heat production (Table 2). The wide range of values of heat production (Figure 26) observed at 10 and 15° C. suggests individual variation in the onset and magnitude of shivering. The need for studies specifically designed to elucidate the factors involved in these relationships are indicated.

The lowest metabolic heat production was observed at 30° C. with only a slight increase (1.8%) noted at 25° C. A larger increase (8.5%), although non-significant (Table 2) was measured at 20° C. Shivering was not observed concurrently with these increases of metabolic heat production. Since non-shivering thermogenesis has not been reported for adult sheep, it is presumed that "thermal muscular tone" which preceeds shivering (Burton and Edholm, 1955) accounts for increased heat production during mild cold stress (15 and 20° C.). Critical temperature I is coincident with the ambient temperature where cold stress begins.

On the basis of the initial increases in heat production below the thermoneutral zone, the results of this study indicate that critical temperature I of sheep (as previously defined) is greater than 20° C. Table 2 shows that only a slight (1.8%) increase in heat production is noted at 25° C. as compared to a substantial (8.4%) increase at 20° C. These data suggest that critical temperature I may be near 25° C. although the slight increase (1.8%) does not warrant this as a conclusion. The 5° C. intervals of ambient temperature studied limit a more accurate assessment of critical temperature I. Comparable data reported by Blaxter *et al.* (1959a) suggests 26° C. as the critical temperature for shorn sheep on a maintenance ration. Dukes (1956) reports critical temperatures for swine, cattle (sheared) and goats (fasted) as 21° C, 18.3° C. and 20° C., respectively. It is concluded that critical temperature I for sheep (as defined) is greater than 20° C.

Hyperthermal rise, termed critical temperature II, and defined as the upper limit of the thermoneutral zone has not been reported in sheep. Before critical temperature II can be accurately determined, the relationship of its determinants (respiratory rate, respiratory and evaporative water loss) to heat stress must be clarified. The absence of these relationships has predicated the impression that critical temperature

II is of minor importance. However, the role of the critical temperature in determining the thermoneutral zone and in describing the initiation of heat loss mechanisms identifies it an important factor in the description of thermoregulatory mechanisms of sheep. On the basis of increased heat loss, this critical temperature is equal to or less than 30° C.

The investigation of physiological responses of homeotherms to thermal stresses requires the establishment of the thermoneutral zone. Numerous workers (Slee and Sykes, 1968; Blaxter _et al._, 1959b; and Armstrong _et al._, 1960) have considered 30° C. as thermoneutral for shorn sheep, although it can be modified by many variables (i.e., exercise, diet, etc.). This value was primarily based on vasomotor activity in the ear as indicated by rapid changes in ear skin temperature (Blaxter _et al._, 1959a). The use of this criterion to describe the thermoneutral zone in sheep is questionable due to the diversity of vasomotor activity observed in different body regions. It may be more appropriate to define the thermoneutral zone for sheep as the range of ambient temperature between critical temperature I (initial cold stress) and critical temperature II (initial heat stress). Based on these criteria the lower limit of the thermoneutral zone for sheep (as defined in this experiment) is equal to or greater than 20° C. while the upper limit is equal to or less than 30° C.

TABLE 1

Rectal, Skin, and Body Temperatures Recorded at Ambient Temperatures From 10 to 45° C. 1/

	Ambient temperature °C.							
	10	15	20	25	30	35	40	45
Rectal temp.	39.49	39.53	39.65	39.67	39.91	40.10	40.22	40.62
Face temp.	20.17	22.80	28.21	31.51	34.87	36.84	39.34	41.36
Ear temp.	15.17	18.53	23.72	27.70	34.19	37.65	39.24	41.44
Forelimb temp.	17.74	21.75	27.10	30.42	34.58	36.37	38.47	40.32
Stifle temp.	28.05	30.25	31.62	34.30	36.19	37.52	38.50	39.73
Trunk temp.	27.84	27.86	30.92	32.88	35.39	37.80	39.20	41.16
Mean skin temp.	36.83	27.17	30.46	32.58	35.31	37.71	39.18	41.15
Mean body temp.	37.06	37.08	37.83	38.10	39.14	39.47	40.02	40.72

1/ Temperature values are means of six observations in degrees centigrade. Means underlined are not significantly different ($P < .05$).

TABLE 2

Physiological Parameters Recorded at Different Ambient Temperatures 1/ 2/

a	0.46(10)	0.52(25)	0.68(20)	0.68(15)	1.01(30)	1.51(35)	3.53(40)	4.09(45)
b	0.042(25)	0.045(20)	0.046(15)	0.060(10)	0.070(30)	0.113(35)	0.123(40)	0.127(45)
c	.00013(45)	.00027(40)	.00068(35)	.00165(30)	.00233(25)	.00246(10)	.00077(20)	.00396(15)
d	.00073(45)	.00090(40)	.00158(35)	.00160(30)	.00176(25)	.00199(20)	.00225(10)	.00244(15)
e	21,189(15)	21,181(10)	21,232(20)	21,250(25)	21,321(30)	21,344(35)	21,382(40)	21,429(45)
f	19.33(15)	23.62(20)	24.12(25)	27.33(10)	49.08(30)	84.91(35)	150.70(40)	179.08(45)
g	65.13(30)	66.32(25)	71.94(20)	73.07(15)	74.43(35)	84.40(40)	80.25(45)	114.95(45)

1/ Each value is the mean of six observations. Means underlined are not significantly different ($P < .05$).

a = Cutaneous evaporative water loss (gm./in^2/24 hr.)
b = Respiratory evaporative heat loss (kcal./kg./hr.)
c = Whole body insulation (^{o}C./kcal.m^2 hr.)
d = Respiratory evaporative heat loss per breath (kcal./kg./hr.)
e = Body heat content (kcal.)
f = Respiratory rate (breaths/min.)
g = Metabolic heat production (kcal./kg.$^{3/4}$/hr.)

2/ Numeral in parenthesis is the ambient temperature in ^{o}C.

TABLE 3

Ambient Temperature Interval and Magnitude of Greatest Change of Rectal and Skin Temperatures

Measurement site 1/	Ambient temp. interval of greatest change 2/	Change per °C ambient temp.3/
Rectal temp.	40-45	0.03
Ear temp.	25-30	0.8
Face temp.	15-20	0.6
Forelimb temp.	15-20	0.6
Stifle temp.	20-25	0.4
Trunk temp.	15-20	0.4

1/ Rectal temperature was measured in lower colon. Skin temperatures were measured at the skin surface.

2/ Ambient temperature interval (°C.) when greatest change in temperature parameters were recorded.

3/ Change in temperature parameters (°C.) recorded per degree centigrade change in ambient temperature.

TABLE 4

Thermal Circulatory Indices at Different Ambient Temperatures 1/

Skin Area	Ambient Temperature °C. 10	15	20	25	30	Percent Change 2/
Ear	0.21	0.16	0.24	0.23	0.78	271
Face	0.58	0.50	0.90	1.00	1.03	106
Forelimb	0.35	0.39	0.59	0.68	0.91	160
Stifle	1.64	1.65	1.48	1.84	1.63	12
Trunk	1.72	1.11	1.25	1.21	1.15	55

1/ Thermal circulatory index = $\frac{T_S - T_A}{T_r - T_s}$

where: T_S = skin temperature (°C.)
T_r = rectal temperature (°C.)
T_A = ambient temperature (°C.)

2/ Percent change = $\frac{\text{Highest TCI} - \text{Lowest TCI}}{\text{Lowest TCI}} \times 100$

TABLE 5

Partition of Q_{10} and Panting Effects on Metabolic Heat Production and Calculation of Panting Index

Ambient temp.	Inc. in metabolic heat prod.1/	Q_{10} effect2/	Panting effect3/	Inc. in resp.evap. heat loss4/	Panting index 5/
35° C.	252	58	194	434	2.23
40° C.	516	155	361	486	1.34
45° C.	680	278	402	510	1.24

1/ Increase in metabolic heat production above lowest value recorded at 30° C. (kcal./24 hr.)

2/ Calculated Q_{10} effect of "deep body" (rectal) temperature on metabolic heat production (kcal./24 hr.).

3/ Effect of panting on metabolic heat production (total increased heat production - Q_{10} effect) (kcal./24 hr.).

4/ Increase in respiratory evaporative heat loss above lowest value recorded at 25° C. (kcal./24 hr.).

5/ Panting index = $\frac{(Hl)_p - (Hl)_r}{(Hm)_p - (Hm)_r}$

where: $(Hl)_p$ = heat loss during panting
$(Hl)_r$ = heat loss during rest
$(Hm)_p$ = heat production due to panting
$(Hm)_r$ = heat production during rest

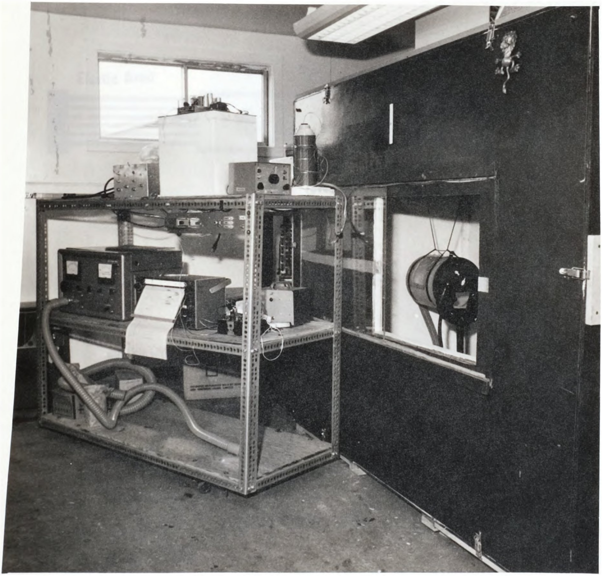


Figure 1. Picture of Temperature - Humidity Control Chamber

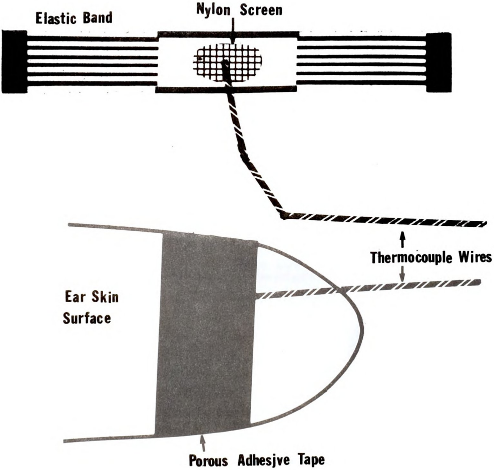


Figure 2. Schematic drawing of thermocouple attachment.

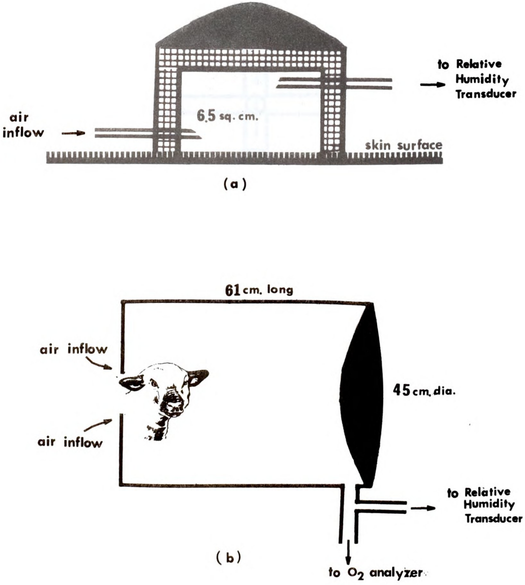
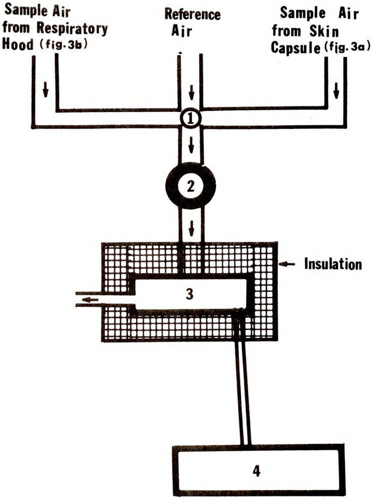


Figure 3. Schematic drawing of evaporative water loss air sampling systems (a-skin capsule, b-respiration hood).



1. **Three way valve**
2. **Air sampling pump**
3. **Relative humidity transducer**
4. **Recorder**

Figure 4. Schematic drawing of air flow system for determination of evaporative water loss.

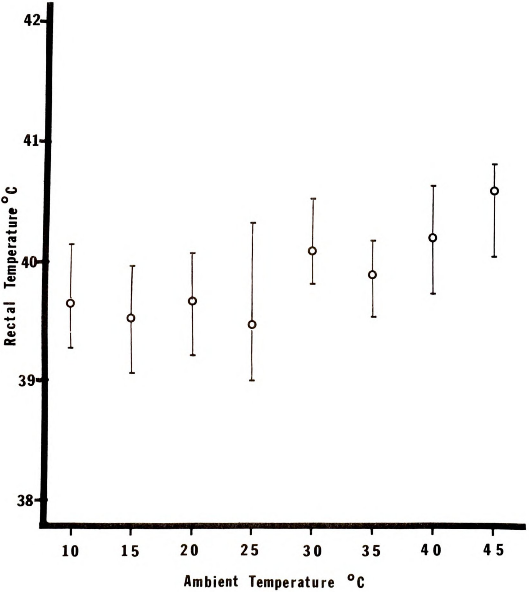


Figure 5. Rectal temperature as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

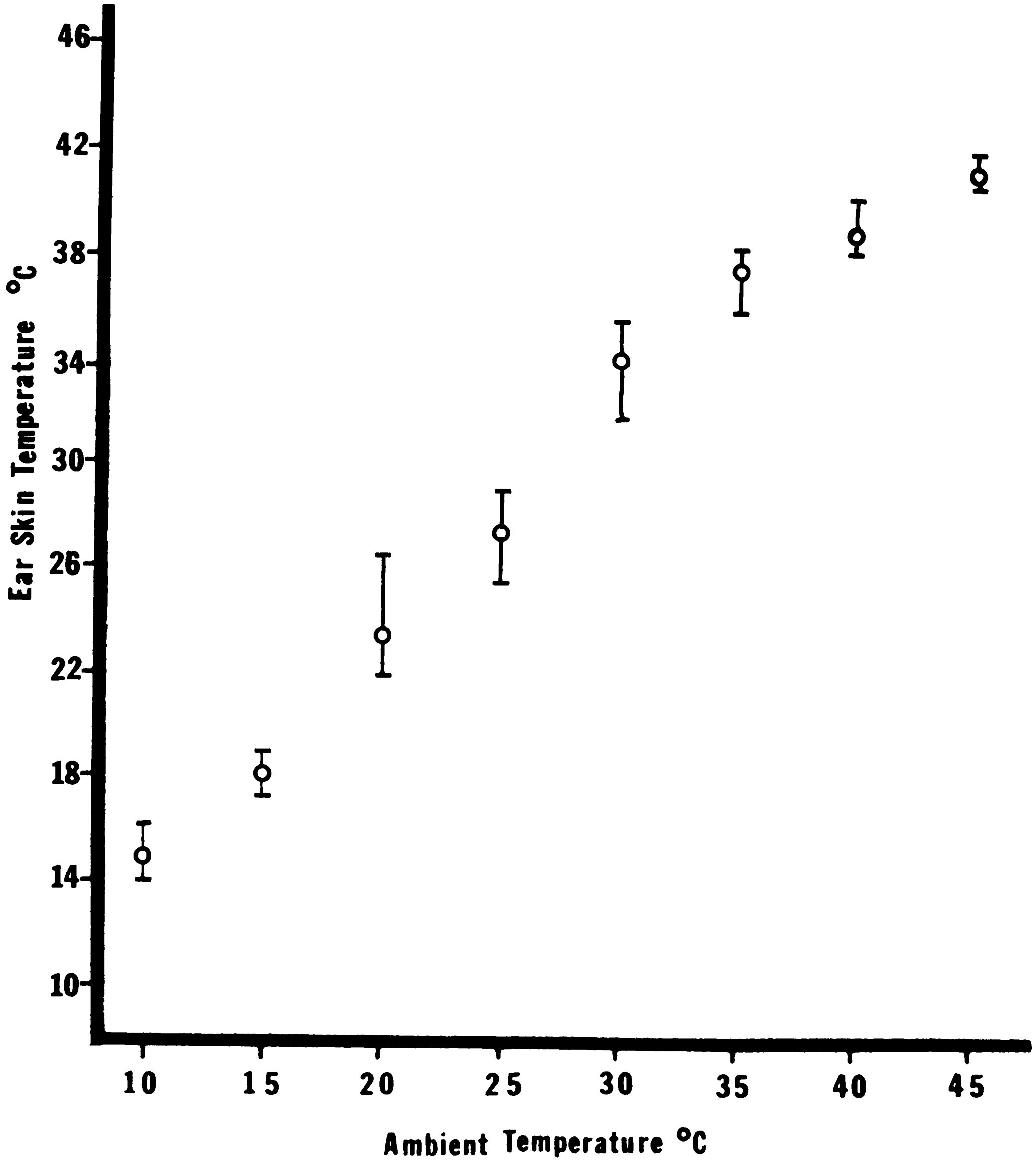


Figure 6. Ear skin temperature as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

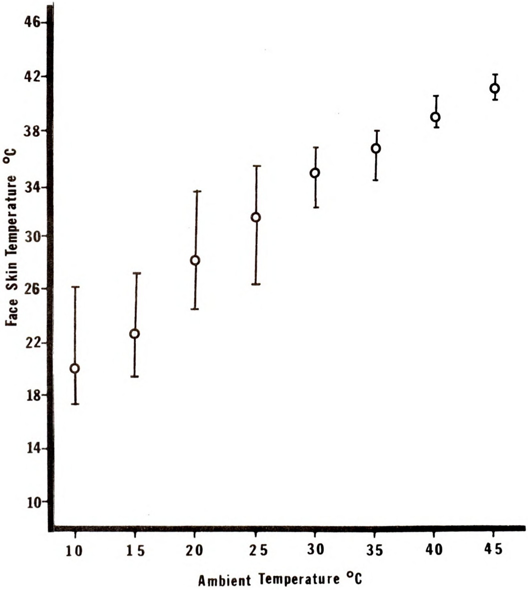


Figure 7. Face skin temperature as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

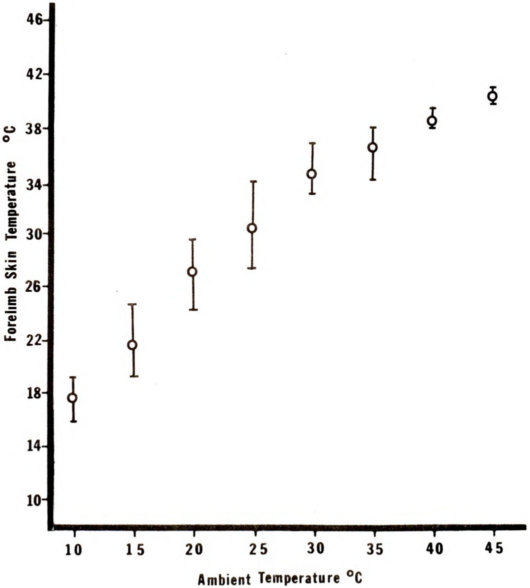


Figure 8. Forelimb skin temperature as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

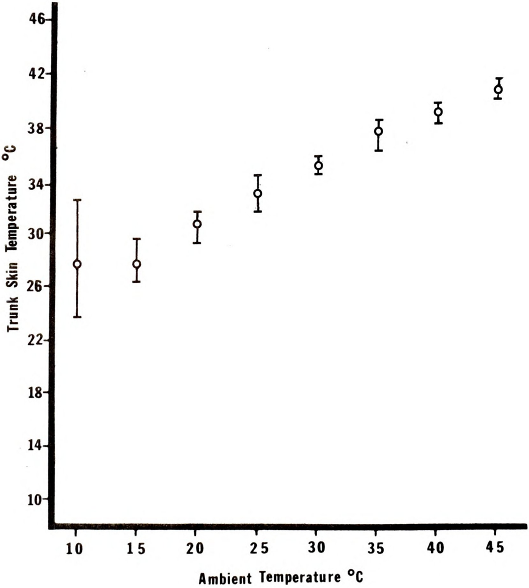


Figure 9. Trunk skin temperature as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

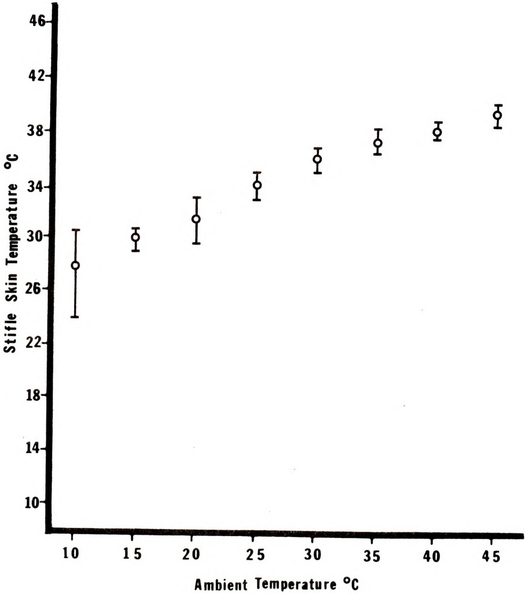


Figure 10. Stifle skin temperature as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

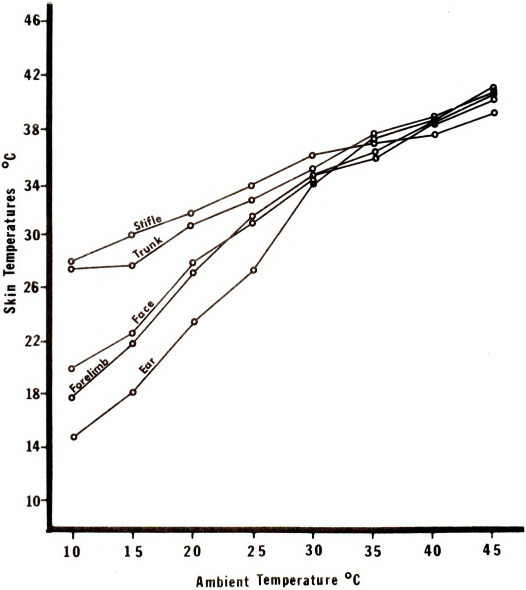


Figure 11. Skin temperatures as a function of ambient temperature.

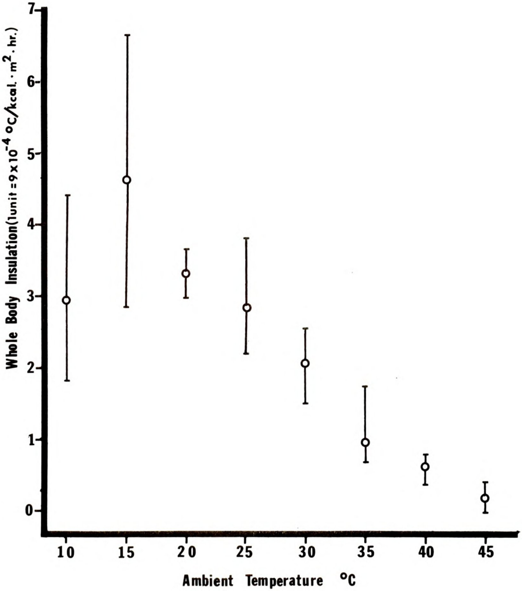


Figure 12. Whole body tissue insulation as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

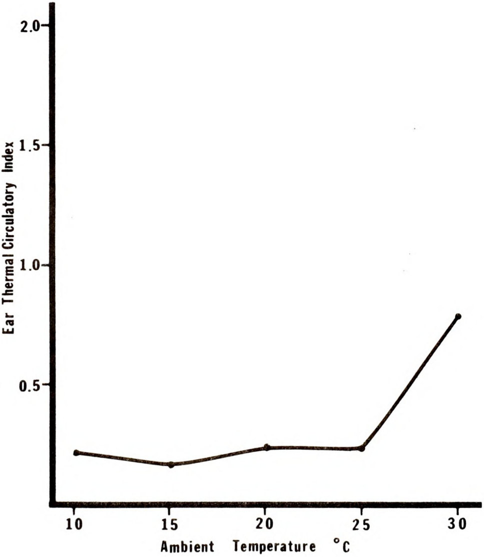


Figure 13. Thermal circulatory index of the ear as a function of ambient temperature.

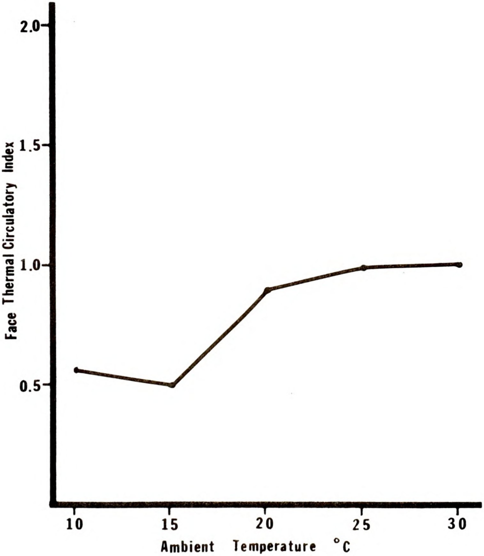


Figure 14. Thermal circulatory index of the face as a function of ambient temperature.

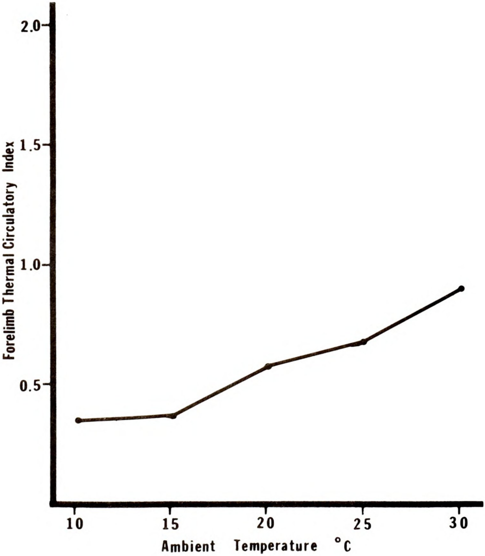


Figure 15. Thermal circulatory index of the forelimb as a function of ambient temperature.

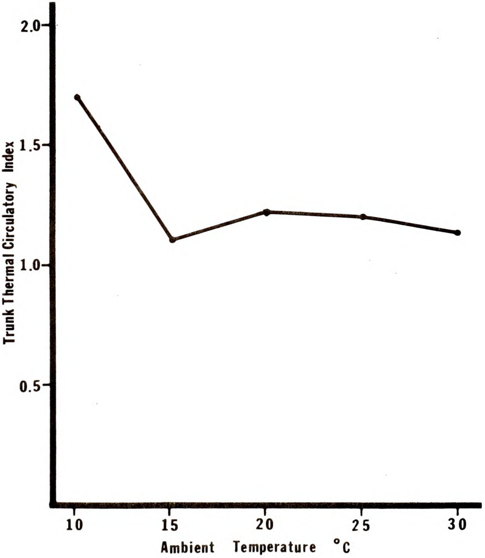


Figure 16. Thermal circulatory index of the trunk as a function of ambient temperature.

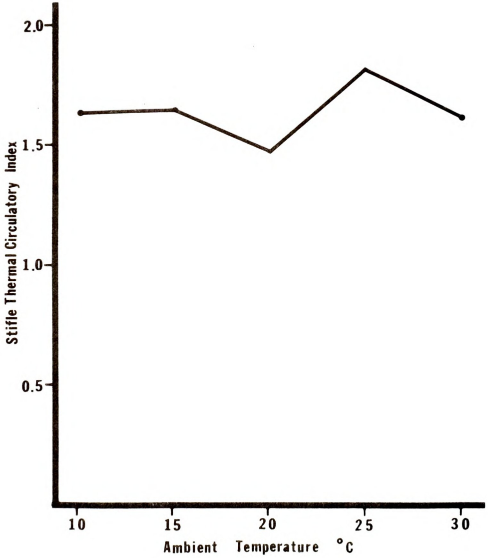


Figure 17. Thermal circulatory index of the stifle as a function of ambient temperature.

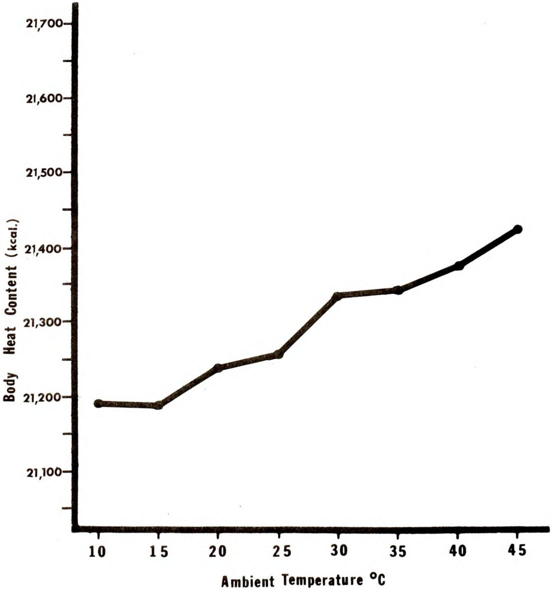


Figure 18. Whole body heat content as a function of ambient temperature.

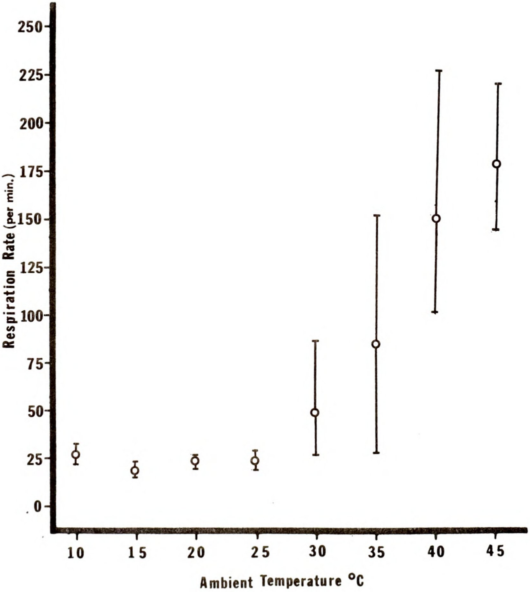


Figure 19. Respiratory rate as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

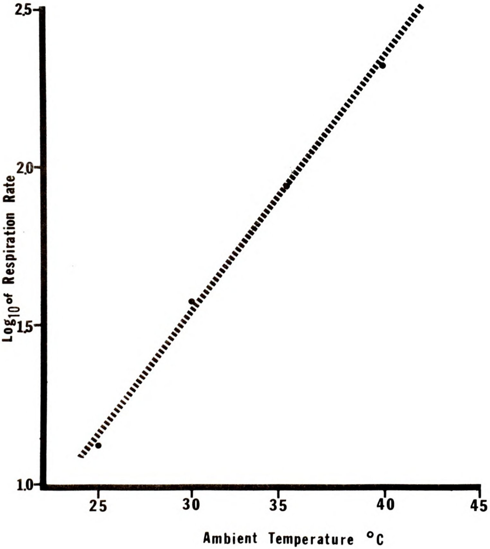


Figure 20. Log of respiratory rate as a function of ambient temperature.

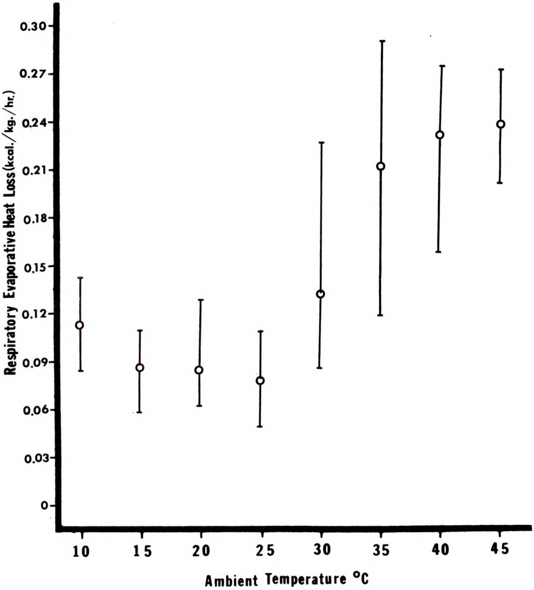


Figure 21. Respiratory evaporative water loss as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

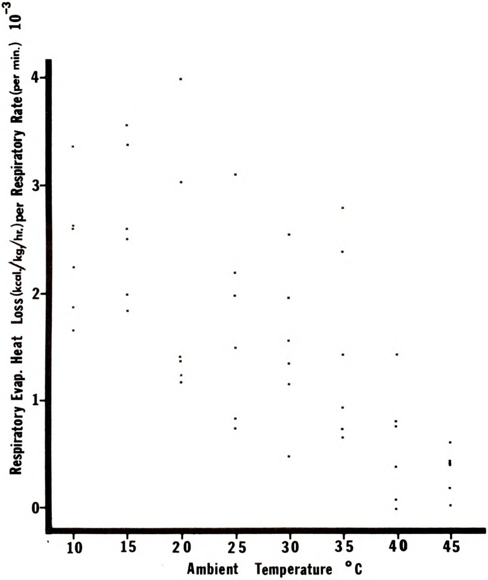


Figure 22. Respiratory evaporative heat loss per respiratory rate as a function of ambient temperature.

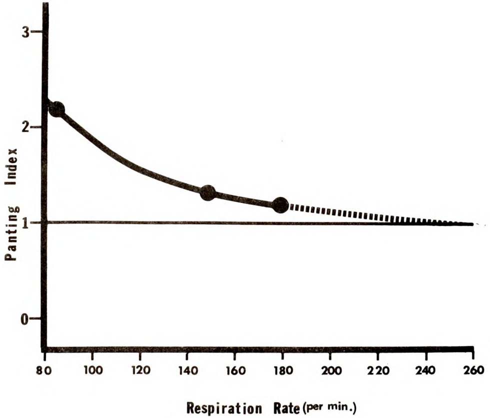


Figure 23. Panting index as a function of respiratory rate.

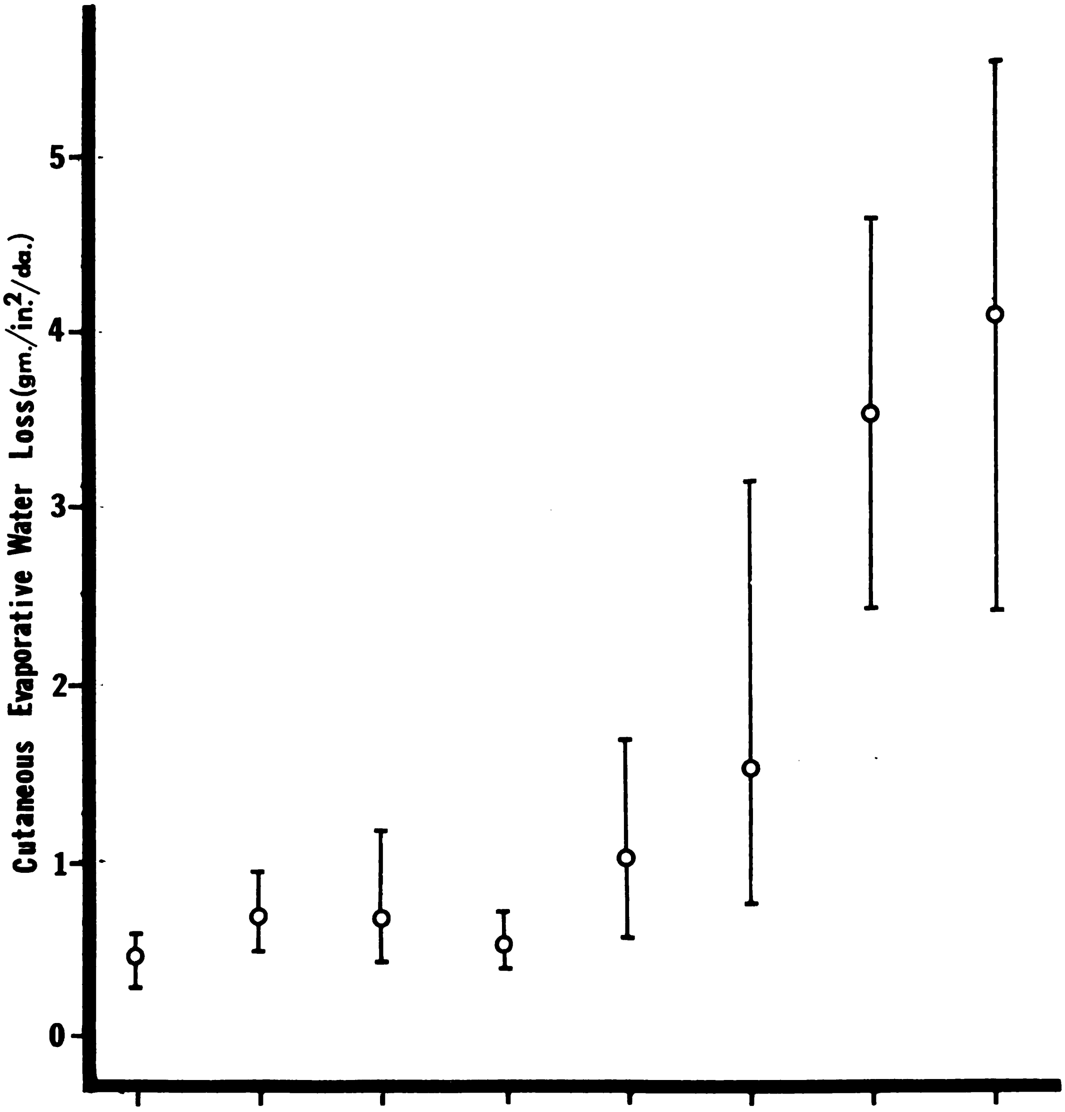


Figure 24. Cutaneous evaporative water loss as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

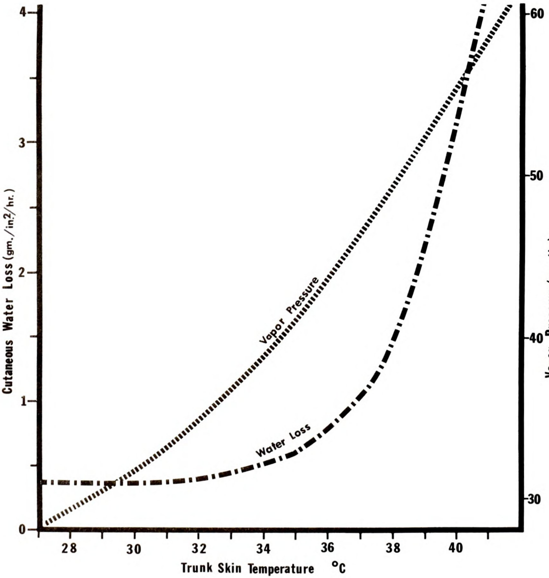


Figure 25. Comparison of vapor pressure and cutaneous evaporative water loss as a function of trunk skin temperature.

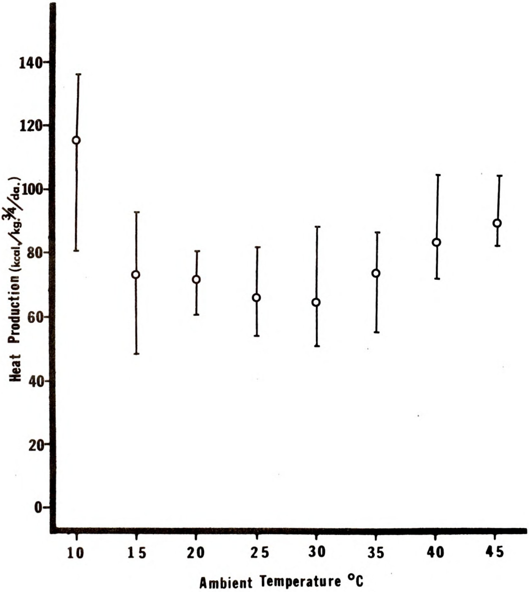


Figure 26. Metabolic heat production as a function of ambient temperature (circles indicate means and vertical lines denote ranges of six observations).

VI. CONCLUSIONS

1. The "normal limit" of rectal temperature in sheep is relatively wide.

2. TCI and changes in skin surface temperatures indicate that the ears, forelimbs and face (characterized by freedom from fleece, high surface area to mass ratio, and overlying areas of little fat or muscle tissue) are capable of vasomotion and are able to modify sensible heat exchange.

3. TCI and skin surface temperatures indicate that the trunk and stifle areas (characterized by the presence of fleece, low surface area to mass ratio and overlying subcutaneous fat and muscle tissue) are probably incapable of altering skin blood flow and consequently unable to modify sensible heat exchange.

4. Sheep do not appear to be capable of reducing skin blood flow to reduce heat gain when ambient temperatures are greater than rectal temperature.

5. Respiratory rate increases logarithmically from critical temperature II until ambient temperature equals rectal

temperature. These data suggest that changes in respiratory rate are valid indicators of thermoregulatory mechanisms.

6. Panting indices suggest that at rates exceeding 240 breaths per minute, panting is a thermal liability.

7. Comparison of obligatory and observed cutaneous water loss indicated the presence of active sweating on sheep.

8. It is hypothesized that cutaneous and respiratory evaporative water loss are both important avenues of heat loss in shorn sheep during heat stress. It appears that respiratory evaporative water loss is relatively more important during mild heat stress (35° C.) but that sweating is relatively more important during severe heat stress (40 and 45° C.).

9. Increases of heat production during cold stress are due to shivering. Increases during heat stress are due to the respiratory activity of panting but more importantly to the Q_{10} effect. The latter, which has received little attention in the past, deserves careful consideration in sheep because of the wide "normal" range of rectal temperatures.

10. The 5° C. intervals of ambient temperature used in this study do not allow accurate determination of critical temperatures. The data suggest that critical temperature I is equal to or greater than 20° C. and that critical temperature II is equal to or less than 30° C.

11. On the basis of physiological responses indicative of heat and cold stress, the lower limit of the thermoneutral zone for sheep (as defined in this experiment) is equal to or greater than 20° C. while the upper limit is equal to or less than 30° C. The use of skin surface temperature to estimate the thermoneutral zone is questioned.

APPENDIX

APPENDIX I

FREQUENTLY USED SYMBOLS

TNZ	Thermoneutral zone
CTI	Critical temperature I
CTII	Critical temperature II
T_A	Ambient temperature
T_r	Rectal temperature
T_e	Ear skin temperature
T_f	Face skin temperature
T_{fl}	Forelimb skin temperature
T_t	Trunk skin temperature
T_{st}	Stifle skin temperature
$T_{\bar{b}}$	Mean body temperature
$T_{\bar{s}}$	Mean skin temperature
ΔT_r	Change in rectal temperature
RR	Respiration rate
Rewl	Respiratory evaporative water loss
Cewl	Cutaneous evaporative water loss
BHC	Whole body heat content
H_m	Metabolic heat production
TCI	Thermal circulatory index
CIVD	Cold induced vasodilation
I_t	Tissue insulation
R.H.	Relative humidity

APPENDIX II

CORRELATION COEFFICIENTS

x	y	r
T_r	T_f	0.67
T_r	T_e	0.65
T_r	T_{fl}	0.64
T_r	T_{st}	0.64
T_r	T_t	0.67
T_r	RR	0.68
T_r	H_m	0.15
T_r	Rewl	0.52
T_r	Cewl	0.74
T_r	Rewl/RR	-0.51
T_r	$T_{\bar{s}}$	0.16
ΔT_r	RR	-0.70
ΔT_r	Rewl	-0.67
ΔT_r	Rewl/RR	0.43
T_A	T_r	0.66
T_A	$T_{\bar{s}}$	0.97
T_A	$T_{\bar{b}}$	0.95
T_A	I_t	-0.85
T_f	T_e	0.96
T_f	T_{fl}	0.96
T_f	T_t	0.91
T_f	$T_{\bar{s}}$	0.93
T_e	T_{fl}	0.98
T_e	T_{st}	0.96
T_e	T_t	0.96
T_e	$T_{\bar{s}}$	0.97
T_{fl}	T_{st}	0.96
T_{fl}	T_t	0.95
T_{fl}	$T_{\bar{s}}$	0.96
T_{st}	T_t	0.94
T_{st}	$T_{\bar{s}}$	0.94
RR	Rewl	0.80
Rewl	Rewl/RR	-0.40
Rewl	$T_{\bar{s}}$	0.72
RR	$T_{\bar{b}}$	0.81
RR	$T_{\bar{s}}$	0.78
Cewl	T_t	0.74
Cewl	$T_{\bar{b}}$	0.79
Rewl	Cewl	0.74

APPENDIX III

REGRESSION EQUATION*

x	y	a	b
T_A	$T_{\bar{s}}$	0.439	21.71
T_A	$T_{\bar{b}}$	0.110	35.66
T_A	RR	4.590	56.45
T_A	Rewl/RR	-4.70×10^{-5}	2.95×10^{-3}
T_A	I_t	-1.0×10^{-4}	4.6×10^{3}
T_A	H_m	-0.261	87.27
T_A	Cewl	0.101	-1.23
T_A	Rewl	0.003	0.01
T_A	T_t	0.412	22.80
T_A	T_{fl}	0.651	12.93
T_A	T_{st}	0.339	25.19
T_A	T_f	0.620	14.85
T_A	T_e	0.797	7.78
T_A	T_r	0.028	39.15
T_r	Rewl/RR	-8.1×10^{-4}	0.03
T_r	Rewl	0.043	-1.64
RR	Rewl	4.9×10^{-4}	0.04

*$y = a + bx$

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