TOPIC 3. THERMOREGULATION

A homeothermic animal maintains a balance between heat production and heat loss. Since heat production and heat loss are constantly changing, the animal is in a continual state of dynamic equilibrium. When the animal is in a thermoneutral zone, the balance between heat production and heat loss may be maintained without special thermoregulation.

Physiologists have usually defined the thermoneutral zone as the range of temperatures which do not cause a metabolic response to maintain homeothermy during basal metabolic measurements. This dependence on temperature has been useful for physiologists who needed to establish some laboratory standard for comparative work, but it is quite inadequate for ecologists concerned with the free-ranging animal. Many animals spend a considerable portion of their time outside of such a physiologically defined thermoneutral range, yet they survive and reproduce.

The homeothermic animal maintains a balance between heat production and heat loss by distributing the heat produced during normal life processes and increasing the heat production when the animal is in a critical hypothermal environment. The heat production by metabolic processes is often localized in a specific areas of the body. Muscle metabolism and rumen fermentation, for example, are two exothermic processes that are quite localized, and it is necessary for the animal to distribute this heat energy throughout its body.

The use of the term "thermoneutral range" in an ecological context implies that there is a balance between heat production during normal activity and heat loss in a complex thermal regime that includes radiation, convection, conduction, and evaporation as the four modes of heat transfer. The thermal environment includes all factors that are a part of the heat production-heat loss relationship. A critical thermal environment (Moen 1968) occurs when the animal must make a response in order to maintain homeothermy. The continual adjustment of physiological and behavioral responses results in short-term temperature transients in the animal, a normal part of life for a homeotherm.

A thermal regime may occur in which the heat production of an animal is greater than the heat loss even though the animal may attempt to maintain a balance. When this occurs, the animal is in a critical hyperthermal environment. If heat loss is greater than heat production, the animal is in a critical hypothermal environment (Moen 1968).
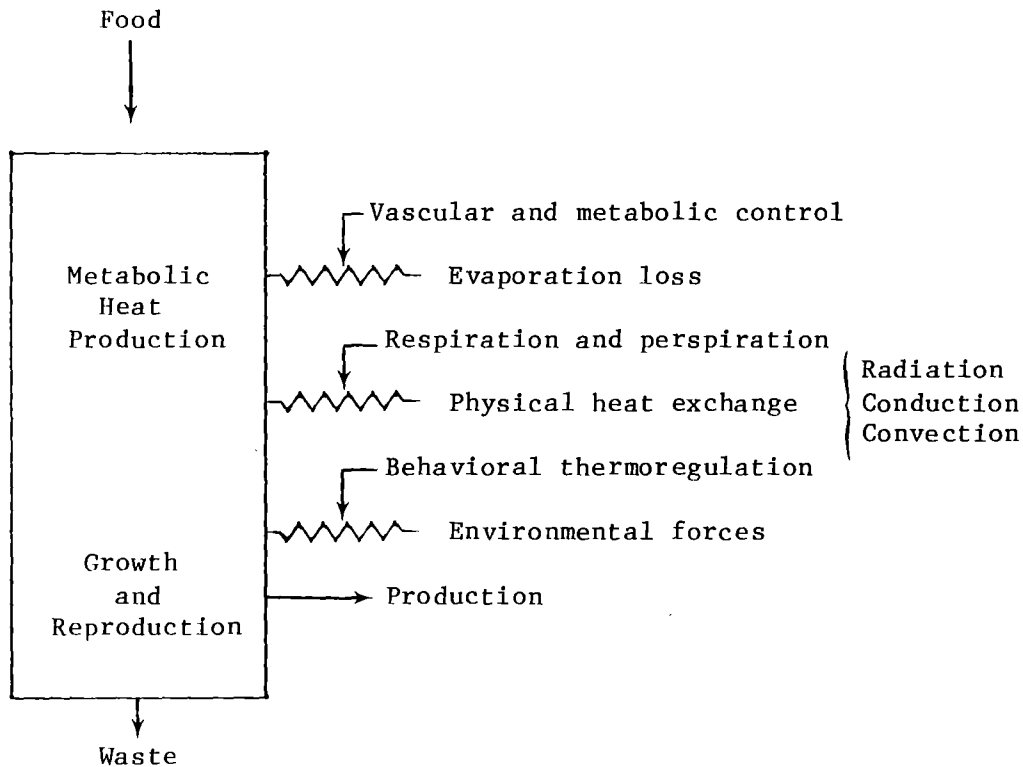
Situations can develop when the many factors that make up the thermal regime, including both heat production and heat loss factors, may result in a critical thermal environment that is partly independent of existing weather conditions. A deer being chased by dogs on a cool fall day, for example, may reach a critical hyperthermal environment because heat production has increased greatly due to running. The weather is not critical; running is the critical factor. A deer may reach a critical hypothermal environment during a spring rain when the molt is in process and the new summer coat becomes soaked with water. The effect of this rain might be critical during the molt, but could have been quite unimportant when the animal was still in winter coat. Thus the critical factor is the stage of the molt rather than the rain. These examples illustrate how combinations of conditions may interact to cause one factor to become important under particular conditions.

Any factor that is a part of the thermal regime could become critical if some of the other thermal conditions were near critical. In a high wind, for example, there could be a critical orientation of the animal that would result in a favorable balance between heat production and heat loss. A critical wind velocity, critical radiant energy level, critical activity level, critical posture, or any other critical variable is meaningful only when all other thermal factors are identified.

Many different combinations of thermal factors can occur for free-ranging animals. Recognizing this, one immediately realizes that the traditional idea of upper and lower critical temperatures to identify the end points of the thermoneutral zone is entirely inadequate in ecology. It has served a useful purpose in the laboratory where chamber conditions are quite well represented by a temperature measurement, but data from these simplified laboratory experiments cannot be applied to the dynamic thermal regimes of free-ranging animals.

The time has come to analyze rather than merely correlate weather data with animal responses. The ecological definition of the thermoneutral range is more of a concept that includes an understanding of the principles of heat exchange rather than a precise definition composed of a set of factors. Further, an understanding of the principles of heat exchange enables one to separate the physiological and behavioral responses to the thermal environment from the responses to social interaction between animals or other stimuli that are not related to weather factors.

The thermal exchange system consists of input and output energy. Input energy includes food that is the source of energy for metabolic processes, and solar and infrared radiation that add to the heat load. Output energy includes the energy that goes into activity, growth and reproduction. The several variables in this system include vascular control over physical heat exchange, respiratory and perspiratory control over evaporation losses, behavioral control over physical heat exchange, and production. A schematic of this system is given at the top of the next page.

```
        Food

          │
          ▼
┌─────────────────┐
│                 │      ┌─Vascular and metabolic control
│   Metabolic     │      │
│     Heat        │  ───┤ ᐯᐯᐯᐯᐯ ─ Evaporation loss
│  Production     │      ┌─Respiration and perspiration
│                 │      │                              ⎧ Radiation
│                 │  ───┤ ᐯᐯᐯᐯᐯ ─ Physical heat exchange ⎨ Conduction
│                 │      ┌─Behavioral thermoregulation   ⎩ Convection
│                 │      │
│    Growth       │  ───┤ ᐯᐯᐯᐯᐯ ─ Environmental forces
│     and         │  ──────► Production
│ Reproduction    │
│                 │
└─────────────────┘
          │
          ▼
        Waste
```

An animal that maintains a balance between heat loss and heat produc-
tion is constantly adjusting the variables over which it has some control.
These can be grouped into two classes: physiological controls and be-
havioral controls. They are not biologically distinct, though, since no be-
havioral response can occur without a physiological function. These two
controls over thermoregulation are discussed in the next two UNITS.

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    concept. BioScience. 18(11):1041-1043.

UNIT 3.1: PHYSIOLOGICAL THERMOREGULATION

An animal can respond to the thermal environment in two ways, including 1) a heat-producing or a thermogenic response, and 2) a heat-conservation response. The heat-producing response involves metabolic processes and thermogenesis. The heat-conservation response involves regulation of the animal-to-environment thermal gradient. These two processes occur together so it is the net effect--whether a change in the heat production is greater or less than a change in the heat loss--that is important.

Heat-producing or thermogenic responses can occur within seconds, and metabolic patterns occur in daily and seasonal cycles also. The metabolic rate is higher during the day for diurnally active animals, and higher at night for those that are nocturnal. White-tailed deer exhibit a seasonal rhythm in metabolic rate, with lower metabolic rates in the winter and higher rates in the summer (Moen 1978).

Heat-conservation or thermoregulatory responses can occur within seconds too, and seasonal cycles such as changes in the hair coat and in the behavior of the animals also occur over periods of several months.

Coat characteristics are an important adaptation for survival in the colder regions of the earth. It is generally thought that the insulation of the coat is the major adaptation of northern species, but the winter metabolic depression is also important. Marked differences do occur between depth and structure of summer and winter coats. White-tailed deer have a summer coat of sparse and fine hair. The winter coat is thick and coarse, with depths over 2.0 centimeters on the trunk. The hairs in the longer winter coat also are hollow and crinkled, with an underfur that consists of very fine hairs that are about as numerous as the longer hairs.

Coat color is a genetic characteristic of interest in analyzing the radiation exchange of an animal, especially because of seasonal changes in color, thickness, and depth. From a thermal point of view, it is advantageous for a rough-coated animal to be white in the winter so a maximum amount of solar radiation can be absorbed by reflection into the hair coat (see CHAPTER 15, UNIT 1.2).

Two ecological rules that relate body structure to climate factors have become firmly entrenched in the ecological literature. Bergman's Rule states that northern members of a species have a larger body size than southern members. This is interpreted as a genetic adaptation to cold since a larger body has a higher volume to surface area ratio than a smaller one. Allen's Rule states that northern species have smaller appendages than southern ones. This is interpreted as an adaptation for the conservation of heat in the north with less surface area on legs and ears, and for the dissipation of heat in southern climates as the appendages act as cooling fins.

The validity of interpreting Bergman's and Allen's Rules on the basis of a climatic gradient may be questioned. Both of the rules are logical in theory, but the number of factors involved in thermal exchange and the compensatory effects of interaction between physiological and behavioral factors indicate that the body size or appendage size differences may be quite insignificant compared to other thermoregulatory mechanisms. Further, the younger members of each species are usually smaller than the mature animals in either north or south, so the rules are violated by each individual during its life span.

An animal may increase its heat production by increasing gross body activity or by increasing the rate of metabolism in specific organs or tissues. Raising the level of gross body activity is not a 100% efficient process since greater body movement results in a greater heat dissipation due to the effect of movement in the hair-air interface. Heat exchange by convection is also increased as the animal moves through the air, increasing the effective wind velocity at its surface.

The increase in metabolic rate due to elevated activity levels may be sufficient to offset heat losses during cold conditions, but it cannot be kept up for long periods of time because of muscle fatigue. Thus it is effective only if the activity level is somewhat similar to normal daily patterns. Less obvious but very important thermogenic responses are found in metabolic potentials that do not involve overt muscular activity. Animals conditioned to cold weather (Acclimatization, Folk 1966) are more capable of withstanding cold than animals that have had no previous exposure to cold.

A general relationship has been observed between heart rate, oxygen consumption, and heat production; an increased heart rate is indicative of a higher heat production. This general relationship between heart rate and metabolism shows considerable variation between individual animals, however, so it is necessary to calibrate each animal to determine its own heart rate:oxygen consumption curve.

One metabolic response that has received considerable attention by physiologists is non-shivering thermogenesis which involves an increase in heat production that results from the metabolism of brown fat. Larger species such as cattle apparently do not have brown fat. Bruck et al. (1969) formulated a general rule, documented also by Jansky et al. (1969), that the bigger the animal, the less brown fat it possesses. This conclusion was reached after careful consideration of their own work and of others reported in the literature. Wild ruminants apparently do not rely on non-shivering thermogenesis for the maintenance of homeothermy.

The metabolic rate of white-tailed deer confined to a temperature-controlled metabolic chamber rose as the chamber temperature was lowered. The actual rate of metabolic increase in relation to chamber temperature cannot be applied directly to temperature data in the field because of the many other thermal factors that need to be considered in the field. The experiments were useful, however, for determining the metabolic potential of deer without a significant increase in gross body activity.

Another metabolic process important in thermogenesis in ruminants is the effect of the heat of rumen fermentation. Ingested forage is digested by rumen microorganisms, and the exothermic fermentation process provides heat energy that contributes to the maintenance of homeothermy. Absorption of nutrients follows digestion, and then these nutrients are metabolized in the cells of the animal, resulting in an additional source of heat attributed to nutrient metabolism.

Experiments on sheep in chambers show that the critical temperature based on the chamber environment is higher when the sheep are at a low feeding level, lower on a medium feeding level, and lowest on the highest feeding level (Graham et al. 1959:23 and Graham 1964:982). This is the pattern one would expect, but it must be emphasized that an animal has several alternative pathways to maintain heat production or regulate heat loss. In the absence of sufficient food, for example, fat catabolism occurs under cold conditions so heat production may be maintained at a necessary level. New-born lambs, not yet developed as homeotherms, survived longer when confined in a room at 23°C than those at 9°C, indicating that a lower heat production was possible as the warmer room resulted in a reduced rate of heat loss from the animal (Alexander 1962:144). This is similar to the conclusions of Moen and Severinghaus (1981) for white-tailed deer that exhibited higher death weights in colder and less protected areas than in warmer, more sheltered areas.

The rate of depletion of the fat reserve is an important consideration when food is inadequate and shelter conditions vary. The significance of fat reserves to wild ruminants may be considered when calculating carrying capacity for different time periods

Heat-conservation responses are dependent on reductions in thermal gradients. Heat energy is distributed to different parts of the body when the circulatory system functions as a thermal transport mechanism. The flow of blood from a warmer area to a cooler area results in the transport of heat energy by convection processes. This is a passive event unless the organism exhibits some control over the flow characteristics in order to maintain a thermal balance.

Both passive and active mechanisms are found in animals. A heat exchanger, illustrated at the top of the next page, is a passive mechanism that has been suggested as one adaptation of caribou for the maintenance of sharp temperature gradients in the extremities (Irving and Krog 1955). This arrangement permits the exchange of heat without an exchange of arterial and venous blood. The heat flow is simply a conduction process from the warm arterial walls through the body tissue to the cooler venous blood that is returning from the extremity. This results in colder tissue temperatures in the extremities, and a reduction in the thermal gradient between animal and environment.

Arterial   Venous
flow   flow
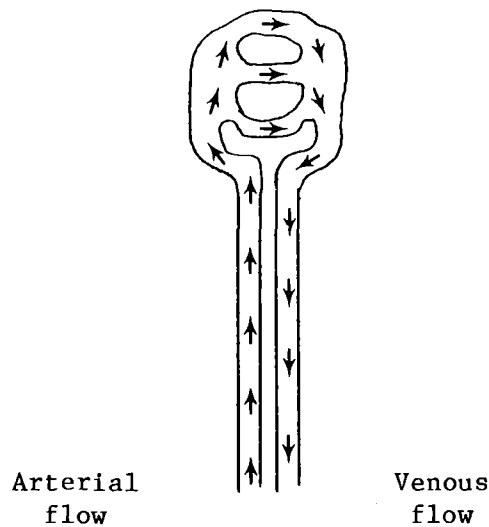
A vascular shunt is an active mechanism for the distribution of heat energy as the blood is shunted from an artery to a vein, diminishing the blood supply in the terminal capillary beds as illustrated below. This results in a reduction in heat loss from the extremity since the blood flow is reduced, but this also causes a reduction in the oxygen supply.

Arterial   Venous
flow   flow
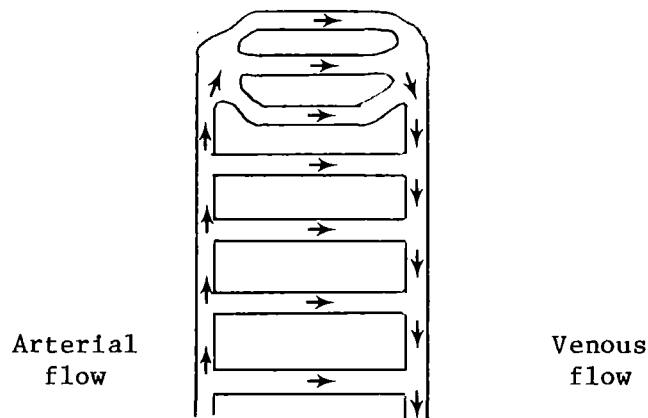
Regulation of heat loss by the control of blood flow is not precise enough to result in a constant temperature of the extremity. Ear temperatures of caribou, for example, showed phasic changes from lows of nearly freezing (0°C) to 15°C, back to 0°, etc. This indicates that the different parts of the anatomy of homeotherms are not in thermal balance, but that the whole body over longer time periods is.

The importance of vascular control of heat flow is related to the insulation characteristics of the coat. The amount of vascular control in the extremeties is relatively more important because of the shorter, sparser hair than on the trunk. The importance of blood flow and hair insulation is further modified by the distribution of subcutaneous fat and piloerection. A fat layer also reduces the heat loss from the animal's surface since fat tissue is a good insulator.

Pilo-erection has traditionally been considered a heat-conservation mechanism because of the increase in the depth of the insulation layer. This increase in depth, however, is compensated for to an unknown extent by the more open characteristic of the hair coat. The loss of heat through a more open hair layer is greater because of increased penetration by wind and subsequent convective heat loss. Thus the decrease in the thermal conductivity due to the greater depth of erected hair is counteracted by the increase in heat flow through the more open erect hair. If the net effect were an increase in heat loss, pilo-erection would not be a heat conservation mechanism.

My theory is that pilo-erection is a heat-producing adaptation as well as a mechanism for heat-conservation. During warm conditions, normal muscle tonus results in a small amount of heat production from the metabolic processes involved in muscular contraction. A small temperature gradient exists between the external surface of the skin and the subcutaneous muscle later. If heat loss increases, the temperature gradient from skin to muscle increases and the thermal receptors in the skin sense the colder conditions. The central nervous system relates the signal to the muscle tissue beneath the skin and the muscles contract with a concomitant release of heat energy. This heat energy raises the temperature in that area of the skin and reduces the temperature gradient. As the muscles contract and release heat, the hair is erected. Pilo-erection is then a secondary effect, with the ex-othermic muscular contractions a heat-producing process of importance in altering the temperature gradients and subsequent flow of heat. Changes in the temperature gradients are illustrated below.

Warm: no pilo-erection

Temperature gradient ———————————————————— Skin
———————————————————— Muscle layer

| | | | | | |
10   15   20   25   30   35   40
Temperature (C)

Cold: before pilo-erection

Temperature gradient ———————————————————— Skin
———————————————————— Muscle layer

| | | | | | |
10   15   20   25   30   35   40
Temperature (C)

Cold: after pilo-erection

Temperature gradient ———————————————————— Skin
———————————————————— Muscle layer

| | | | | | |
10   15   20   25   30   35   40
Temperature (C)
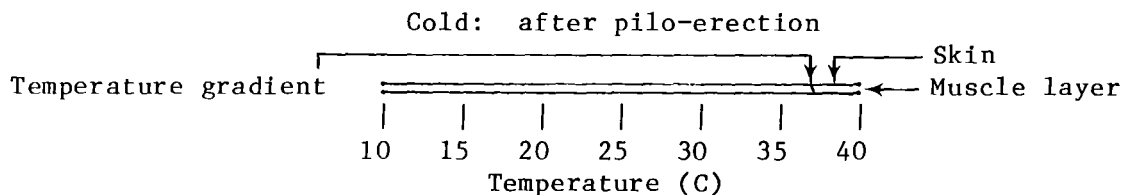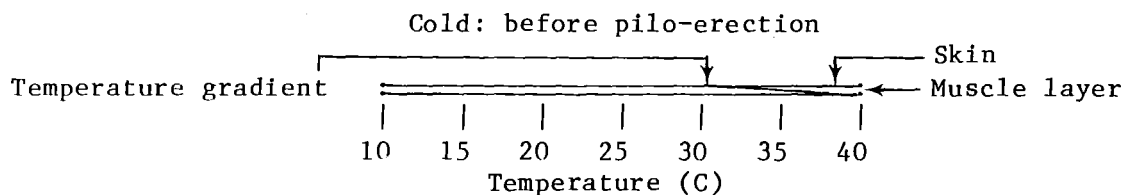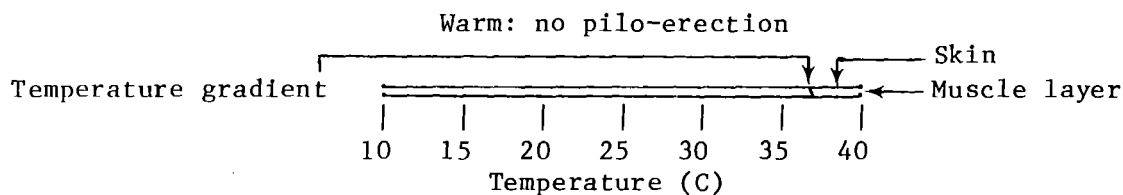
Evaporation of body fluids is a thermoregulatory response that occurs under hot conditions. The balance between heat loss and heat production in hot environments can be regulated by a reduction in nutrient intake and an increase in evaporative heat losses. Thus water is consumed at high levels during hot weather. When the effective environmental temperature is equal to or greater than body temperature, evaporative heat loss is the only kind of heat loss that can occur. Radiation, conduction, and convection result in a heat input rather than a heat loss.

The evaporative heat loss from respiratory surfaces can be increased by panting. This is, in part, an inefficient process because exothermic reactions occur as muscles are used for panting. This increases heat production, which must be offset by increases in heat loss by evaporation. There are few data available that provide an indication of the relative magnitude of the two opposing forces.

Wetting of an animal's surface results in an increase in heat loss by evaporation. An increase in heat production may result; infant caribou with wet fur had a heat production up to 10 times the basal rate (Hart et al. 1961). The heat loss due to evaporation has been suspected as a cause of mortality in the newborn of several different species.

Several other physiological responses are observed when animals are exposed to thermal regimes that are beyond the zone of thermoneutrality for any length of time. Body growth and production are retarded in hot environments, and reproduction is generally less successful. Hypercritical thermal environments for a few hours or days can result in mortality as body tissue is not adapted to the maintenance of metabolic processes at temperatures much over 2°C above normal.

The physiological effects of cold environments are frequently less critical than those of hot environments. The effect of cold environments can be compensated for by higher planes of nutrition that permit increased heat production up to the maximum metabolic potential of the animal. If the amount of ingested food is insufficient to meet the energy needs in the cold, body tissue can be mobilized. Fat is mobilized in such a way by wild ruminants during each winter. Pregnant females may resorb the fetus, thus reducing the reproductive rate. While these responses are known to be possible, there are no field data on population effects except for documented winter mortality for some species in selected areas.

Behavioral thermoregulation is discussed in the next unit (UNIT 3.2). It is closely tied to physiological thermoregulation since behavioral acts cannot be completed without physiological functions.

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PHYSIOLOGICAL THERMOREGULATION

SERIALS

TYPE	PUBL	CITY	PAGE	ANIM	KEY WORDS----------------	AUTHORS/EDITORS--	YEAR
edbo	apso	wadc		mamm	p 361, terres anim in cold	bill,db	1964
aubo	lefe	phpa	308	----	intro, environmntl physiol	folk,ge,jr	1966
edbo	acpr	nyny	1967	mamm	p 412, resistance to cold	rose,ah	1967

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS----------------	AUTHORS----------	YEAR
BISNA	18--11	1041	1043	odvi	criticl thermal environmnt	moen,an	1968
CJZOA	53--6	679	685	odvi	ambien temp effect, physio	holter,jg; urban/	1975
ECOLA	57--1	192	198	odvi	energy conservat in winter	moen,an	1976
JWMAA	35--1	37	46	odvi	effect falli temp, heat pr	silver,h; holter/	1971
JWMAA	42--4	715	738	odvi	seas chan, heart rate, act	moen,an	1978
NFGJA	28--2	162	177	odvi	annual wt cycl, survivl,ny	moen,an; severing	1981

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS----------------	AUTHORS----------	YEAR
CJZOA	56--11	2388	2393	ovca	winter bioenerget, rocky m	chappel,rw; hudso	1978
JWMAA	35--3	488	494	ovca	variat of rectal temperatu	franzmann,aw; heb	1971

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS----------------	AUTHORS----------	YEAR
				odhe			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS----------------	AUTHORS----------	YEAR
				ceel			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS----------------	AUTHORS----------	YEAR
				alal			

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CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

APSCA 105-3 268  273  rata spitzberg. womt-dorman ung ringberg,t       1979

CBPAB 60A-2 123  126  rata seas change growth hormone ringberg,t; jaco/ 1978

CJZOA 39--7 845  856  rata clima, metab, therm, infan hart,js; heroux,/ 1961
CJZOA 48--2 391  392  rata energy metab, barren groun mcewan,eh         1970


CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

              anam


CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

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CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

JWMAA 35--3 488  494  ovca variat of rectal temperatu franzmann,aw; heb 1971


CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

              ovda


CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

              obmo


CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

              oram


CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

CJZOA 56-11 2388 2393 ovca winter bioenerget, rocky m chappel,rw; hudso 1978
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CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

ANYAA 53--3 600  607  many role piliary sys,therm env herrington,lp    1951

JAPYA 7---4 355  364  many tem skin in arctic, reg he irving,l; krog,d 1955

SSEBA 18--- 31   48   many insul, met adap to cold in hart,js          1964



CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

RSPYA 4---3 353  362  doca oxy cost, induc hyperventi hales,jrs; findla 1968



CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

AJAEA 13--1 82   99   dosh eff wind, evap on meta rat alexander,g       1962
AJAEA 15--6 982  988  dosh inf amb tem, heat prod pre graham,nmcc       1964

CNJNA 43--1 39   46   dosh eff low temp, physiol resp hess,ea           1963

JASIA 52--1 13   24   dosh energ met, closely clipped graham,nmcc; wai/ 1959



CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR

BIBUB 99--- 259  271  mamm adap, cold, arctic, tropic scholander,pf; h/ 1950

FEPRA 19--4 59   563  ---- thyroid secr, cold acclima cottle,hw         1960
FEPRA 28--3 1053 1058 ---- non-shiv thermogen, inters jansky,l; bartun  1969

PNUSA 37--1 29   43   ---- energy exchanges &  injury richards,jr; dru/ 1978

SCAMA 214-1 94   101  mamm adaptations to cold       irving,l           1966
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Behavioral responses. Animals respond behaviorally to the thermal re-
gime, altering the balance between heat loss and heat production by changes
in orientation, posture, activity, or the selection of cover.   This be-
havioral thermoregulation has an effect on the physiological responses that
result from thermoregulation, since behavioral responses cannot occur with-
out the contraction of muscles.

Individual responses.   Each individual animal can assume an ori-
entation with respect to the distribution of thermal energy, especially wind
and radiation, that will result in the conservation or dissipation of heat.
For example, an animal that stands perpendicular to the wind direction may
have a greater convective heat loss than one oriented with the direction of
air flow. The orientation of the hair with respect to wind direction also
has an effect on the heat loss by convection.

Direct solar radiation is distributed with distinct shadows that re-
sult from the distribution of cover. Indirect or diffuse solar radiation is
scattered throughout the cover, but with a reduction in intensity as the
cover density increases. The amount of radiation absorbed depends in part
on the angle with which the radiation strikes the animal.

Infrared energy has a distribution that is dependent on physical
characteristics of the environment too. A "thermal profile" of a tree at
night is a predictable thing; the radiant energy extends outward to a radial
distance that is approximately the same as the height of the tree (Moen
1968; 6).

The surface area of an animal that is in contact with the snow or soil
is an important consideration in the amount of conductive heat loss.   A
standing animal has little area in contact with the substrate, so conduction
losses are small. An animal bedded in the snow has about 25% of its surface
area in contact with the snow, and heat loss by conduction is an important
part of the total heat loss.

Many descriptions of thermoregulatory behavior are found in the
literature. Severinghaus and Cheatum (1956) report that deer will remain in
a bed for one to three days after a storm, usually under low-hanging con-
ifers or windfalls. During sub-zero weather in Maine, beds were found under
conifer branches that were bent down and covered with snow, or under
hardwoods which had retained their leaves (Hosley 1956; 216). On very cold
nights, deer in the Adirondacks were observed moving slowly on the trails,
and Severinghous and Cheatum (1956) suggested that it was too cold for the
deer to remain bedded.   Deer in the Edwards Plateau in Texas con-
centrated in a valley protected from a cold north wind (Taylor 1956; 147).

Henshaw (1968; 22) noted that caribou bedded in areas of irregular
topography during continued high winds. Their bodies were generally broad-
side to the wind. No apparent discomfort due to low temperature with little

or no wind could be detected. Observations of white-tailed deer in the cold, continental climate of western Minnesota also indicated that cold temperatures without wind had no apparent effect on the animals (Moen 1966).

How significant are the above observations and others similar ones in the literature when considered in the entire ecological picture? Do the animals really conserve a significant amount of heat by behavioral thermoregulation?

The questions above cannot be answered without an examination of the dynamics of heat flow. Early calculations with a standing model of white-tailed deer indicated that this was feasible, (Moen 1966 and Moen 1968). Additional experiments at the Wildlife Ecology Laboratory, Cornell University, have resulted in a considerable amount of information that is of value in intepreting the behavior of deer in the winter.

On cold days an animal is faced with the choice of either producing more heat or conserving more heat. An increase in body activity results in a greater heat production. This additional heat will counteract the great heat loss in a cold environment. It is not a completely efficient process, however. Moving about increases the flow of heat through the hair coat as it flexes, and it also increases convective losses. Heat production during sustained body activity will usually exceed the heat loss, however, so the net effect is to keep the animal warm.

More body activity results in an increase in the energy requirement. The additional energy required may not be available on the range, or it may not be available fast enough to support the higher level of activity. Thus, increasing body activity is not a feasible long-term solution for a free-ranging animal.

In cold conditions an animal can increase its feed intake to benefit from the increased heat of fermentation and nutrient metabolism. A reduction in intake in hot environments has the opposite effect. Other factors that influence the level of ingestion of a free-ranging animal may be more important than the thermal regime of the animal. Endocrine effects seem to be extremely important on a seasonal basis for white-tailed deer. It appears that food intake by wild ruminants is not related to the thermal effects of weather except in a very general way. Factors affecting ingestion are discussed further in another chapter.

Groups of wild ruminants seem to respond to general weather conditions in somewhat predictable ways. Caribou have been observed to be more gregarious during cold weather (Henshaw 1968; 23). White-tailed deer move or are confined to yards, especially during winters with deep snow. White-tails in western Minnesota formed larger groups during periods of reduced visibility without apparent relation to temperature (Moen 1966 and unpublished data). Elk migrate from summer to winter range and this seems to be triggered by weather changes. Heavy snowstorms are a factor in starting the fall migration of mule deer to winter range while the migration back to summer range is related to plant growth (Russell 1932; 39). Moose bed in soft snow and this may reduce the energy requirements of the animals because snow is a good insulator (Des Meules 1964; 55).

Some studies have been done to evaluate the different directions of slopes that are used, and the usual conclusion is that the southern exposures are used more than northern ones. There is a greater energy flux on south slopes than on north slopes because of the distribution of solar radiation. Northerly winds are also more common in the winter, resulting in generally harsher conditions on the north slopes. The preference for south slopes may not be related to weather conditions or energy flux alone, however. Snow depths are frequently less on south exposures, especially in late winter and early spring when melting begins. A decrease in snow cover results in an increase of available food, and this may have a considerable effect on the distribution of animals.

Grouping of animals has some potential benefit in the reduction of heat loss. Animals that are huddled together exchange heat with each other, thus conserving it within the group. Caribou move in bands when feeding and the water vapor released by respiration sometimes condenses and forms a cloud that can reduce heat loss by radiation. The physiological benefits from grouping may be secondary effects only however. The stimulus for grouping may be social, with heat conservation benefits only incidental. The "cloud cover" that forms above a herd of caribou may have little real benefit since the heat production of the animals is higher when active and the cloud is not necessary for the maintenance of homeothermy.

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REFERENCES   UNIT 3.2

BEHAVIORAL THERMOREGULATION

SERIALS

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS---------------	AUTHORS----------	YEAR
ECOLA	57--1	192	198	odvi	energy conservat in winter	moen,an	1976
JWMAA	42--4	715	738	odvi	seas chan, heart rate, act	moen,an	1978

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS---------------	AUTHORS----------	YEAR
ECMOA	2---1	1	46	odhe	seasonal migration, mule d	russel,cp	1932a

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS---------------	AUTHORS----------	YEAR
				ceel			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS---------------	AUTHORS----------	YEAR
JOMAA	50--2	302	310	alal	odvi,structrl adapta. snow	kelsall,jp	1969
QSFRA	3----	51	73	alal	influence of snow on behav	des meules,p	1964

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS---------------	AUTHORS----------	YEAR
ATICA	12--3	158	179	rata	snow, winter ecolo, bar gr	pruitt,wo, jr	1959
IJBMA	12--1	21	27	rata	act wint cari, snow, alask	henshaw,j	1968

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS---------------	AUTHORS----------	YEAR
				anam			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS---------------	AUTHORS----------	YEAR
				bibi			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS---------------	AUTHORS----------	YEAR
				ovca			

        ovda

        obmo

        oram

        ovda

        obmo

CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR
CJPPA 47--8 719 724 dosh cold thermogenes in sheep webster,ajf;heit/ 1969

CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS---------- YEAR
FEPRA 19--4 19   24   ---- calorigen in organ systems depocas,f   1960
FEPRA 28--3 1053 1058 ---- non-shiv thermogen, inters jansky,1· bartun 1969

PAREA 18--1 291 301 ---- catecholam cold adaptation carlson,1d   1966

CLOSING COMMENTS

This CHAPTER 16 has included a review of the more traditional approaches to the calculation of heat loss and the measurement of animal responses, an introduction to the concept of the thermal boundary region as the overall layer of insulation, and the use of overall heat transfer coefficients for calculating heat loss. While I have extensive data on overall heat transfer coefficients for white-tailed deer, the analyses have not been completed yet so the discussions here have been limited to general patterns. Results of these analyses will be published in a scientific journal as soon as possible

Aaron N. Moen
November 18, 1981

AITE = Air temperature

BLMD = Base-line metabolism

DCYC = Diameter of the cylinder in centimeters
DLTT = Delta T = Delta temperature

ELMD = Ecological metabolism

HADE = Hair depth

KCAL = Kilocalories

MBLM = Multiple of base-line metabolism

OHTC = Overall heat transfer

PHOU = Per hour
PSMH = Per square meter per hour
PSQM = Per square meter

QFCV = Quantity of forced convection
QHCO = Quantity of heat transfer by conduction
QHLK = Quantity of heat lost
QNCV = Quantity of natural convection

SAFC = Surface area in forced convection
SANC = Surface area in natural convection
SQMH = Square meters per hour

WIVE = Wind velocity
WTKG = Weight in kilograms

SERIALS are identified by five-character, generally mnemonic codes called CODEN, listed in 1980 BIOSIS, LIST OF SERIALS (BioSciences Information Service, 2100 Arch Street, Philadelphia, PA 19103).

The headings for the lists of SERIALS are:

CODEN VO-NU BEPA ENPA ANIM KEY WORDS----------------- AUTHORS---------- YEAR

The volume and issue numbers (VO-NU) are given after the CODEN entry, followed by beginning page (BEPA), ending page (ENPA), species discussed (ANIM), KEY WORDS from the title, AUTHORS [truncated if necessary, slash (/) indicates additional authors], and year.

AGMYA   Agricultural Meteorology
AJAEA   Australian Journal of Agricultural Research
AJPHA   American Journal of Physiology
ANYAA   Annals of the New York Academy of Sciences
APSCA   Acta Physiologica Scandinavica
ATICA   Arctic

BIBUB   Biological Bulletin
BIOJA   Biophysical Journal
BISNA   Bioscience
BJLSB   Biological Journal of the Linnean Society
BVJOA   British Veterinary Journal

CBPAB   Comparative Biochemistry and Physiology A Comparative Physiology
CJPPA   Canadian Journal of Physiology and Pharmacology
CJZOA   Canadian Journal of Zoology
CNJNA   Canadian Journal of Animal Science
COPMB   Computer Programs in Biomedicine

EAFJA   East African Agriculture Forestry Journal
ECMOA   Ecological Monographs
ECOLA   Ecology

FEPRA   Federation Proceedings

IJBMA   International Journal of Biometeorology
IJLAA   Indian Journal of Animal Sciences
IJMDA   Israel Journal of Medical Sciences

JAPYA   Journal of Applied Physiology
JASIA   Journal of Agricultural Science
JDSCA   Journal of Dairy Science

JOMAA   Journal of Mammalogy
JPHYA   Journal of Physiology
JTBIA   Journal of Theoretical Biology
JWMAA   Journal of Wildlife Management
JZOOA   Journal of Zoology

NAWTA   North American Wildlife and Natural Resources Conference,
         Transactions of the,

PAREA   Pharmacological Reviews
PNUSA   Proceedings of the Nutrition Society
PYSOA   Physiologist

QSFRA   Quebec Service de la Faune Rapport

RSPYA   Respiration Physiology

SCAMA   Scientific American
SSEBA   Symposia of the Society for Experimental Biology
SZSLA   Symposia of the Zoological Society of London

TRJOA   Textile Research Journal

VCSZA   Vestnik Ceskoslovenske Spolecnosti Zoologicke

XARRA   U.S. Forest Service Research Note RM

ZETIA   Zeitschrift fuer Tierpsychologie
ZOTCA   Zootechnia

The headings for the lists of BOOKS are:

TYPE PUBL CITY PAGE ANIM KEY WORDS---------------- AUTHORS/EDITORS-- YEAR

      All essential information for finding each book in the library is given on just one line. The TYPE of book could have either AUTHORS (aubo) or EDITORS (edbo). Publishers (PUBL) and CITY of publication are given with four-letter mnemonic symbols defined below. The PAGE column gives the number of pages in the book; ANIM refers to the species discussed in the book (given as a four-letter abbreviation of genus and species), and KEY WORDS listed are from the title. The AUTHORS/EDITORS and YEAR of publication are given in the last two columns.

acpr	Academic Press	New York	nyny
apso	American Physiological Society	Wshington, D. C.	wadc
jwis	John Wiley and Sons, Inc.	New York	nyny
lefe	Lea and Febiger	Philadelphia, PA	phpa
pepr	Pergamon Press	Oxford, England	oxen
spve	Springer-Verlaug, Inc.	New York	nyny
usup	Utah State University Press	Logan, Utah	lout
whfr	W. H. Freeman Co.	San Francisco, CA	sfca

GLOSSARY OF ANIMAL CODE NAMES

Wild ruminants are referred to in this CHAPTER by a 4-character abbreviation from the family, genus and genus-species. These are listed below under Abbreviation.

Scientific names of North American wild ruminants are those used in BIG GAME OF NORTH AMERICA, edited by J.C. Schmidt and D. L. Gilbert (1979: Stackpole Books, Harrisburg, PA 17105, 494 p.), and may be different from the scientific names given in the original literature.

The abbreviations used for North American wild ruminants are listed below.

CLASS: MAMMALIA

   ORDER: ARTIODACTYLA   Abbreviation

	Abbreviation
FAMILY: CERVIDAE	cerv
GENUS: Odocoileus (deer)	od--
SPECIES: O. virginianus (white-tailed deer)	odvi
O. hemionus (mule deer)	odhe
GENUS: Cervus (Wapiti, elk)	ce--
SPECIES: C. elaphus	ceel
GENUS: Alces (moose)	
SPECIES: A. alces	alal
GENUS: Rangifer (caribou)	
SPECIES: R. tarandus	rata
FAMILY: ANTILOCAPRIDAE	
GENUS: Antilocapra	
SPECIES: A. americana (pronghorn)	anam
FAMILY: BOVIDAE	bovi
GENUS: Bison (bison)	bi--
SPECIES: B. bison	bibi
GENUS: Ovis (sheep)	ov--
SPECIES: O. canadensis (bighorn sheep)	ovca
O. dalli (Dall's sheep)	ovda
GENUS: Ovibos	
SPECIES: O. moschatus (muskox)	obmo
GENUS: Oreamnos	
SPECIES: O. americanus (mountain goat)	oram

The abbreviations used for European wild ruminants are listed below.

CLASS: MAMMALIA

ORDER: ARTIODACTYLA   <u>Abbreviation</u>

    FAMILY: CERVIDAE   cerv
      GENUS: <u>Capreolus</u> (roe deer)   ca--
        SPECIES: <u>C. capreolus</u>   caca
      GENUS: <u>Dama</u> (fallow deer)   da--
        SPECIES: <u>D. dama</u>   dada
      GENUS: <u>Cervus</u> (Wapiti, elk)   ce--
        SPECIES: <u>C. elaphus</u> (red deer)   ceel
      GENUS: <u>Alces</u> (moose)
        SPECIES: <u>A. alces</u>   alal
      GENUS: <u>Rangifer</u> (caribou)
        SPECIES: <u>R. tarandus</u>   rata

    FAMILY: BOVIDAE
      GENUS: <u>Bison</u> (bison)
        SPECIES: <u>B. bonasus</u>   bibo
      GENUS: <u>Capra</u> (ibex, wild goat)   cp--
        SPECIES: <u>C. aegagrus</u> (Persian ibex)   cpae
              <u>C. siberica</u> (Siberian ibex)   cpsi

OTHERS

Abbreviations for a few other species and groups of species may appear in the reference lists. These are listed below.

<u>Axis axis</u> (axis deer)   axax
<u>Elaphurus davidianus</u> (Pere David's deer)   elda
<u>Cervus nippon</u> (Sika deer)   ceni
<u>Hydropotes inermis</u> (Chinese water deer)   hyin
<u>Muntiacus muntjac</u> (Indian muntjac)   mumu
<u>Moschus moschiferus</u> (musk deer)   momo
<u>Ovis nivicola</u> (snow sheep)   ovni
<u>Ovis musimon</u> (moufflon)   ovmu
<u>Ovis linnaeus</u> (Iranian sheep)   ovli
<u>Rupicapra rupicapra</u> (chamois)   ruru

big game   biga
domestic sheep   dosh
domestic cattle   doca
domestic goat   dogo
domestic ruminant   doru
herbivore   hrbv
mammals   mamm
three or more species of wild ruminants   many
ruminants   rumi
ungulates   ungu
vertebrates   vert
wildlife   wldl
wild ruminant   wiru

JULIAN DAY: MONTH AND DAY EQUIVALENTS*

Day	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Day
1	001	032	060	091	121	152	182	213	244	274	305	335	1
2	002	033	061	092	122	153	183	214	245	275	306	336	2
3	003	034	062	093	123	154	184	215	246	276	307	337	3
4	004	035	063	094	124	155	185	216	247	277	308	338	4
5	005	036	064	095	125	156	186	217	248	278	309	339	5
6	006	037	065	096	126	157	187	218	249	279	310	340	6
7	007	038	066	097	127	158	188	219	250	280	311	341	7
8	008	039	067	098	128	159	189	220	251	281	312	342	8
9	009	040	068	099	129	160	190	221	252	282	313	343	9
10	010	041	069	100	130	161	191	222	253	283	314	344	10
11	011	042	070	101	131	162	192	223	254	284	315	345	11
12	012	043	071	102	132	163	193	224	255	285	316	346	12
13	013	044	072	103	133	164	194	225	256	286	317	347	13
14	014	045	073	104	134	165	195	226	257	287	318	348	14
15	015	046	074	105	135	166	196	227	258	288	319	349	15
16	016	047	075	106	136	167	197	228	259	289	320	350	16
17	017	048	076	107	137	168	198	229	260	290	321	351	17
18	018	049	077	108	138	169	199	230	261	291	322	352	18
19	019	050	078	109	139	170	200	231	262	292	323	353	19
20	020	051	079	110	140	171	201	232	263	293	324	354	20
21	021	052	080	111	141	172	202	233	264	294	325	355	21
22	022	053	081	112	142	173	203	234	265	295	326	356	22
23	023	054	082	113	143	174	204	235	266	296	327	357	23
24	024	055	083	114	144	175	205	236	267	297	328	358	24
25	025	056	084	115	145	176	206	237	268	298	329	359	25
26	026	057	085	116	146	177	207	238	269	299	330	360	26
27	027	058	086	117	147	178	208	239	270	300	331	361	27
28	028	059	087	118	148	179	209	240	271	301	332	362	28
29	029	[060]	088	119	149	180	210	241	272	302	333	363	29
30	030		089	120	150	181	211	242	273	303	334	364	30
31	031		090		151		212	243		304		365	31

* For leap year, February 29 = JDAY 60. Add 1 to all subsequent JDAYs.

LIST OF WORKSHEETS – CHAPTER SIXTEEN