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Research Reports

The Critical Thermal Environment: A New Look at an Old Concept

The thermoneutral range for a homeotherm includes the heat exchange conditions which do not elicit a metabolic response to maintain a normal body temperature. There is a lower limit to the thermoneutral range, below which the animal experiences a drop in the body temperature, and an upper limit which, if exceeded, results in a rise in the body temperature, unless compensated for by a metabolic response. The maintenance of "normal" body temperature depends on two basic processes. One, the metabolic process, an exothermic reaction, that results in the release internally of heat energy, and two, the physical exchange of heat between the organism and the environment. The homeotherm must constantly maintain a caloric balance between the heat produced metabolically and the heat lost from its surface.

There is frequent use of the term "critical temperature" in establishing the upper and lower limits of the thermoneutral range. It is a useful index in the physiology laboratory where chamber conditions may be quite thermally stable, but the term is not appropriate when one considers the complexity of the heat exchange phenomena in the field. The amount of heat flux at a particular moment in time and space is dependent on several gradients rather than on a single temperature value. There is increasing use of the term environmental temperature rather than air temperature, presumably to represent the thermal conditions in the entire environment by a single value. This term is better than air temperature, but in reality no single environmental temperature can be meaningful, either as a mean, mode, or any other numerical representation of the thermal conditions in the environment.

The animal does not sense air temperature or environmental temperature, but rather perceives impulses generated by the neurological state of its thermal receptors. These receptors are affected by the heat flux in the environment, and temperature is but one of the parameters involved.

Heat is exchanged between an animal and its environment in four ways: radiation, conduction, convection, and evaporation. In radiant heat exchange, the energy travels by electromagnetic waves, and any object with a temperature above absolute

zero gives off radiant energy. The amount of radiation given off from the surface of any object is $Q_r = E\sigma T^4$, where E is the emissivity of the object — a comparison of its radiation characteristics to those of a black body, σ is the Stefan-Boltzmann constant, and T the surface temperature on the Kelvin scale.

In addition to emitting radiant heat, an animal also receives solar radiation from the sun and infrared radiation from objects in the environment. The albedo or reflective characteristics of the animal will determine how much of the solar energy is absorbed and how much is reflected. A white animal reflects more solar energy than does a black animal, and the reflected solar energy cannot contribute to the internal heat load of an animal.

The infrared energy which reaches the animal is also reflected or absorbed, and the emissivity (E) of any surface is equal to the absorption coefficient. Thus an animal surface with a high emissivity in the infrared — and biological materials generally have high emissivities — will also have a high absorption coefficient.

Heat is transferred by conduction as molecules collide with one another. The more heat energy in a given substance, the more rapid is molecular oscillation, and a larger temperature gradient within a substance results in a faster rate of heat transfer by conduction. The formula $Q_c = K\Delta T/d$ includes the basic factors involved in conductive heat transfer. The thermal conductivity of the conducting material is K , and ΔT is the temperature gradient between two points separated by distance d .

Convective heat transfer occurs in two ways: natural and forced. Natural convection, also called free convection, results from density differences in the fluid surrounding an object, while forced convection results from external pressure on the fluid as it flows past an object. The basic factors involved are $Q_h = h_c\Delta T$, where h_c is the convection coefficient, a number representing the heat lost from the object in a given orientation in a fluid flow with particular thermal characteristics and velocity, and ΔT is the temperature difference between the fluid and the surface of the object.

Evaporation is dependent on the vapor pressure gradients that exist between the

animal and the environment, and the resistance to the movement of mass (water vapor) across the gradient distance. The amount of energy lost from an object by evaporation is determined by multiplying the mass of water changed from one state to another by the heat of vaporization at the temperatures involved. In the living animal, this includes both external surface evaporation and internal evaporation from the lung surfaces.

None of the formulas above include area and time factors. The area involved in heat exchange is dependent on the size and posture of the animal, and the appropriate time factor is selected by the researcher, of course.

An equally important consideration in the analysis of heat exchange is the metabolic heat produced by the animal. This quantity includes the basal heat production necessary to sustain life, and the heat increments due to diet, activity, and several other less important factors. An increase in the quantity of food consumed and an increase in the muscular activity both contribute to a greater heat production. Thus total heat production is equal to the basal metabolism multiplied by the ratio of total heat increment. The two increments due to food and activity can result in a total heat production several times greater than basal metabolism.

It is clear from the basic formula presented above that heat exchange is dependent on several factors, including solar and environmental radiation, the albedo of the animal surface, infrared emissivity of the animal, surface temperature, thermal conductivity of the animal's covering, thermal conductivity and temperature gradients in the substrate, wind velocity, air temperature, and vapor pressure gradients. Other factors are also important. For example, the surface area participating in heat exchange depends on the animal's posture, and a reduction in the net heat loss results when an animal curls up to rest. This is similar to the relationship implied in Allen's Rule, which states that northern species tend to have smaller extremities. When an animal curls up tightly or lays its ears back against its head, it is, in effect, decreasing the area of the appendages participating in heat exchange with the physical environment.

The surface area: weight ratio decreases as the animal increases in weight; this is a geometric relationship between volume and area. Equating volume with weight assumes that no change in the overall density occurs as the animal becomes larger. Total heat production increases as the animal's weight increases, although the heat production per unit of weight decreases.

A tendency toward a larger body size has been observed in northern species (Bergman's Rule), and this is an advantage to a homeotherm in cold weather. There are size differences within a population, of course, and the larger individuals have an advantage over the smaller ones in maintaining homeothermy because of their more favorable surface area: weight ratio.

The animal can also exhibit thermoregulatory behavior so the environmental energy regime compliments, within limits, its physiological state. Thus an animal seeks wind on hot days to increase convective heat loss. On cold days, it may seek solar radiation during the day, and heavy cover at night for protection from the cold night sky. Dogs are frequently observed digging in preparation for lying down on cool soil in the shade on a hot day. Animals alter their posture according to thermal stress too; racoons (Folk, 1966) and dogs lie on their backs with legs out-

stretched when hot, and animals are commonly observed to be curled up tightly when cold. Deer mice (*Peromyscus maniculatus*) salivate on their bodies which increases evaporative heat loss (Brower and Cade, 1966). Huddling decreases the heat loss from chicks as part of their surface exchanges heat with the other chicks in the group (Kleiber and Winchester, 1933).

Diets are also regulated according to thermal conditions. Man, for example, prefers cold salads in the summer and foods high in carbohydrates and fats in the winter. This is a reflection, in part at least, of the differences in the heat increments of various foods.

Since there is variation in the heat exchange that can be attributed to change in any one of the many thermal parameters, it is obvious that temperature is not the only critical factor. Temperature gradients are included in some of the heat exchange calculations, but they are by no means the only factors, nor are they always the most important. The rise in convective heat loss which occurs when wind velocity increases illustrates the latter point; the convection coefficient increases while ΔT decreases, but the net result is a greater heat loss.

I suggest that the term "critical thermal environment" is appropriate when considering all factors which determine the

limits of the thermoneutral range. Critical temperature is appropriate only when all other thermal parameters are held constant. The critical thermal environment may include internal gradients as well as external ones. Thus the distribution of heat energy within the body due to muscular activity and blood flow is appropriately included in the total animal-environment thermal relationship.

Figure 1 illustrates some critical values which have been determined for white-tailed deer (*Odocoileus virginianus*) in a standing posture in an open field under clear, nocturnal skies. The assumptions underlying these energy balance calculations are described in further detail in Moen (1966, 1968a and 1968b). Note that Figure 1 is based on a constant air temperature of -30°C . This temperature is used as a reference point in these calculations for predicting radiation flux under clear skies at night, based on measurements in the field (see Moen, 1968a).

Three body sizes and three dietary levels are shown in Figure 1. A 30 kg deer on a full diet has a less favorable thermal balance than does a 70 kg deer on the same diet level. Specifically, the full-fed 30 kg deer reaches a negative thermal balance at less than 4 mph (V_c^1), a 50 kg deer at 8 mph (V_c^3), and a 70 kg deer at 11-12 mph (V_c^5). Thus, with heat production held constant at the full diet level, the lower limit of the thermoneutral range is dependent on body size and surface area relationships implied in Bergman's Rule.

If the diet is at the starvation level, none of the body weights are sufficiently large to maintain a positive energy balance when the animal is standing in an open field under clear, nocturnal skies with an air temperature of -30°C . On a maintenance diet, the 30 kg deer reaches a negative thermal balance at less than 2 mph, the 50 kg deer at 4 mph (V_c^2), and the 70 kg deer at just over 6 mph (V_c^4). These data illustrate the effect of diet on the heat production and subsequent thermal balance of deer, as well as the effect of body weight and surface area relationships on their thermal energy balance.

If one defines the diet and the thermal conditions to which an animal is exposed, a critical body weight (W_c) — or the weight necessary to prevent a net heat loss — can be calculated. A deer on a maintenance diet exposed to a wind velocity of 8 mph would be at the lower limit of the thermoneutral range if it weighed 88 kg.

A deer weighing 50 kg and on a full diet would be in a positive thermal balance if the wind velocity was less than 8 mph. Above that velocity, the thermal balance is negative; 8 mph can be considered a critical wind velocity (V_c^3) for the 50 kg deer on a full diet, standing posture, and in an open field under clear skies at night.

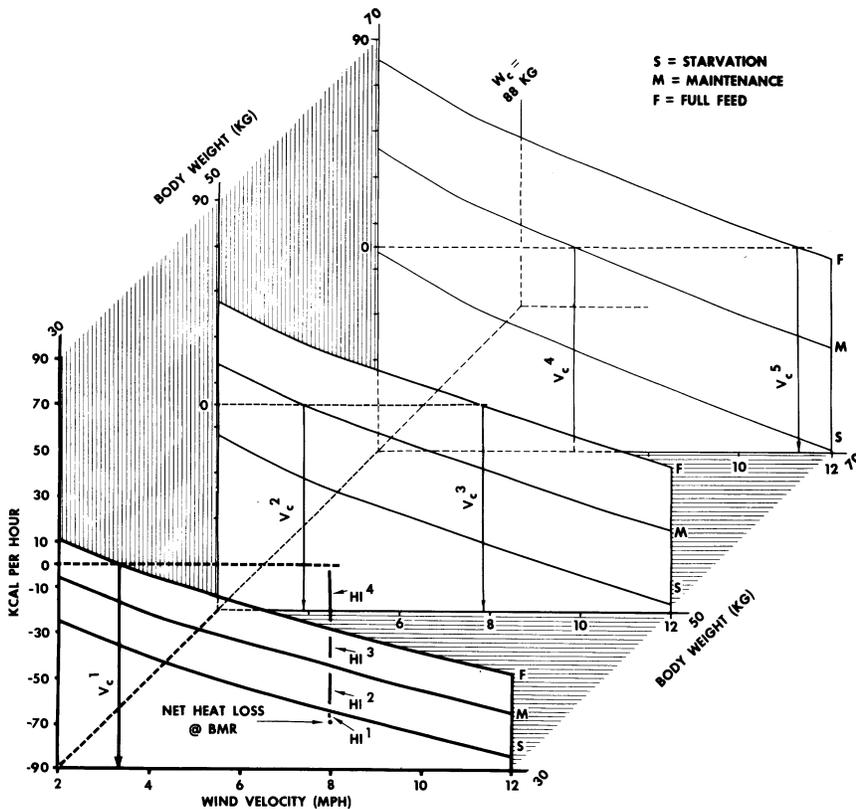


Fig. 1. The thermal balance (x axis) of deer exposed to wind velocities (y axis) from 2 to 12 mph. Body weights of 30, 50, and 70 kg are considered (z axis), and three dietary levels are used (see key). Calculations are for a standing deer in an open snow field under clear skies at night, with an air temperature of -30°C .

The critical wind velocity for a 50 kg deer on a maintenance diet, when exposed to these thermal conditions, is 4 mph (V_c^2).

The heat increments of deer on different levels of diet and activity are shown on the 30 kg graph. The basal metabolic rate of heat production is about 70 kcal per hour less than the rate of heat loss by a deer exposed to 8 mph winds, -30 C air temperatures, and clear night skies. The animal on a starvation diet has no heat increment due to diet. HI^1 is an increase in the heat production due to a standing posture, and is expressed by the ratio 1.1:1.0 (Brockway, 1965), with the latter number representing the basal level. HI^2 is the increment due to a maintenance diet; the ratio used is 1.47:1.0 (Blaxter, 1962), and the net heat loss is about 45 kcal per hour. $HI^3 + HI^2$ is the increment due to a full diet; the ratio used is 1.88:1.0 (Blaxter, 1962), and the net heat loss is about 30 kcal per hour. The heat increment due to diet and the standing posture is not enough to offset heat loss from a 30 kg deer exposed to these thermal conditions; the deer is still losing about 30 kcal per hour more than it is producing. An additional heat increment (HI^4) raises the heat production to the point of balancing heat loss, and this could result from an increase in the activity of the animal. The heat increment that would be required for the 30 kg deer is about 2.8 times the basal metabolism, with 1.88:1.0 being the diet component and 1.5 being the activity component of the increment. Thus, one can define a critical heat increment which is necessary to maintain homeothermy when the animal is exposed to known thermal parameters in the environment.

The living animal can alter its thermal balance in many ways. In addition to those mentioned above, it can also erect its hair or fluff its feathers. This may alter the thermal conductivity of the insulating coat and K , ΔT , and d are changed for conductive heat transfer from the inside of the animal to the outer surface of its coat. A critical hair or feather conductance could be calculated if one defined the other parameters in the energy balance calculations. A change in the orientation of the animal with respect to wind direction also changes the convection coefficient, thus generating a whole new series of calculations to represent the heat flux occurring, and a new series of "critical orientations" or critical convection coefficients for the animal in given thermal environments.

One must also recognize that changing one surface parameter causes changes in the amount of heat lost by other modes of heat transfer. If the hair conductance decreases, for example, more heat is lost by conduction and the surface temperature of the animal increases. The net radiation

loss also increases as the absolute temperature of the surface increases, and ΔT is larger in the convective heat transfer formula, resulting in an increase in convective heat loss. In reality, then, the heat exchange is a complex system of flux which changes at different rates due to variations in the time factors involved in each type of heat transfer.

The formulas and data illustrate a number of parameters that must be considered in analyzing thermal relationships. Other supporting formulas have not been included here, but are available in elementary texts on heat transfer and meteorology.

The extreme fluctuations in the surface temperature of an animal are illustrated by data I have on pheasants (*Phasianus colchicus*). One example of a measurement with a remote-reading Barnes IT-3 infrared thermometer responsive to wavelengths of 8 to 14 μ will illustrate the point. With a bright sun shining and free convection conditions, the surface temperature was measured at 45 C, or 4 to 5° higher than internal temperature. Thus heat flow was from the outside surface to the interior of the animal. With cloud cover and a slight breeze, the surface temperature decreased nearly to air temperature, or 21°, and heat flow was from the inside of the animal to the outside surface. These variations were observed to occur in a matter of seconds, and the air temperature did not change during this period of time. The insulation of the feathers is a thermal buffer which ameliorates these rapid fluctuations in environmental energy flux. It helps prevent hyperthermia when the bird is exposed to intense solar radiation, and hypothermia when thermal conditions have the capacity to increase heat loss to a critical level.

It is clear that air temperature alone cannot be an adequate representation of thermal conditions at either the upper or lower limits of the thermoneutral range. The "critical thermal environment" includes all thermal factors which enter the active heat exchange between an organism and its environment. External thermal flux is included, as well as the internal factors related to heat production. The upper limit of the thermoneutral range can be designated the "critical hyperthermal environment" and the lower limit the "critical hypothermal environment." In practice, of course, the ecologist does not know all of the gradients at any one point in time and space. Recognition of their existence and the basic modes of heat transfer clarifies the concept. The animal can by thermoregulatory behavior select those environmental conditions which permit homeothermy, or the animal can make a physiological adjustment in heat production. When the behavioral and

physiological capabilities have been exhausted in a rigorous thermal environment, the animal faces death from thermal stress.

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