Some Physiological Costs of Cold Climates

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Some Physiological Costs of Cold Climates

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"Fact alone is sterile; hypothesis and integration are the real stuff of science:" this statement was made by Dr. K. L. Blaxter on the occasion of the 4th Samuel Brody Memorial Lecture. Samuel Brody was one who had the great ability to integrate facts and observations and produce a clear, concise picture. This ability is well demonstrated in his book "Bioenergetics and Growth." To put a new twist to an old proverb one could say that Brody not only could see the trees and the woods but also see the path through the woods. One of Brody's abiding interests was bioenergetics or the transformation of energy in living things, an interest he maintained through his belief that energy is the common denominator which relates to much of the physiology of an animal. During this lecture I will deal with three aspects of animal physiology that are influenced by cold. In concluding I will suggest possible extensions to the list. Our laboratory in Edmonton has been established but a short time and to date the scope of investigation has been limited to a few studies on cattle and sheep. Therefore, the examples I will use will be drawn mainly from these species.

The modeling of biological systems has become increasingly popular over the last decade and has proved to be a most useful tool for organization and evaluation of research efforts. In 1961 Professor Max Kleiber produced a model of animal bioenergetics. Subsequently, various models have been developed and adapted by nutritionists, physiologists, and engineers in attempts to relate the energy consumed by animals to animal performance (Maynard and Loosli, 1969; Crampton and Harris, 1969; Paine and Nelson, 1971; Baldwin and Smith, 1971; Teter *et al.*, 1973). A schematic representation of the flow of energy through an animal is shown in Figure 1. This scheme represents food energy intake by the animal and its utilization for various bodily and productive functions. A reservoir (tissue stores) is represented and acts as a buffer whenever the energy intake does not equal energy output. The scheme can be visualized as a funnel into the top of which enters the chemical energy of food. The funnel has outlets or faucets from which flow chemical, heat and work energy. The outlets are of various sizes and continually vary in magnitude depending on the animal's physiological state and the impinging environmental factors. As in any biological system, the various components are not independent. If one is modified the others will be affected.

The total dietary energy or gross energy intake by an animal is largely determined by appetite and opportunity. Management decisions such as restrictive feeding practices and dieting restrict expression of appetite capacity.

Let us turn now to the various ways energy may leave an animal. Firstly, there is a loss in feces. Characteristics of the food influence digestibility and thus the amount of energy lost in the feces. Various foods are more or less digestible by the different species and age of animals. For example, the ruminant species because of their specialized digestive system can digest fibrous foods which are generally unavailable to the simple-stomached animals. Other forms of chemical energies (or material wastes) leaving the animal are the combustible gases from microbial fermentation in the digestive tract, and urine. Gross energy intake less the losses in feces, urine and combustible gases is the metabolizable energy of the food or that portion of the total food energy available for metabolic activities.

A primary use of metabolizable energy is for the maintenance of the integrity of the animal's body, that is, basal metabolism. The classical work of Brody (1945) showed the relationship between the basal or minimal metabolism of mature animals of different species and an exponential expression of body weight. Kleiber (1961) and Scholander *et al.* (1950) concurred with Brody's general conclusion on the exponent of body weight. The expression of metabolic body size (body weight raised to the three-fourth power, $W^{3/4}$) is now widely recognized and used (NAS-NRC, 1966; EAAP, 1965).

There are expenditures of energy by animals to obtain nutrients. These include the costs of locomotion between feeding and watering areas, the costs of eating, as well as the costs of translocation and conversion of food into forms usable by the body.

Animals are consistently faced with stress, the type and magnitude of which vary continually. Substantial energy may be expended in combating stresses such as severe deviations in the climatic environment. On the other hand, the costs of other stresses such as parasite and pathogen loads are largely unknown.

Production requires energy, but energy is not available for production unless the maintenance needs of the animal are met. The metabolizable energy available for production is not entirely incorporated into products. Because of the inefficiencies of the productive processes, energy is given off in the form of heat during the formation of products. Under cold conditions this additional heat energy or heat increment of production may be of benefit to an animal in combating cold. The scheme shown in Figure 1 has been simplified by grouping the various forms of production. It should be noted, however, that some products are harvestable only upon slaughter of the animal while other products such as milk or wool can be harvested at regular intervals.

Direct Consequences of Cold Requiring Thermoregulation

If the ambient temperature is decreased a point will be reached where the heat production arising from normal metabolic functions is just inadequate to maintain the body temperature of the animal. With any further decrease in ambient temperature extra metabolic heat must be produced to compensate for the increased rate of heat loss to the environment (Kleiber, 1961). The ambient temperature below which extra metabolic heat must be produced for an animal to

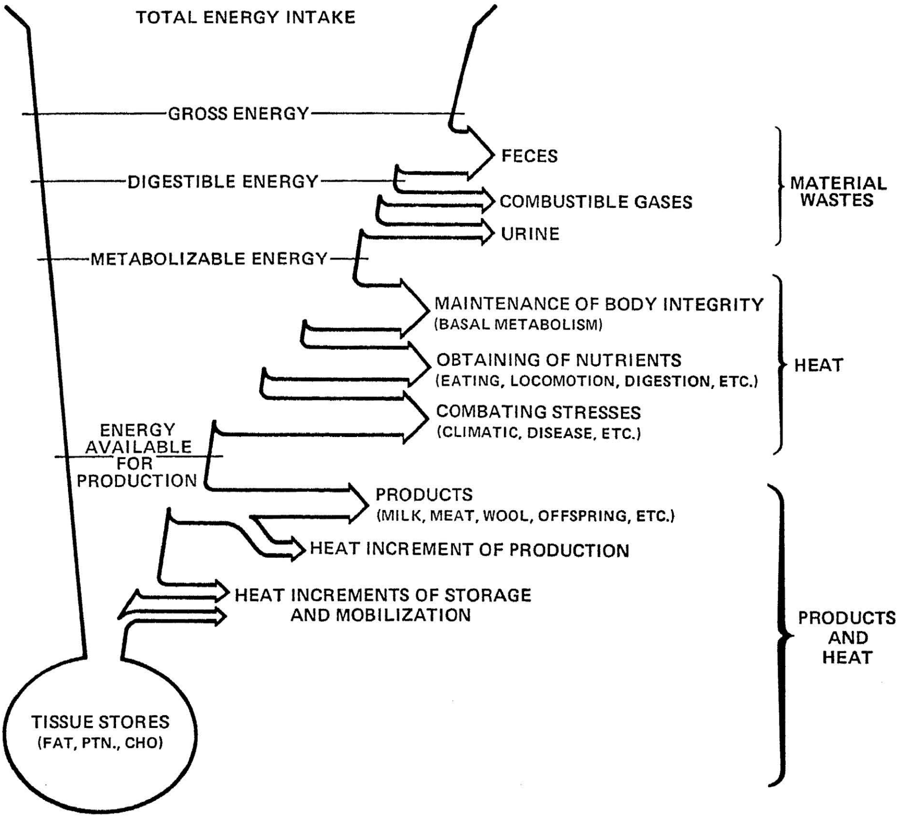

Fig. 1—Schematic representation of the flow of energy through an animal.

maintain homeothermy is its lower critical temperature. There is an approximately linear increase in the rate of heat production as ambient temperature decreases further until the point of summit metabolism where the animal's rate of heat production is maximal. With a further decrease in ambient temperature the heat loss from the animal is in excess of maximum heat production and consequently body temperature falls and death results (Kleiber, 1961). The lower critical temperature and the temperature and magnitude of summit metabolism of an animal are not unalterable. Given the opportunity, an animal will respond either voluntarily or involuntarily to lessen a cold stress. There is insufficient time in this lecture to consider these topics. I, therefore, refer you to excellent recent reviews by Jansky (1971), Whittow (1971), Smith *et al.* (1972), and Bligh (1973).

The lower critical temperature of an animal is theoretically determined by—(a) the thermoneutral rate of heat production, and (b) the thermal insulation, or inversely the thermal conductivity of the peripheral tissues, the coat and the air immediately surrounding the animal. The derivation of thermal insulation values was dealt with by Dr. Blaxter in the 4th Brody Memorial Lecture (1964) and extensive work has been done by him and others on measurements of insulation values of animals (Scholander *et al.*, 1950, Blaxter *et al.*, 1959, Blaxter and Wainman, 1961 and 1964, Webster *et al.*, 1969). With a knowledge of the insulation of an animal and a measure of its thermoneutral heat production the lower critical temperature can be estimated from rearrangement of heat flow equations (Blaxter, 1964). In a steady state the critical temperature of an animal is given by the expression

$$\text{CRITICAL TEMPERATURE (C)} = T_B - H(I_T + I_E) - V_B I_E$$

where:

T_B = body core temperature (C)
H = thermoneutral heat production (Mcal. m^{-2}. 24 h^{-1})
I_T = tissue insulation (C.m^2 . 24h . $Mcal^{-1}$)
I_E = external insulation (C. m^2 . 24 h. $Mcal^{-1}$)
V_B = minimal evaporative heat loss during cold exposure (Mcal. m^{-2} . 24 h^{-1})

As a ready and practical means of predicting critical temperatures of cattle the nomogram presented in Figure 2 was devised (Young, 1971). It was derived from the equation above with the prediction of heat production per unit surface area based on the daily metabolizable energy intake and the assumption of a constant 50 percent efficiency of utilization of metabolizable energy for production. Actual estimates of efficiency of utilization of metabolizable energy for body weight gain range from about 33 to 66 percent and for lactation from about 60 to 70 percent (ARC 1965). The assumption of a constant 50 percent utilization does not introduce a large error nor limit practical application of the nomogram. Body weight (W,Kg) to surface area (A,m^2) conversion was based on the Meeh formula, $A = kW^{2/3}$, with the coefficient k = 0.09 (Blaxter, 1967; Mitchell, 1963).

The nomogram incorporates a means for adjusting for the added cooling power of the environment because of the presence of wind (Siple, 1964). A windy

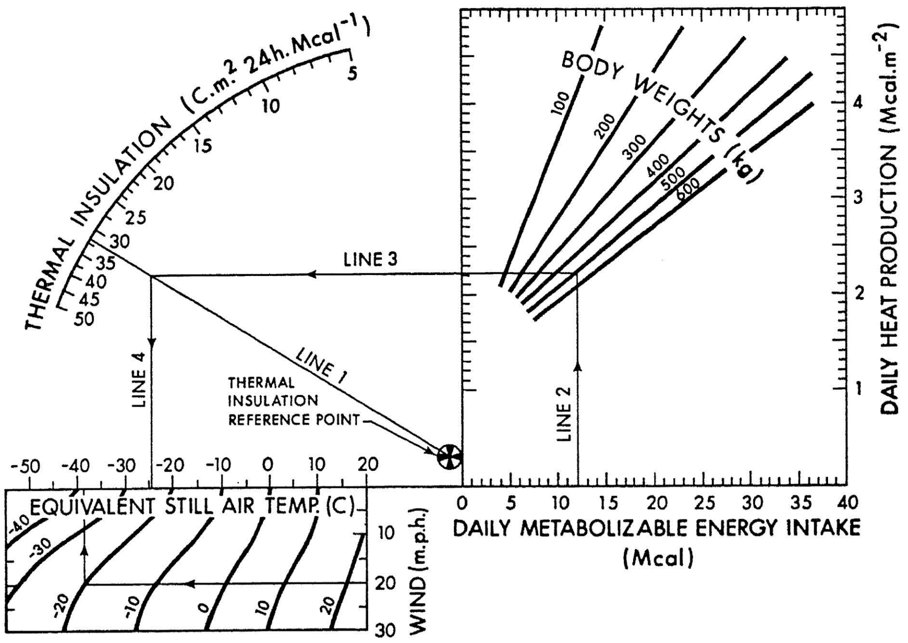

Fig. 2—Scheme for estimating the critical temperature of an animal from its thermal insulation, body weight and daily metabolizable energy intake. Four lines are drawn on the graph to estimate the critical temperature of an animal. For the example shown values of 32 C. m^2. 24 h. Mcal^{-1}, 12 Mcal and 500 kg have been used for thermal insulation, daily metabolizable energy intake and body weight respectively.

Line 1 - from the thermal insulation reference point to the appropriate value for the animal on the thermal insulation scale.

Line 2 - drawn perpendicular from the daily metabolizable energy intake value for the animal, to intercept the line for the body weight of the animal.

Line 3 - horizontal from the point of interception of Line 2 and the weight line, across to the left side of the graph to transect Line 1.

Line 4 - directly down from the intersection of Line 1 and Line 3 to the equivalent still air temperature scale. The critical temperature for the animal is given by the point where line 4 meets the temperature scale.

Below the temperature scale the insert graph indicates the extent to which wind increases the cold stress. This graph allows estimation of the equivalent still air temperature at different winds at animal height by drawing a horizontal line from the wind velocity scale to intercept the line on the graph representing actual air temperature. A perpendicular line is drawn from the intercept the equivalent still air temperature scale. For example, a wind speed of 20 m. p. h. and an air temperature of -20C is equivalent to still air temperatures of -38C.

environment, therefore, can be expressed in terms of an equivalent still air temperature. The nomogram does not incorporate any adjustment for the added cooling power arising from the presence of moisture or precipitation (rain or snow) as no adequate method was available. The moisture can considerably increase the cooling effect of the environment.

Information on an animal's thermal insulation, daily metabolizable energy intake, and body weight are required to use the nomogram. Four interconnecting lines are then drawn on the nomogram to estimate the lower critical temperature of the animal. Two additional lines are used to express a windy environment in terms of an equivalent still air temperature. Details of procedure are contained in the legend of Figure 2.

To permit application of the nomogram to practical farming situations a simplified means was needed for estimating thermal insulation (Table 1). The values in Table 1 are derived from reports by Scholander *et al.* (1950, Blaxter *et al.* (1959) and Blaxter and Wainman, (1961) and from measurements made in our laboratory (Webster *et al.*, 1969 and 1970, and unpublished observation). The factorial estimation of thermal insulation is based on an assignment of a base value to which adjustments are made depending on the characteristics of the animal. As considerable subjective judgement is required in making the adjustment a high level of precision cannot be expected. The derived values are, however, generally adequate for practical situations.

From the nomogram (Figure 2) it is possible to estimate the lower critical temperatures of an animal and obtain estimates of the extra feed that would be required by an animal to combat a cold stress without loss of body tissue stores. An animal is subjected to a direct cold stress if the equivalent still air temperature of the environment is below the animal's lower critical temperature. An estimate of the extra metabolizable energy required to compensate for a direct cold stress can be obtained by tracing backwards through the nomogram parallel to lines 4, 3 and 2, from the equivalent still air temperature scale to the energy intake scale. The extra feed required is the difference between the two intercepts on the energy intake scale. In some instances, because of limitations in appetite, availability, etc., it may be not possible for an animal to fully compensate for cold by consuming more food. The animal must then draw upon body reserves to produce the extra metabolic heat to maintain homeothermy.

The Effects of Cold on the Apparent Digestibility of Feed

During the last decade there have been several reports in which animals kept in the cold appeared to digest dietary energy and nitrogen less completely than did animals kept in the warm (Graham *et al.*, 1959; Graham, 1964; Fuller, 1965; Fuller and Boyne, 1972). There has been some hesitation to accept the idea of a reduction in apparent digestibility of a ration during cold exposure as a true physiological response (Graham, 1964; Fuller, 1965). Examination of experimental procedures and subsequent suggestions of possible artifacts of experimentation have failed to show the depression in apparent digestibility to be other than a true physiological shift (Fuller and Cadenhead, 1969).

Recently we have carried out several digestibility experiments in which animals exposed to warm and cold conditions were given the same ration (Christopherson and Milligan, 1973; Christopherson and Thompson, 1973; Young and Christopherson, 1974). Apparent digestibility of dry matter of rations (Table 2) generally shows a similar magnitude of depression in digestibility for each degree C decrease in animal exposure temperature as has

Table 1. PRACTICAL METHOD FOR ESTIMATING THERMAL INSULATION OF CATTLE. A VALUE IS ASSIGNED FOR ANIMAL TYPE AND THEN ADJUSTMENTS ARE MADE FOR VARIOUS ANIMAL AND ENVIRONMENTAL CHARACTERISTICS. THE EXAMPLE SHOWN IS FOR A MATURE BEEF COW IN FAT BODY CONDITION, AFTER EXPOSURE TO SUB-FREEZING TEMPERATURES FOR SEVERAL MONTHS. THE COW HAS ABOUT AN INCH OF HAIR COAT DEPTH AND IS KEPT IN AN AREA FREE FROM WIND (From Young, 1971).

		Example		
Animal Type				
Beef type animal	22	22		
Dairy type animal	19			
Adjustment for age				
Mature	0	0		
18 - 24 months	- 2			
12 - 18 months	- 4			
6 - 12 months	- 6			
Adjustment for Body Condition				
Very fat	+ 4	+ 2		
Fat	+ 2			
Average	0			
Thin	- 2			
Very Thin	- 4			
Emaciated	- 6			
Adjustment for Cold Acclimatization				
Immediate previous exposure to sub-freezing temperatures		+ 2		
1 month	+ 1			
2 or more months	+ 2			
Adjustment for Hair Coat Depth				
Add 1 unit for each 4 mm. (1/6 in.) of coat depth or 6 units per inch of coat depth		+ 6		
Adjustment for Wind				
5 m.p.h.	- 2	0		
10 m.p.h.	- 4			
15 m.p.h.	- 7			
20 m.p.h.	-10			
THERMAL INSULATION (C. m^2. 24h. $Mcal^{-1}$)		32		

been reported previously. We found an average depression of 0.24 percent DM digestibility per degree C. However, in one experiment in which two rumen fistulated cows were exposed to alternate four week periods of warm and cold in controlled temperature rooms, a difference in apparent digestibility of DM was not observed. The reason for this inconsistent result is unclear as is the

Table 2. APPARENT DIGESTIBILITY OF RATION DRY MATTER (DM) IN WARM AND COLD ENVIRONMENTS (From Young and Christopherson, 1974).

Animal	Ration	Exposure temperature (C)	Apparent DM digestibility (C)	Change in % DM digestibility per 1 degree C decrease in exposure temperature
Sheep	Alfalfa pellets	21	52.0	
		- 6.5	44.5	-0.27
	Alfalfa-grass pellets	20	55.3	
		- 8	48.4	-0.25
	Grain and alfalfa pellets	20	69.0	
		- 8	57.9	-0.40
Calves	Grain and chopped alfalfa	18	70.4	
		-10*	65.1	-0.19
	Grain and chopped alfalfa	18	69.8	
		- 9*	60.7	-0.34
Cows	Alfalfa-grass long hay	21	61.3	
		-11	61.6	+0.01
			average	-0.24

* Average temperature of outdoor environment.

physiological mechanism involved in the influence of environmental temperature on the apparent digestibility of rations.

Metabolic Adaptation to Cold

Where a persistent or repeated external stress is imposed an animal may develop an improved ability to withstand the stress. An increase in basal metabolic rate (BMR) has been observed in small animals and birds exposed to cold (Galino, 1964; Hart, 1971) but for adaptation to a naturally occurring cold climate an increase in BMR has been questioned (Hart, 1971; Heroux *et al.*, 1959). There is some evidence of an increased BMR in man with repeated cold exposure (Yoshimura *et al.*, 1966; Hong, 1973) and suggestions from studies of Webster *et al.* (1969) and Slee (1971) that the metabolic rate may be elevated in sheep adapted to cold.

Recently we have examined the heat production of calves and cows following prolonged exposure to warm and cold either in controlled temperature rooms or in the naturally occurring climatic conditions (Young 1972 and 1973). When the resting heat productions of the animals were measured while the animals were temporarily in a warm environment, those which had been previously exposed to cold had significantly higher (8 to 40%) heat productions than those which were kept in warm conditions (Table 3). Expressed in terms of an increased daily heat production, the average increase was 0.6 Kcal. $Kg^{-3/4}$ for each degree C decrease in ambient temperature to which the animals were adapted. It appears that metabolic adaptation takes substantial time to develop and to subside, and is probably the consequence of thyroxine, catecholamine, and other hormonal adjustments (Gale, 1973). Metabolic adaptation to cold makes an animal more resistant to further cold by increasing its capacity to produce heat during severe cold stress (Bartunkova *et al.*, 1970). Adaptation, however, entails modifications which result in a higher heat production by the animal, even when there is no direct cold stress and consequently the animal has an increased maintenance requirement. This increase in maintenance requirement is a penalty that the animal must pay for being more prepared to combat the stresses of cold.

Practical Implications

The increase in maintenance requirement and the concomitant decrease in ration digestibility with reduced ambient temperature have practical implications for the livestock industries. These long-term effects of cold occur in addition to the direct and immediate thermoregulatory responses arising from exposure to sub-critical ambient temperatures. In Figure 3 are shown estimates of the increased maintenance requirements which could arise for a cow kept at various ambient temperatures. It is of interest to note that in most cold regions where there is livestock production, the major effect of cold is apparently not the direct consequence of an animal's need to produce heat to maintain homeothermy. Such thermogenesis, however, may be of vital importance to an animal during periods of acute cold such as may occur during a winter storm. The primary increase in feed requirements apparently arises from the prolonged effects of cold involving a reduction in the efficiency of digestion and the physiological adaptive changes which increase maintenance requirements (Young and Christopherson, 1974).

Shown in Figure 4 are estimated feed requirements of steers kept in feedlots in northern Colorado (Knox and Handley, 1973) and Saskatoon in central Canada (Milligan and Christison, 1973) expressed relative to that which would be predicted from the National Academy of Sciences-National Research Council recommendations for beef cattle (NAS-NRC 1970). The data have been plotted against average monthly ambient temperatures. Also shown in Figure 4 is the relationship between relative feed requirements and ambient temperature that would be predicted, taking into account the effect of temperature on digestibility, metabolic adaptation, and the direct effects of cold. The NAS-NRC recommendations were used as a basis for these calculations and adjustments were made for temperatures below 18 C (Young and Christopherson, 1974). The high relative requirement values for the calculated data probably arises because the

Table 3. EFFECT OF PROLONGED EXPOSURE TO WARM AND COLD ENVIRONMENTS ON RESTING HEAT PRODUCTION (From Young and Christopherson, 1974).

Animal	Feeding level	Exposure temperature (C)	Measurement temperature	Heat production (Kcal.kg$^{-3/4}$.24h^{-1})	Change in heat production per 1 degree C decrease in exposure temperature
Calves	Fasting	18	21	65	0.37
		-12*	18	76	
	Maintenance	18	18	81	0.56
		- 5*	11	94	
	Ad lib	18	12	110	0.40
		- 5*	5	119	
Cows	Maintenance	22	21	60	
		- 3	24	79	0.71
	Maintenance	18	16	64	
		-14	22	83	0.58
	Maintenance	18	30	73	
		- 1*	30	91	0.95
	Maintenance	18	30	77	
		-21*	30	109	0.82
	Maintenance	18	30	80	
		- 4*	30	89	0.41
				average	0.60

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*Average temperature of outdoor environment.

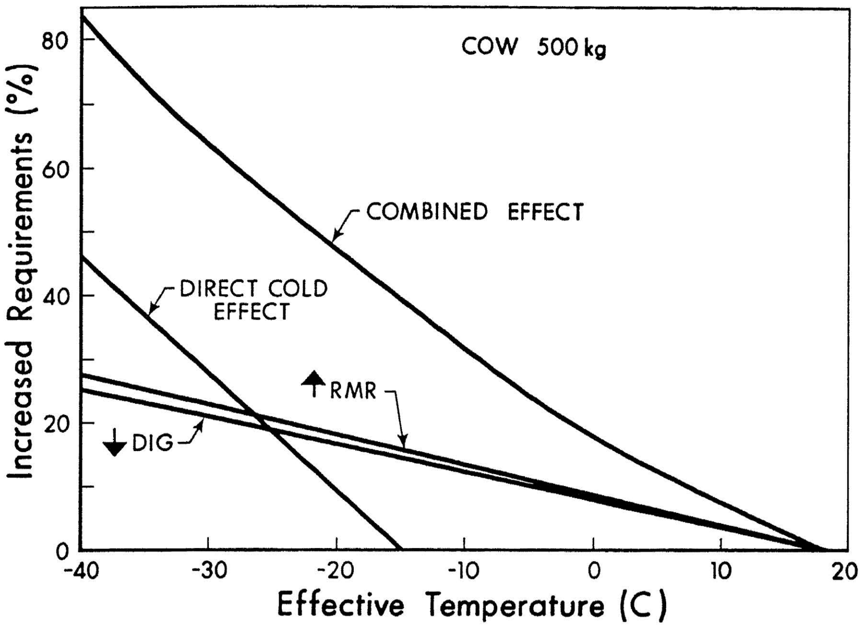

Fig. 3—Estimated increased feed requirements of a mature beef cow in relation to effective ambient temperature. Values have been calculated as percent increase in requirements for temperatures below 18C. The direct cold effect is the increased requirement arising from exposure to sub-critical temperatures. The more long-term effects on metabolic adaptation and digestibility are shown ↑RMR and ↓DIG respectively.

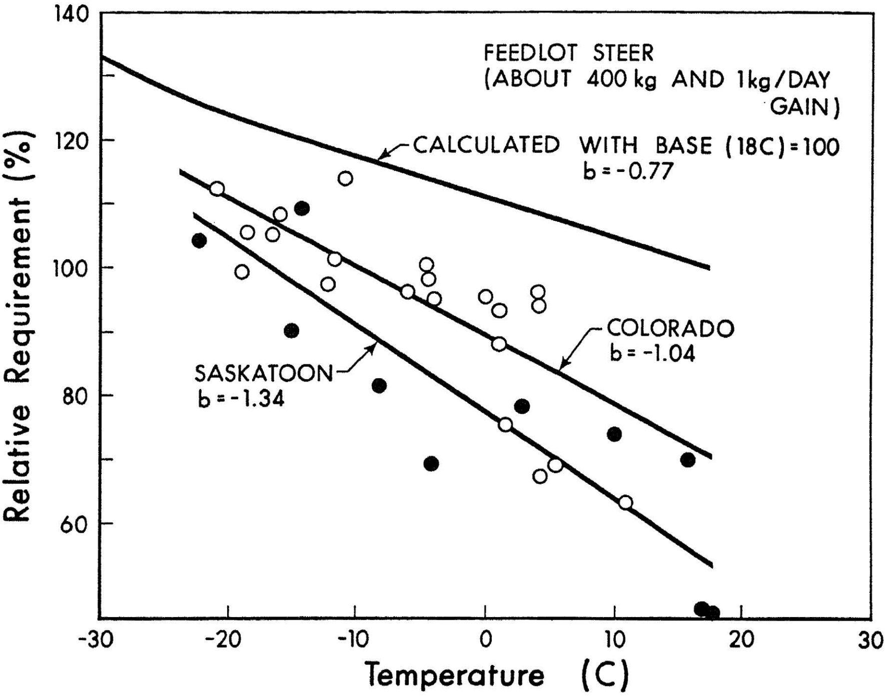

Fig. 4—Feed requirements of feedlot steers relative to NAS-NRC recommendations, in relation to average ambient temperatures. The upper line was calculated from estimates of critical temperature and the direct effect of cold and the effects of cold on metabolic adaptation and digestibility (see text). Also shown are feedlot data from northern Colorado (Knox and Handley, 1973) and Saskatoon (Milligan and Christison, 1973). The slope (b, % relative requirement per degree C) of each line is given.

NAS-NRC recommendations are for temperatures somewhat below 18 C although in the recommendation there is no suggested adjustment for temperature. The gradient (b) of the calculated line is less than that of the observed data which suggests that the present calculations account for some, but probably not all, of the effects of cold on cattle.

Concluding remarks

During this lecture I have described three aspects of the effects of cold on animals: First, the direct effects requiring immediate thermoregulation; second, the effects of cold on digestibility of the ration; and third, the consequences of metabolic adaptation. Our understanding of the nature and magnitude of the physiological costs of cold climates is quite incomplete, especially the changes and mechanism of adaptation.

I have compiled in Table 4 some food for thought. It is a time spectrum of possible effects of cold on animals. This spectrum is by no means complete and

Table 4. SPECTRUM OF RESPONSES OF ANIMALS TO COLD

MINUTES	DISCOMFORT
	PSYCHIC STRESS
	HEAT LOSS INCREASE
	HEAT CONTENT DECREASE
	THERMAL INSULATION INCREASE
	Vasoconstriction
HOURS	Piloerection
	BEHAVIOURAL ADJUSTMENTS
	Avoidance
	Huddling
	HEAT PRODUCTION INCREASE (ACUTE)
DAYS	BODY MASS DECREASE
	DIGESTIBILITY DECREASE
	APPETITE INCREASE
	METABOLIC ADJUSTMENTS (CHRONIC)
	Basal (Thermoneutral) Increase
WEEKS	Heat Producing Capacity Increase
	MORPHOLOGICAL ADJUSTMENTS
MONTHS	Skin, Hair, Sweat Glands
	Tissue Composition
YEARS	SURVIVAL CHALLENGED
	POPULATION CHANGE

does not attempt to account for possible interactions between the various factors. The list contains some items which have received considerable research effort, while others have received only nominal recognition. Some of the factors have obvious importance in livestock production, while others are of unknown importance. Those factors involved in an immediate animal response include discomfort and psychic stress. There is an increased rate of heat loss followed by activation of various voluntary and involuntary neural mechanisms to reduce the rate of heat loss and, if necessary, assist in replenishment of lost body heat. Taking still longer time to respond are the slowly established changes involving hormonal and metabolic shifts. Finally, if the cold persists we may see morphological changes, actual survival may be challenged and there may even, through natural selection, be a change in the population.

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