COMPARATIVE PHYSIOLOGY OF TEMPERATURE REGULATION

PART 2

Editors
JOHN P. HANNON
ELEANOR VIERECK

ARCTIC AEROMEDICAL LABORATORY
FORT WAINWRIGHT
ALASKA
1962

COMPARATIVE PHYSIOLOGY OF TEMPERATURE REGULATION

PART 2

Editors
JOHN P. HANNON
ELEANOR VIERECK

ARCTIC AEROMEDICAL LABORATORY
FORT WAINWRIGHT
ALASKA
1962

THE HETEROTHERMOUS CONDITION OF THE TISSUES OF WARM-BLOODED ANIMALS

Laurence Irving

Appreciation for the universality of physical laws began to develop toward the close of the eighteenth century as the metabolic production of animal heat was ascribed to combustion. Lavoisier (1777) estimated that the heat caused by formation of the carbon dioxide expired by a rabbit was nearly equivalent to the heat which the animal gave off to a calorimeter, and he confidently attributed the production of heat by animals to processes of oxidation.

In 1840 Julius Robert Mayer, a young physician in Java, followed the then prevailing custom of bleeding sailors as they arrived in a tropical port. When he observed that the venous blood appeared arterial red he consulted with a colleague and was informed that in Java venous blood appeared arterial in color. His imagination led him to think that the diminished need for metabolic heat in a tropical climate brought about less reduction of oxygen in the venous blood than was usual in a colder climate. Reflecting upon this dubious explanation, he was led to produce comprehensive physiological and astronomical illustrations of the transformation of energy, from which he developed the general view of the conservation of energy (Tyndall, 1898). Mayer's explanation of the color of venous blood does not sound valid, however, for people in warm and cold climates have about the same basal production of heat, adjusting the elimination of heat to the climate by varying the circulation and temperature in their skin.

ARCTIC CLIMATE

Cold northern climates are advantageous for studying thermal reactions of animals because the winter weather is so much colder than the bodies of warm-blooded animals. Over the northern interior of Asia and America extreme seasonal changes occur. At Allakaket

in the Koyukuk Valley of interior Alaska just north of the arctic circle the lowest temperature during the mild winter of 1959 was -59° C, and the warmest day in June was +29° C. On April 3, -36° C was recorded, and on April 11, the temperature rose to +13° C (U. S. Weather Bureau, 1960). Residents of the Arctic encounter large annual variations and precipitous rise of temperature in spring.

Stable Physiology of Arctic Populations

History indicates the presence of Eskimo people in the American arctic for 1,000 years before the first Norse settlers described them in southwest Greenland. Archaeological study of flint implements indicates that an Eskimo type of culture has been in the American Arctic for 2,000 years, and the ancestry of the Eskimo race in Alaska is probably as old as the traces of its culture. The stability of these people shows that their arctic existence was not uncertain and that it was secured by good adaptation to arctic life.

Relics of mammals indicate that species now living have been stable in form for several hundred thousand years. In the last part of this period drastic climatic changes have occurred; 6,000 years ago the north was warmer than now, and some 20,000 years ago most of Canada and much of Alaska was thickly covered by great ice fields. The ancestors of arctic animals have been exposed to pronounced variations in climate during a few thousand years. Although many generations succeeded each other in that time, the evolution of new species is not apparent. The arctic species must have long possessed physiological characteristics which were adaptable without evolutionary change in form to the recent climatic variations through which they have successfully passed.

Although relics of animals of the past provide little direct evidence about their physiology, systematic comparisons of physiological characteristics indicate that the principal mammalian and avian thermal processes have been stable since nearly the origin of the warm-blooded habit. In arctic Alaska John Krog and I (1954) found a fair sample of the few species of arctic mammals and resident birds and observed that their body temperatures did not differ significantly from those of animals of warmer climates. In fact among all of the

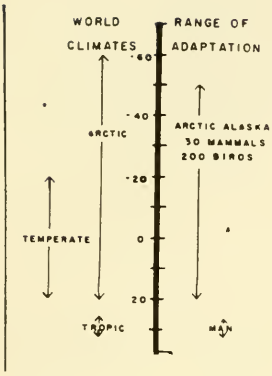


Figure 1. Temperature ranges for which warm-blooded animals are physiologically adapted compared with those of the world's climates. Redrawn from Figure 16, page 33, "Birds of Anaktuvuk Pass, Kobuk, and Old Crow." Bulletin 217, U. S. National Museum. 1960.

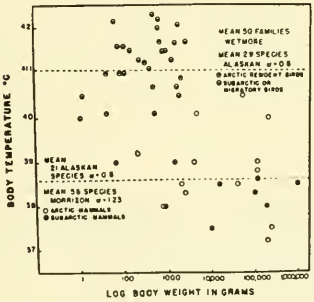


Figure 2. Mean body temperature of arctic and aubarctic birds and mammals. Figure 6, page 677, "Body Temperatures of Arctic and Subarctic Birds and Mammals." JAP. 6(11):667-680. 1954.

species of mammals that regulate their temperature well when at rest, there is a difference of only a few degrees. Body temperatures do not now differ geographically, and the comparative view indicates that little scope for variation in warm body temperature has occurred in the course of evolution. There may be evidence for ancient separate development of warm body temperature in birds and mammals, but the heat producing machines of the two warm-blooded classes operate at nearly the same temperature. The reptilian metabolic system was already so elaborately developed that its evolutionary modification for warmer operation was limited within a narrow range of temperature (Fig. 2).

Economy of Heat Among Arctic Animals

Watching the caribou in winter in Alaska, I have been impressed by the large amount of time that they expend resting and carrying on individual and social activities that bring them no food, for while living in warmer climates I had thought that arctic mammals must feed diligently in order to combat the arctic cold with metabolic heat. But Scholander and I (1950a) found at the Arctic Research Laboratory that even in the coldest temperatures the warmth of well-insulated arctic birds and mammals could be sustained with metabolism at the resting rate. Because of this economy the cost of maintaining bodily heat for existence in arctic cold does not exceed the metabolic cost of living in warm climates. Insulation adaptive to the vicissitudes of the arctic climate opens the north for occupation by warm-blooded animals without economic handicap.

Natural populations of birds and mammals including man engage in a great variety of time-consuming individual and social activities which organize their societies in order to pursue their annual programs. Although these programs differ to suit seasons in various environments, the organization of avian and mammalian populations demands so large a share of each individual's time that only limited periods can be utilized for feeding without endangering the structure of the population, which is as complex in the arctic as in milder climates.

The Variable Insulation of Arctic Animals

The thick fur of arctic animals is obviously an insulator that protects them from excessive loss of heat (Scholander et al., 1950b). In fact fur is so effective an insulator that a man clothed in winter caribou (Rangifer tarandus) fur becomes overheated when he walks, and we do not yet know how animals with thick fur get rid of the heat generated by their long, swift running. A portal for the exit of surplus metabolic heat is provided by the thin covering of the limbs and noses. When active, these extremities become nearly as warm as the body, but at rest their skin cools. We found that the bare skin of the toe pads of arctic sled dogs and the hooves of caribou at rest might be near the freezing temperature. The large webbed feet of Alaskan Glaucous-winged Gulls (Larus hyperboreus) are nearly as cold as the icy water in which they swim (Irving and Krog, 1955). When we tried to measure the heat emitted to cold water from the extensive webbed foot of an Arctic Gull, the amount was so small that at first we regarded the results with suspicion (Scholander et al., 1950b) (Fig. 3).

Effective conservation of heat by cold skin is shown by the coldness of the entire surfaces of swine (Sus scrofa) in Alaskan winter weather (Irving, 1956). The value of their cool skin as an insulator is apparent in the practicability of raising hogs outdoors in Alaska, where our estimate indicated that they consumed about the same amount of food as in temperate climates (Irving, Peyton, and Monson, 1956).

An even more impressive indication of the insulating effectiveness of changing the temperature of bare skin was shown by the hair seals (Phoca vitulina and P. groenlandica) that J. S. Hart and I examined in winter at St. Andrews, N. B. (Irving and Hart, 1957). In ice water their skin was only a degree warmer than the surrounding water, and their metabolic production of heat was little greater than in warm air. Thus cooling of bare skin provides insulation against excessive loss of heat in arctic waters, which have the greatest capacity of any inhabited environment for removing heat. This thermal economy allows great numbers of seals, walrus, and narwhals to live throughout the year in the icy arctic seas.

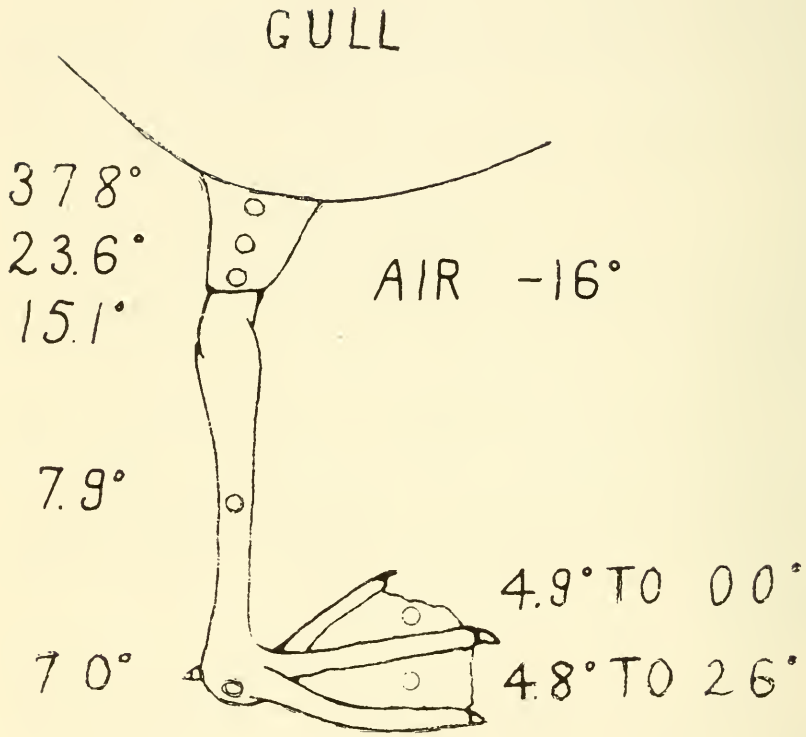


Figure 3. Topographic distribution of superficial temperatures in the leg of a gull (Larus glaucescens). Figure 9, page 361, "Temperature of Skin in the Arctic as a Regulator of Heat," JAP. 7(4):355-364. 1955.

It is an interesting indication of the general pattern of climatic adaptability of animals that while land animals shed fur in summer, northern harbor seals (Phoca vitulina) lose part of their physiological insulation in warm summer water at Woods Hole (Hart and Irving, 1959). As fur covered mammals vary the thickness of their coats to suit the season, seals reduce the effectiveness of their physiological insulation in warm weather. A number of examples illustrate that thermal adaptations of individuals are reduced as well as enhanced to suit seasonal climates.

Varying temperature of superficial tissues can thus efficiently adapt warm-blooded heat producing machines to operate economically in a variety of environments. In fact heat producing machines cannot work without thermal gradients. Until we examined arctic animals, however, I did not appreciate the extent of the swift changes in the thermal gradients of the tissues of warm-blooded animals. Now I find this variability in tissue temperature to be one of the most interesting characteristics of warm-blooded life, and I suspect that it is the primary insulator of the warm-blooded mechanism and that fur and feathers are secondary developments.

At the start of intense activity in cold weather bare skin may suddenly warm to nearly 40° C and then cool when rest is resumed. From measurements of thermal gradients extending for 6 to 8 cm beneath the skin surface in swine and seals, we have found that large masses of tissues are frequently involved in extensive thermal changes. In the temporal and topographic variations of superficial temperature, the warm-blooded animals differ fundamentally from the cold-blooded kinds. In warm-blooded forms only the center is relatively homeothermous, while the organism is heterothermous.

Variations With Temperature in Activities of Cold- and Warm-Blooded Animals

In summer on the tundra near the arctic coast of Alaska at Barrow, I noticed that when the sun shone intermittently through the clouds, the flies (Grensia) which I was pursuing escaped by flying. When the sun was covered by a cloud the flies became grounded, slow, crawling insects that I could easily catch. I inserted fine thermocouples in several of the flies and found that in shade they were

about 8° C and in sunshine they warmed to 12° C. The change of a few degrees converted the flies from slow, crawling to alert, flying organisms.

Not only do habits of living change critically in cold-blooded animals at certain temperatures, but many measurable physiological frequencies and velocities of their activities commonly double in warming 10° C. Aquatic cold-blooded animals do not usually survive the quick changes through which heterothermous tissues of northern warm-blooded animals rapidly and frequently pass, but some northern terrestrial insects can survive large and swift changes in temperature. If their activity changed continuously from 0° C to 40° C with the common Q_{10} of two, it would increase 16-fold, but the discontinuity in activity seen in the tundra flies shows that critical transitions in their cold-blooded activity occur at certain temperatures and drastically alter their manner of living.

The physiological systems of cold-blooded animals do not operate consistently over wide ranges of temperature, but the heterothermous superficial tissues of birds and mammals act in continuous coordination with the homeothermous centers so that each animal steadfastly remains one individual operating in its characteristic manner. This integrated action of heterothermous tissues may be the most informative distinction between warm- and cold-blooded life.

Our knowledge about processes in the heterothermous tissues of warm-blooded animals is too sparse to provide profitable speculation on how they are integrated in the continuous life of individual organisms, but I can add some examples of heterothermous operation in the adaptative reactions to cold of people living in northern climates.

Cooling of Hands and Feet of People Adapted to Cold

A few years ago I was fortunate in making the acquaintance of members of a sect accustomed to going with light clothing and bare feet in Alaska. Two of their members who were university students have helped us to understand some thermal reactions by their ability to manifest and describe their adaptation to cold (Irving, 1959). While

one student was sitting for 100 minutes in sparse clothing in a room at 0° C, a toe cooled, in 40 minutes, below 10° C and then warmed in two typical slow warming cycles. The toes of the other student cooled to 5° C at 65 minutes and were colder for the remainder of the 100 minute test period. During the tests the students studied for examinations and neither expressed or showed much disturbance by the cold. At 6° C the toes of one became insensitive to light touch, but both individuals remained sensitive and alert to small thermal changes when their toes were 8° C. One of them notified me that a certain toe was rewarming while its change was recorded from 10.0° C to 10.2° C and remarked upon similarly small cooling before the change was recorded. I suspect that their peripheral circulation is carefully monitored through alert sensations of temperature. Exposure to cold must train the conscious and unconscious observation of temperature for precise and vigorous reaction to meet temporal and topographic requirements (Fig. 4).

In the same condition and similar scant clothing, the toes of a young airman, who had been for two years an assistant in the Aeromedical Laboratory at Ladd Air Force Base, Alaska, cooled to 10° C in eight minutes and were very uncomfortable. At 14 minutes they were very painful, and his general discomfort became so great in 41 minutes that I asked him to give up for fear that his violent shivering would be injurious (Fig. 5).

I was at first unimpressed when one of the students told me that he had noticed sweating in his armpits while he was exposed to cold. When the adhesive tape holding thermocouples to a finger and toe were removed after his cold test, he pointed to droplets of sweat on rewarming fingers that had not yet reached 20° C. Airman Henson also looked for and showed me droplets of sweat on his fingers and toes as he was rewarming but still shivering. The paradoxical appearance of sweat on cold skin may give a clue to a common process of regulation in the simultaneous sweating and warming of cold tissues.

In their two years in Alaska the two students had developed the ability to work undisturbed while exposed to cold that we could not stand. Although they felt no pain in fingers and toes so cold as to be extremely painful for a person unpracticed in exposure, their

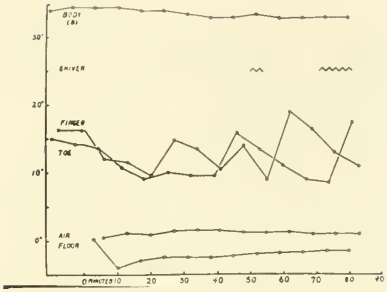


Figure 4. Temperature on skin of a young man accustomed to light clothing, bare feet and hands. Figure 1, "Human Adaptation to Cold." Nature. 185(4713): 572-574. 1960. Macmillan and Co., St. Martins Street, London, W. C. 2.

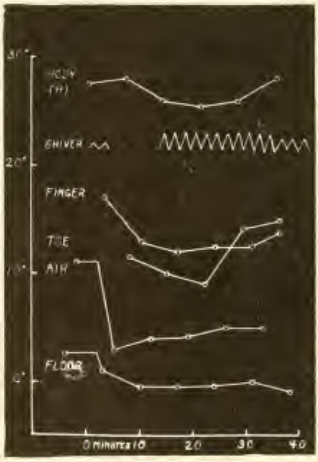


Figure 5. Temperature on skin of a young airman accustomed to regular military clothing. Figure 2, "Human Adaptation to Cold." Nature. 185(4713):572-574. 1960.

thermal sensations were not numbed but remained alert. Their tolerance of cold appears to be an active accomplishment and not the result of insensitivity. I think it is right to say that they are adapted to cold, because their accurately developed reactions enable them to achieve the simplicity and comfort that they seek by wearing light clothing.

Reactions of Eskimos' Hands to Cooling

Since we are biologists we should look for adaptation as a function of populations and not look merely in the samples of young men whom we usually test. But it is hard enough to make observations on vigorous young men when they are exposed to cold, and experimental exposure to cold might appear to be cruel treatment of delicate women and frail children. Since 1947 I have often enjoyed the good company and been aided by the intelligent appreciation of arctic life of the vigorous Nunamiut Eskimos who live by hunting caribou in the mountains of arctic Alaska. While we were visiting with Simon Paneak and his pleasant family at Anaktuvuk Pass last March, Keith and Jo Ann Miller and I were able to examine the reactions of a sample of the population to cold. The men wear warm fur clothing while traveling, hunting, and working. Their small children set out to play in warm clothing, but in excited enjoyment of their strenuous sport they may play for hours after they have lost their mitts and after their disordered clothing becomes infiltrated with snow. It was no problem to get them to sit outside in air temperatures just below freezing with bare hands while we observed them from the comfort of the sod house (Figs. 6-11).

The hands of five Eskimo men and two young ladies remained a little warmer than those of three white men and two ladies. I think it is significant that the hands of the adult Eskimos showed marked rewarming reactions earlier than the white people, for we had noticed that when immersed in cold water the hands of Indian men at Old Crow began to rewarm earlier than the hands of the white men whom we tested there (Elsner, Nelms, and Irving, 1960). The tiny fingers of the tough little Eskimo boys cooled rapidly and very quickly began rewarming cycles which continued at short intervals as lively as their play. The boys' hands were often colder than 10° C.

Figure 6. Nunamiut Eskimo camp at Chandler Lake, Brooks Range, Alaska, November, 1947. Photo by Laurence Irving.

Figure 7. Nunamiut Frank Rulland, Simon Paneak, and Jesse Ahgook with P. F. Scholander, Chandler Lake, November, 1947. Science. 107(2777): Cover. Photo by Laurence Irving, 1515 Massachusetts Ave., NW Washington 5, D. C.

Figure 8. Nunamiut boys with Jo Ann Miller at Anaktuvuk Pass, March, 1960. Photo by Keith Miller.

Figure 9. Nunamiut boy at play, Anaktuvuk Pass, March, 1960. Photo by Keith Miller.

Figure 10. Nunamiut boy after losing gloves at play, Anaktuvuk Pass, March, 1960. Photo by Keith Miller.

Figure 11. William Tobuk with hands exposed for cold test, Bettles, March, 1960. Photo by Keith Miller.

Another important difference was in the expression of pain. Most white people find fingers around 10° C painful, and our white subjects spoke very plainly about the cold as disturbingly painful. The two Eskimo young ladies said their fingers pained a little. The Eskimo men and boys did not openly express or demonstrate pain or appear anxious to terminate the test as did the white people; but on questioning two of the nine said their fingers became a little painful. Most of the Eskimos said, however, that their hands became very cold. Keith Miller is now analysing records obtained at the Arctic Research Laboratory, Barrow, during exposure of hands to just below freezing air in 12 Eskimo men, 4 women, 15 children, and 14 white men, 7 of whom were accustomed to work outdoors. His records substantiate with details the general impressions gained from Eskimos at Anaktuvuk Pass.

With fingers so cold that the pain would have disturbed us the Eskimos seemed undisturbed. But the lively thermal reactions of the Eskimo boys showed that their vasomotor regulation was sensitive. After they had been happily and noisily at play for several hours their hands were so cold as to appear beyond our safe tolerance. Although they do not appear to depend upon warning by pain they cannot be insensitive to cold, for when the children's fingers verge upon dangerous cold conscious and unconscious attention for rewarming must be especially accurately controlled in order to protect the little fingers with their relatively feeble supply of heat.

Eskimos cannot safely expose their hands to severe arctic cold longer than a few minutes; therefore this adaptation of part of the surface of Eskimos is small in comparison with the degree and extent of the adaptation of the extremities of arctic animals. But even this small adaptation extends their ability to work sufficiently to allow for many essential acts which can only be performed with hands unencumbered by mitts. That frostbite is so rare among Eskimos is the result of their keen conscious and unconscious appreciation for the limits of time and intensity of cooling that they can endure.

Oberservations on the Integration of Heterothermous Tissues

For individual existence to be coherent it must be continuously related to information about its internal condition and external circumstances. Apparently an individual must always appreciate certain

physical dimensions in absolute terms. For example, the force required to move the mass of a leg does not change with temperature, but physiological processes involved in sensory detection of physical forces do change with temperature. Mammals and birds appear to differ from the cold-blooded animal, however, in the large inconstancy of temperature in superficial tissues and in the integration of individuality in this heterothermous condition.

After seeing that the fingers of people adapted to cold were usefully coordinated when very cold, I have been trying to find a pertinent measure for their sensitivity. It seemed to me that terrestrial animals would need constant appreciation for force and mass in order to move. Stimulation by impact is a convenient test because mass and the distance through which it falls can easily be varied and measured.

Cabbage seeds selected for uniform weight, about a miligram, were found detectable after falling about 20 mm onto the ball of the warm mid-finger. The impact of a seed of double the size was noticeable after falling 10 mm, or the threshold for stimulation varied about as the kinetic energy of the impact. Other parts of the skin differed in sensitivity, and as the skin was cooled, a heavier weight or longer fall was required for the impact to be detectable.

It was easier to discharge mercury droplets weighing from 1 to 3 mg by Scholander's micrometer burette which, with a plunger 1.59 mm in diameter, measured volumetrically the drop discharged through a hypodermic needle to within a few hundredths of a milligram. The kinetic energy of the impact on the ball of my middle finger that I could just detect increased rather regularly about eight times as my finger was cooled from 35° C to 20° C (Fig. 12).

Keith Miller is now using small steel ball bearings for weights and finding that when measured as kinetic energy of detectable impact the threshold stimulus increases regularly in a trained subject as the skin cools. Individuals differ in sensitivity and in the rate of diminishing sensitivity with cold. We have not discovered whether this measure of sensitivity of cold fingers will distinguish differences in the people accustomed to cold whom we regard as adapted.

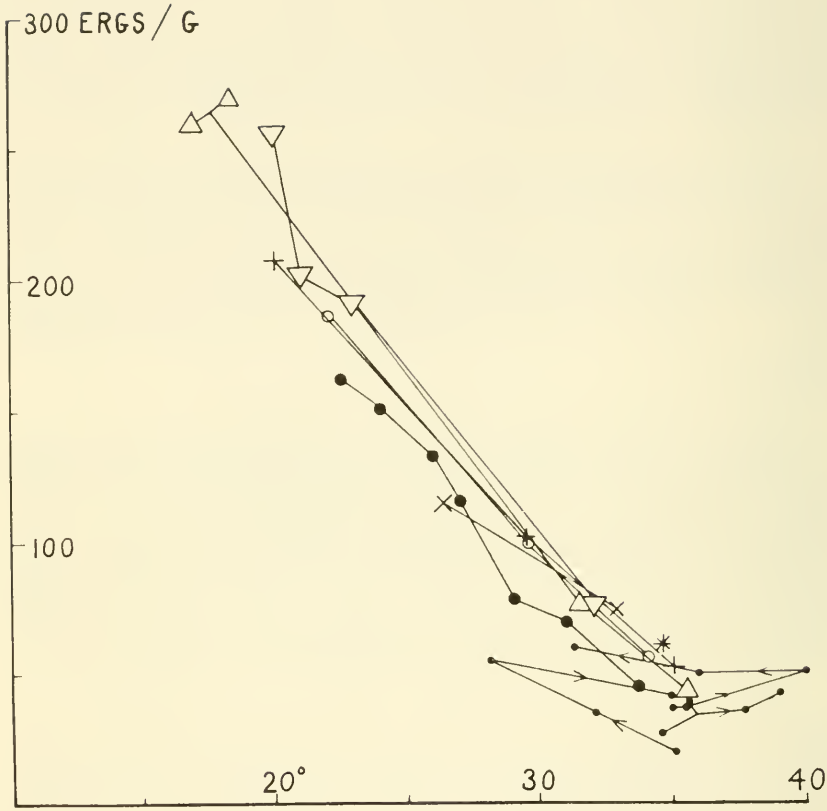


Figure 12. Change in threshold with temperature for detection of impact on the ball of one individual's finger. Abscissa:temperature of skin of fingertip. Ordinate: impact of falling droplet of mercury. Unpublished.

The report of sensation involves complex neural mechanisms which we cannot analyze physiologically. Since only part of the hand or of a finger is cooled and we cannot control effectively the amount of tissue cooled, we suspect that the regular thresholds observed in day after day tests indicate that cooling of the hand affects the local peripheral agents of sensation. But we are still only measuring a threshold and not the sensation that is involved in our estimation of the physical dimensions of stimulation. It is nevertheless interesting to consider this test an illustration of the integration of heterothermous tissues in an individual organism. Certain characteristics of the external world must be appreciated in constant dimensions, and yet the signals for those dimensions are submitted through peripheral transducers that change characteristics as the tissues which contain them warm and cool.

In comparison with the natural adaptation of animals to cold, the best physiological adaptation developed in people is only of small magnitude, and cultivated human habits and economy provide the main protection from cold. Some people resident in cold climates are motivated to utilize to the utmost their small physiological adaptability to cold. They find it worthwhile to practice exposure that seems very unpleasant for us who are accustomed to sheltered urban life. We face the test of cold with anxiety and respond in the irregular manner that characterizes untrained physiological reactions.

Power and equipment from foreign sources are used to relieve soldiers and transient workers in the north from adaptation to its cold climates. In each successive war in history power and technology have improved the protection of armies from cold and enabled them to live and move effectively in any climate and on any terrain. In spite of improving protection from the weather it is surprising that in every war winter cold blocks operations in the field and continues to be a major cause of injury. The reason lies in dependence upon power susceptible to accidental disruption. Military tactics aim to damage the enemy's vulnerable heating system or to lead him into a position where its effectiveness diminishes. Then troops accustomed to sheltering warmth are immobilized by the protection that has left them inexperienced in cold, while those less dependent upon artificial warmth may retain a small but decisive ability to maneuver.

The necessity for independence requires Eskimo populations to utilize their adaptability in winter. Even the limited human physiological adaptation is important in the natural economy of arctic life, and it is interesting to see how this adaptation is used by the Eskimo children for enjoyment of their environment. If it were considered worthwhile we could doubtless dispense with some of the expensive protection from cold that complicates living and restricts our experience. Whether or not physiological adaptation to cold is economical, I hope that some people will continue to practice ways leading to adaptation so that by their reactions we can gain insight into the interesting physiological components that appear in human adaptation to cold.

Subject	Age	Air (°C)	Rewarming (Minute)	Pain (Minute)	Body
White:					
LI	65	- 6	9	10 moderate	Warm
JLA	39	-11	12	8 severe	Warm
NG	22	-15	10	17 moderate	Warm
AB	40	- 7	17	14 moderate	Warm
JAM	26	- 6	6	3 moderate	Warm
			10		
Eskimo:					
JR	31	- 9	5	---	Warm
CH	45	-14	11	---	Warm
			8		
RN	36	-12	10	---	Shivering
Robt. P	23	- 5	4	---	Shivering
Ray P	20	- 4	8	---	Shivering
MP	19	- 9	5	17 moderate	Warm
RM	20	- 8	7	3, 21 moderate	Shivering
			7		
HH	11	-18	1	---	Warm
GP	11	-16	0	---	Warm
WT	12	-12	1	---	Shivering
Roos. P	14	-16	3	---	Warm
			1		

Table I.

LITERATURE CITED

1. Elsner, R., J. D. Nelms, and L. Irving. 1960. Circulation of heat to the hands of arctic Indians. J. Appl. Physiol. 15(4):662-666.

2. Hart, J. S. and L. Irving. 1959. The energetics of harbor seals in air and in water with special consideration of seasonal changes. Can. J. Zool. 37:447-457.

3. Irving, L. 1956. Physiological insulation of swine as bare-skinned mammals. J. Appl. Physiol. 9(3):414-420.

4. Irving, L. 1959. Human adaptation to cold. Nature 185(4713):572-574.

5. Irving, L. and J. S. Hart. 1957. The metabolism and insulation of seals as bare-skinned mammals in cold water. Can. J. Zool. 35:497-511.

6. Irving, L. and John Krog. 1954. Body temperatures of arctic and subarctic birds and mammals. J. Appl. Physiol. 6(11):667-680.

7. Irving, L. 1955. Temperature of skin in the Arctic as a regulator of heat. J. Appl. Physiol. 7:355-364.

8. Irving, L., L. Peyton, and M. Monson. 1956. Metabolism and insulation of swine as bare-skinned mammals. J. Appl. Physiol. 9(3):421-426.

9. Lavoisier, A. L. 1777. Experiences sur la respiration des animaux et sur les changements qui arrivent a l'air en passant par leur poumon. Mem. Acad. Sci. Paris, 1777, p. 185. (Oeuvres de Lavoisier, vol. 2, p. 174).

10. Scholander, P. F., R. Hock, V. Walters, and L. Irving. 1950a. Adaptations to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull. 99(2):259-271.

11. Scholander, P. F., R. Hock, V. Walters, and L. Irving. 1950b. Body insulation of some arctic and tropical mammals and birds. Biol. Bull. 99(2):225-236.

12. Tyndall, J. 1898. Fragments of Science, Vol. 1, p. 428, New York.

13. U. S. Dept. of Commerce. 1959. Climatological data, Alaska. Asheville.

DISCUSSION

MILLER: As Dr. Irving stated, Figure 13 summarizes one aspect of a study made at Barrow late last winter involving Eskimo and white subjects. Several of the whites were normally cold-exposed to a considerable extent, while others received little if any cold exposure. In Figure 13 you see finger cooling rates of Eskimo girls, aged about 11 to 12, Eskimo boys of the same age, outdoor or cold-exposed whites, and indoor, non-cold-exposed whites and Eskimo adults with varying degrees of cold exposure. The lines connect points representing cooling rates of five different fingers averaged for the individuals in each group. Cooling rates were calculated from temperature determinations made at 30-second intervals during an initial five-minute cooling period. There appears to be a definite relationship between hand volume and the initial five-minute cooling rate. The smaller fingers of the children show a more rapid initial cooling rate than the adult fingers. Ignoring the group of indoor or non-cold-accustomed whites for the moment, it may be seen that the relationship between initial cooling rate and hand volume among the various groups is approximately linear, the cooling rate being decreased with increasing hand volume. The most striking feature exhibited by the slide is the fact that the indoor non-cold-exposed white group exhibits an anomalously high cooling rate in comparison with adult Eskimos and cold-exposed whites. This more rapid cooling rate is most prominent in the little finger, although it is exhibited to a noticeable degree even by the thumb. Another point of interest is the degree of variation among different fingers within each subject group. Variation among cooling rates of different fingers is greatest in the group with the smallest hand size, the Eskimo girls, and decreases steadily with increasing hand volume, again with the exception of the indoor whites. The degree of variation within the whites not accustomed to cold was almost identical to that of the Eskimo boys. The fact that white men not accustomed to cold exhibited a finger cooling response significantly different from that of Eskimo men, despite almost identical average hand volumes, would seem to indicate that a difference in circulatory response to hand cooling is present between the two groups. Whether this difference, if real, is due entirely

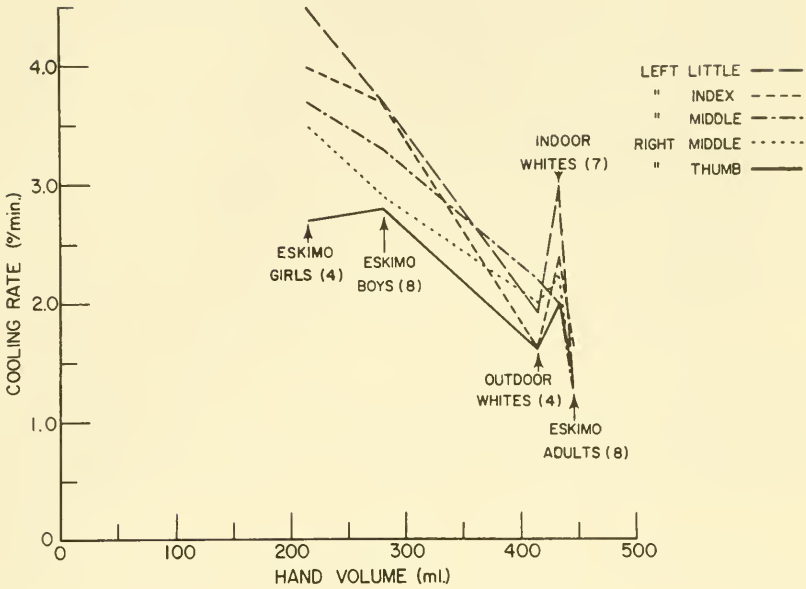


Figure 13. Initial (5 minute) cooling rates of various fingers of Eskimos and Whites plotted as a function of average hand volume.

to group differences in regard to previous cold experience, I would not wish to say at this time. The exposure temperatures were from -5° C and -10° C.

EAGAN: Is it possible that whites who worked indoors could afford more expensive clothing?

MILLER: No, not unless you want to insult all the members of the Arctic Research Lab.

HART: Were the hands exposed in open air?

MILLER: Yes.

MORRISON: Is the larger hand volume characteristic of the Eskimos?

MILLER: No, it is not significantly larger. There is just a very slight difference.

MORRISON: It is 10% which would seem to be an appreciable amount.

MILLER: But it does not appear to be statistically important. It is a relatively small group.

HUDSON: Are there any changes in blood flow?

MILLER: I did not make any determinations of blood flow, but other people have correlated blood flow changes with adaptation in Eskimos by cooling them in water. This is, more or less, a complimentary study, using air cooling.

EAGAN: I would like to ask Dr. Irving one thing: your concept of peripheral heterothermy, I believe, presupposes an improvement in sensitivity to all the general factors in the environment at the same or at a lower temperature. Does this also include the ability to cool more and yet maintain sensitivity to environment?

IRVING: Well, there certainly must be improved sensitivity; that would be the conclusion from the fact that they appear better able to monitor what is going on outside. That is, they are more observant of minor temperature changes in exposed skin areas such as the face and fingers. This is not a reduction in sensitivity or simply hardiness. Rather, along with the suppression of pain or the suppression of the impression of pain, there is apparently a more refined observation of the local temperature condition of the skin. As yet, we have not successfully demonstrated that sensitivity is retained at a better level in the cold adapted skin than in the warm adapted skin. So far we have only used these sensory tests with people that were unadapted to cold. There are other tests that indicate that the temperature sensitivity is retained better in the cold skin after the people have been accustomed to exposure.

EAGAN: From the figures you have given on Eskimos, there is a suggestion that their adaptation is an ability to maintain higher peripheral temperatures, so that we cannot say that this is in any way related to peripheral heterothermy as being an economical type of adaptation.

IRVING: Well, you have to qualify the statement and say which Eskimos you are talking about. As Mr. Miller has shown, there is a real difference between men and children, and yet they are all normal components of the population. In addition, he also observed that the skin of the Eskimo children did cool more rapidly and to a lower temperature during the period of exposure than was true of any of the adults.

EAGAN: Children do seem to withstand very low hand temperatures even here in Fort Wainwright.

IRVING: I do not know whether it is true of all children or not. We do not dare to ask parents to lend us their children for experiment, but we have no compunction about asking the Eskimo children to cooperate. They enjoy it.

EAGAN: Glasser's work with habituation or repeated presentation of an extreme cold stimulus shows that there is a change in

the way that the central nervous system handles its appreciation of this stimulus. Thus, after a series of exposures the organism appears to gain confidence in itself. There is every evidence that the discharge of cold receptors proceeds at the same rate, but the change in the sensation of cold is localized in the sensory cortex; that is, there is an habituation to cold. This can be suppressed by anxiety. I would think that possibly the central habituation may often be of much greater importance than peripheral heterothermy as a mechanism of cold adaptation.

IRVING: I would like to know if anyone has ever demonstrated that the discharge of the peripheral sensory endings is maintained during cold exposure.

EAGAN: We only have indirect evidence of this. Dr. Hensel has not done it, but I believe Glasser put on a demonstration before the Physiological Society. He had a subject who was accustomed to immersing one finger in ice water six times per day and who no longer gave any evidence of a pressor response or of a cardiac acceleration response to this measurement. However, when the subject was brought up before the group at the physiological meeting, he did show the pressor response and the tachycardia. He has made other indirect observations on experiments in which they have induced anxiety in the subject, causing him to show this physiological correlate of pain sensation. Also, he had an argument which involved the use of tranquilizer drugs, and from all of this he thought that the simplest explanation was that the discharge of the peripheral receptors is unchanged.

IRVING: Well, I cannot discount the operation of the central part of the system in habituation, as distinct from peripheral adaptation. I would say that adaptation likely involves change in the physiological behavior of peripheral organs or tissue. I think there is sure to be some alteration there; for example, the changes in some of the nerves of the poikilotherms result in the blocking of their conduction and excitability at a lower temperature after they have become used to that temperature. That is the sort of thing I am confidently looking for since we observed that the peripheral nerves of cold adapted sea gulls conducted at lower temperatures than when warm adapted.

PROSSER: It might be that these other more complex integrated functions are superimposed upon peripheral change. I do not think one would expect a single line of defense here, but a double line of defense.

IRVING: I do not see how the nervous system can possibly work, anyway. What I mean is, how can it maintain the constancy of appreciation for external conditions through a thermo-labile system which changes so grossly in many of its velocity and frequency functions? A gram remains a gram, and that is that. A millimeter remains a millimeter and that is that. If the universe changed dimensions as it changed temperature, we would go nuts; we would not be here.

EAGAN: There was an experiment we did in which four subjects exposed one hand in a cold box for 12 hours per day for ten consecutive days, the finger temperatures being maintained between 10° C and 15° C during the period of exposure. The latter was accomplished by having the subject withdraw his finger slightly as the finger temperature increased or decreased towards 10° C or insert it farther into the cold box as it increased towards 15° C. The subjects complained quite a bit at first, especially as it was getting toward the 10° C side of things. As the days passed, their cold tolerance was greatly increased and they would even go to sleep with finger temperature at 10° C, a temperature which was too painful in the beginning to even consider any sleep. Interestingly enough, when they did go to sleep, the finger temperatures invariably rose; we had to awaken them so that they could shove their hands into the cold box a little further. In general, I feel that this experiment nicely demonstrates a decrease in the discomfort due to cold as a result of continuous exposure.

IRVING: I think that is very important. Even though we say "pain" is not physiologically definable as yet, it is nevertheless a very important fact. Pain is pretty real, especially pain from cold. A person unaccustomed to cold just cannot conceal it. I think the mechanisms responsible for this habituation present a most interesting question. As a result of habituation there is repression of the sense of pain, but we do not know whether there is any change in

the rate, the velocity, the thresholds, or the temperature of cold block for the actual nerve tissues in the periphery. There must be some way to get at this question.

PROSSER: What would be the best animal to use? Hensel's work has been done almost exclusively with cats.

IRVING: People are pretty good.

PROSSER: But you cannot go in and record the nerve impulses. I want an animal in which you can go in and record the nerve impulses.

IRVING: I would take a bird like a gull, because for one thing they are not pleasing animals; you have no sympathy for them at all. By just putting blindfolds over their heads you can pretty well immobilize them, and when so quieted you can readily expose their long bare legs to cold.

EAGAN: I think a lot could be done by using Irving's and Miller's ball-bearing test on fingers. When you use bilateral comparisons you can so simply compare the adapted side with the controlled side.

PROSSER: Is this sensory adaptation which may be occurring due to the temperature per se, or might it be due to changes in oxygen supply?

IRVING: Temperature, per se, must be a factor in this habituation. However, since cold does reduce the circulation, then oxygen supply is also a probable factor.

ADAMS: You can superimpose the effects of anxiety, induced either by emotional stress or by pain on the cold induced vasodilation response. In some subjects where we have measured cold induced vasodilation responses, we find that we can prolong the period of the peripheral vasoconstriction (with the finger surface temperature at 0° C) up to 25 minutes in the ice bath by superimposing the effects of anxiety on the basic pattern of the response.

In these studies we found finger temperatures were about 33° C when the subject was supine at a room temperature of about 20° C. After stable measurements were attained at room temperature, the finger was immersed into a stirred ice bath. At this point, of course, a typical "Lewis response" occurs; that is, a rapid cooling to approximately the temperature of the bath, followed by a period of spontaneous rewarming to about 10° C to 12° C. I think that this is an almost classical response and anyone can reproduce the experiment using similar test conditions. This is the type of response that we find in all of the subjects in non-anxiety states. In superimposing the effects of anxiety, however, we can change this pattern to one where the cooling phase is prolonged to 25 minutes after the initial immersion of the finger into the ice bath. This is to be contrasted to the "unstressed" subject, where the spontaneous vasodilation normally occurs in about 7 minutes. This, I think, would probably indicate that there is a functional integrity of at least the efferent nervous components in the peripheral portion of the finger at these temperatures. Incidentally, the temperature that I am discussing is, of course, the temperature at the thermocouple taped to the surface of the finger. It indicates very little, if anything, about temperatures deeper in the finger where one may expect to find the sensory endings and where you may also expect some peripheral vascular changes to come about with mild degrees of adaptation or cold acclimatization.

We became interested in this phenomenon as a possible test site for induced variations in peripheral vascular responses with local chronic cold exposure in the same individual. The conditioning phase in our series of experiments consisted of immersing the same portion of the right index finger in a stirred ice bath for 20 minutes each time for one month; different groups of subjects underwent two, three, or four such exposures each day. In the group of subjects that showed the greatest difference in response to the finger immersion in stirred ice water, we found the finger temperatures cooled to only 10° C in the bath, compared to 0° C in the control experiments. The first thing that we saw was an earlier initiation of the rewarming phase after about one week of cold conditioning. We also carried out digital calorimetric measurements when the finger was maximally vasodilated in the bath and found a statistically

significant difference between the heat dissipation to our digital calorimeter of the control and locally cold conditioned digits.

There is a possibility that this vasodilation, or relatively reduced vasoconstriction, could be due to the destruction of the components or functions in the finger that would allow for maximal vasoconstriction during immersion in the ice bath. That is, the vasodilation we see developing in the locally cold conditioned finger may be due to a destruction of vasoconstriction potential. However, using anxiety again as a variable, we found that with our subjects, all of whom were either medical or graduate students and in whom it is very easy to induce anxiety, the induction of anxiety by verbal suggestion at any point in the phase of vasodilation brought the finger immediately to 0° C, with a cooling pattern similar to the initial vasoconstriction seen in the control experiments. I do not feel, therefore, that the cold conditioned fingers have lost the ability to vasoconstrict maximally. The altered CIVD patterns appear to result from an adjustment in peripheral circulatory control rather than a simple destruction of function.

EAGAN: I would like to point out that you have to be very careful in using thermometry to deduce what is happening in the blood vessels, but you cannot fool a calorimeter if you use exactly balanced systems in testing the two fingers. In similar experiments of recurrent finger cold exposure we have used plethysmography, thermometry, and calorimetry concurrently, and we do not see any of these CIVD differences you report.

ADAMS: I think such calorimeter data are quite acceptable for showing an increase in digital blood flow. It is possible, however, that one could have a change in circulation or circulatory mechanisms, perhaps in an increased blood flow deep in the finger, that would not be reflected in surface temperatures.

EAGAN: How can you fool a plethysmograph? Calorimetry will measure the average response over 30 minutes, if that is the length of immersion. With thermometry you get something intermediate in capability for detecting vascular change. It is slightly more sensitive than calorimetry, but nevertheless, in vasoconstricted tissue, because of the thermal capacity of the tissue and

because of its low thermal conductivity, you will have a considerable delay in detection of vasodilation. We have used the mercury strain gauge, which you can place on the finger and which makes plethysmographic measurements by using either the volume pulse or the measurement of blood flow but does not interfere with the exposure of the finger to the environment. And here we have a very sensitive measure of the most subtle changes in vascular responses. Yet, despite this we have failed to detect any evidence in favor of a local adaptation to cold insofar as the CIVD response is concerned.

FOLK: I would like to ask Dr. Johansen to comment again on his work with huskies. As I understand it they showed high body temperatures after being on the trail. If you are talking about some other animal we might find evidence of cross-acclimatization, but if I understand it correctly, the husky does not show cold acclimatization. Is it possible that there might be heat acclimatization?

JOHANSEN: My studies on the exercising of huskies were essentially not complete in the sense that I studied all the factors involved in thermobalance. I did not measure superficial temperatures, for example. I did find, however, that training lowers to some extent the great increase in temperature that is seen after intense exercise. I do not know if this will hold up statistically, but I do think that the effector systems for heat loss in the husky, the wolf, the fox, and a number of other semi-large arctic mammals are not effective enough to give a steady state thermal balance at high levels of exercise. There seems to be an inevitable accumulation of heat.*

MORRISON: What was the ambient temperature when you were running those huskies?

JOHANSEN: From 30° C to 40° C below zero.

MORRISON: We ran some similar studies with huskies, and in two sets of experiments of about an hour each we did not get any

*Rapid or slow, this heat accumulation is probably related to the whole problem of fatigue.

such increase in body temperature. These measurements were made during a normal regime with the team pulling a loaded sled and with three to five minute rest breaks every 15 minutes.

IRVING: These were trained?

JOHANSEN: Yes, eventually. They were not trained at the start of the season, of course, but they were gradually trained during the course of the winter.

EVONUK: What was your environmental temperature, Dr. Morrison?

MORRISON: It was in February or March; the temperature was near 0° C.

JOHANSEN: I have done similar studies on smaller, well-furred arctic mammals, like the muskrat, and if I dispense with their avenues for heat loss, for instance by occluding the tail as a heat exchanger, then they show a very high body temperature. In other words, heat loss through the feet and the nose and panting is not enough to keep them at a normal body temperature.

ADAMS: There were also some data on beagles* showing that voluntary exercise terminates at a particular level which seems to be determined by the body temperature. The rate of body heating is decreased with training. Untrained dogs will have a more rapid rate of increase in body temperature when exercised on a treadmill, whereas trained dogs will show a slower rate and will reach a particular rectal temperature in a much longer time.

JOHANSEN: I can tell you that just harnessing up a dog team makes them quite excited; it is enough to increase their body temperature more than one degree.

HANNON: Dr. Durrer and I have done a lot of work related to this problem of insulation and metabolism of well-furred, well-insulated dogs versus those that are not so well insulated. Thus,

*Young, D. R., et al. 1959. J. Appl. Physiol. 14:839.

the daily caloric intake of huskies was measured throughout the entire year. In addition, the daily caloric intake of beagles was measured over a period extending from late winter to summer to early winter again. Contrary to what you might suspect from reports in the literature, there is a marked seasonal difference in caloric intake in both groups of dogs--very high rate in winter and low rate in summer. In the husky this occurred despite a large increase in winter insulation. The difference between the amount of calories they took in in summer and winter was in the neighborhood of 60% in the husky and 70% in the beagle.

The data of Scholander and Irving's group at Barrow* indicate that a few arctic animals show no effect on metabolism through a temperature range. We saw a similar thing in the caloric intake of huskies during midwinter, when the environmental temperature made a sudden drop from -7° C to -44° C. This temperature change had no effect on caloric intake. We did not take a look at this type of thing in the beagles, but the beagles between winter and summer showed changes very similar to those seen in the huskies from the standpoint of caloric intake--a little greater, but not appreciably so. As a result of these observations on caloric intake, we are coming to the conclusion that in these animals the basic response appears to be metabolic and the insulative change probably serves to increase their capacity to tolerate even lower environmental temperatures.

In the husky it is interesting that early in the winter, in November in particular, his caloric intake is somewhat above that seen later in the winter. For example, it may go up to 70% above the summer level and then drop back down to a plateau that is maintained for the remainder of the midwinter. This would suggest that as he picks up his winter insulation he is able to compensate somewhat for the increased caloric demand of the environment. We did not carry the beagles far enough into the winter to see if there was a similar sort of reduction in caloric intake. However, no gross changes in fur insulation were apparent.

*Scholander, P. F., et al. 1950. Biol. Bull. 99:259.

HART: You have an increase in food intake of 50% to 60%?

HANNON: This is average daily intake on five huskies.

HART: I do not think that you can conclude that this necessarily represents metabolic temperature regulation. How well did you control activity, sledding and various things?

HANNON: These dogs were tied with six-foot chains. They were only released from these chains a few times, in both summer and winter, to be brought into the laboratory for blood sugar determinations. Furthermore, in the winter the body weight declined, and in the summer it increased, thus suggesting an inability to precisely match the caloric intake to the energy demands of the environment. In other words, in the summer they were eating too much and in the winter too little to maintain a constant body weight from season to season.

HART: Is not 60% a large increase in food intake for a well-insulated animal?

HANNON: It would seem so, yes.

MORRISON: Are they rather limited in their activity in the summer?

HANNON: Grossly, the animals appeared to be most active in the summer and the least active during periods of extreme winter cold. Whether this produced a significant seasonal difference is unknown. It is my guess, however, that they may be more active in summer, because there are more people around them.

DURRER: It is interesting to note that in temperatures of -35° C or -40° C the activity is quite reduced. For example, they are even reluctant to get up and eat and are not as apt to rise in the presence of people at these extreme winter temperatures as they are in summer or in the warmer winter temperatures.

JOHANSEN: One factor that has not been mentioned is the

availability of food to the animal. It is extraordinary when an animal has more food than he can eat every day. This is certainly not what you would expect arctic mammals to be confronted with in his natural environment.

HANNON: That is true, but if we had attempted to control caloric intake we would have biased our results by the mere fact that you are controlling the amount of food available.

IRVING: He is thinking that the dog chooses to eat more when excess food is available. Why he chooses to eat is a different thing.

MORRISON: I might add that our appetite in cold weather exceeds the thermoregulatory needs of the body.

HANNON: After the first two or three weeks of over-eating they reduced their intake and it remained fairly constant from day to day. However, when you consider these daily intakes over a period of months the differences between the seasons are significant, and there is a significant correlation between temperature and food consumption.

HART: Have you done this over the whole winter and summer?

HANNON: On the huskies, we have it starting with November of one year and continuing through November of the following year.

MORRISON: How about the beagles?

HANNON: The reason we used beagles is interesting in itself. We started these feeding experiments on huskies on the first of October and commenced our measurements of food intake on the first of November. As I mentioned earlier, there was a decline in food intake between November and the later portions of the winter. This did not seem quite right; so in midwinter we decided we had better look at dogs that were not so well-insulated as the huskies. Beagles seemed to offer a good choice. They were purchased in California and brought to Alaska, where they were housed indoors for four weeks. During this period they were allowed two weeks to adapt to the same diet as the huskies and two weeks

during which control measurements were made in the laboratory. They were then subjected to outdoor exposure. When we first put them out in the cold the temperature was about 0° F. At first they could not tolerate this cold on their feet and would howl, roll on their backs and put their feet in the air. During subsequent exposures of gradually increasing duration they evidenced cold injury, particularly on the feet, ears and mouth. However, within a period of two or three weeks these injuries began to disappear and they were eventually able to tolerate temperatures as low as -30° C for a full 24 hours with no apparent ill-effects. Such continuous exposure was continued through the remainder of the winter, the summer and into the early months of the following winter, when the experiment was terminated.

MORRISON: Were they eating meat or dog chow?

HANNON: The diet was fairly high in protein; it was a mixture of dry dog food, powdered milk, and fish meal.

WEST: Did you find any difference in efficiency?

HANNON: Do you mean work efficiency?

WEST: No, efficiency of food assimilation; that is, the utilization of the energy that you gave them. Did you get the caloric value of feces, for example, to see if they were using all this food that you were feeding them?

HANNON: No, we did not.

KLEIBER: I may have an answer to that, not for dogs but for baby chicks. There we found a very consistent correlation between food intake and temperature; namely, as we decreased the temperature from 100° F to 95° F to 80° F to 70° F, there was a consistent increase in food intake. There was also a decrease in digestability.

WEST: We found the same decline in efficiency with wild birds. I wonder if this is a part of the explanation for this increase in food intake.

KLEIBER: We measured that and found that there is a definite increase in caloric output.

HANNON: Well, the magnitude of the change in the beagles, at least, between this summer and winter is very similar to what you see in rats going into a 5° C cold room, thus suggesting a similar caloric demand by the environment. In the cold, rats certainly exhibit a high rate of heat production, but as far as I know the efficiency of food utilization has never been measured.

IRVING: To get back to the remarkably high body temperature that Dr. Johansen spoke about, I would like to inquire whether there are reports of domesticated animals having reached similar high temperatures?

KLEIBER: Yes, Kibler and Brody* recorded rectal temperatures in Holstein cows as high as 108° F (42° C). Generally cows are in bad shape in a hot environment.

FOLK: I might make another comment on continuous feeding of dogs, since apparently not too many people have heard about it, but some of the big kennels have been doing that for several generations. Sometimes, in experiments like those you do with white rats, you want to have continuous food there. You do not want a perturbation. If they have had food in front of them when they are quite young they do not overeat. Occasionally there is one dog you will need to eliminate because it does overeat, but they are rather quick to learn to take just enough out of a feeder.

HANNON: Our dogs in the study were two to four years old. Thus, they were adults. Food was placed in front of them and left for a period of one-half hour. But, as I mentioned earlier, they would eat a little bit too much in the summer time and too little in the winter time insofar as the maintenance of a constant body weight was concerned.

MORRISON: I wonder if the specific dynamic action of the food

*Kibler, H. H. and S. Brody. 1953. Influence of humidity on heat exchange and body temperature regulation in Jersey, Holstein, Brahman and Brown Swiss cattle. Univ. of Missouri Res. Bull. 522:14.

would produce enough heat to make them uncomfortable in the summer and if this could modify their intake. Such an effect should not bother them in winter.

HANNON: We do not know, except that in the winter they have heavy insulation. In the summer they do not.

MORRISON: They can lie in the snow and dissipate more heat.

HANNON: I believe Dr. Irving has made some measurements on the amount of heat that huskies dissipate to the snow when they are lying down?

MORRISON: Well, how much they can dissipate and how much they do dissipate depends on whether they are in a heat dissipation "posture" or not.

HANNON: If dogs are lying in the snow dissipating very much heat, a melting of the snow should be evident. This does not seem to occur.

IRVING: There is no melting. John Krog and I measured the temperature under dogs by putting a grid of thermocouples under the place where they slept. We found that the temperature at the surface was not above freezing, and the snow did not melt although it did become compressed. If the snow had melted, the fur would have froze to the snow, and you never see any fur frozen in a place where a normal animal has been bedded down in the snow.

JOHANSEN: If I may switch back to the high temperatures now, I think that we really need a lot more measurements. The only really detailed study available is Asmussen and Nielsen's study of athletes, which showed a rectal temperature of 41° C after long track running. It may be surprising to you, but it is not to me, that the husky, with its tremendous insulation, gets such a great increase in temperature.

IRVING: Have you obtained any evidence that he really develops a better faculty for supporting a high body temperature?

JOHANSEN: No.

IRVING: I think this would be a very valuable thing to determine, especially when sled-dog running is so well cultivated here; you might even use such information to get good teams of dogs.

JOHANSEN: Of course I would like to measure running caribou and, when I get back to Norway, the reindeer, which is domesticated and used for transportation.

HART: I would like to mention this in connection that even in the small mammals such as mice and rats body temperatures up to 40° C or 41° C may be obtained during exercise of 20 or 30 minutes duration. It is commonly possible to do this in a relatively warm environmental temperature. However, in a cool environment, the body temperature may not rise at all.

JOHANSEN: Their insulation of course is poor.

HART: The insulation is markedly inferior. With the husky dog, you apparently never reach the condition where the temperature is low enough to cause this effect.

HANNON: Along similar lines it might be worth mentioning that the rectal temperatures of cold acclimatized rats are quite readily elevated to very high levels when they are injected or infused intravenously with norepinephrine. A number of times, for example, we have observed body temperatures as high as 43° C or 44° C in experiments with this hormone.

JOHANSEN: Of course this concept of heterothermy and the potential of insulation somewhat invalidates the things we have been taught in school about the climatic rules. I was wondering whether Dr. Irving would care to comment about how this might invalidate Allen's Rule about the length of extremities.

IRVING: I think those rules are useless.

PROSSER: There is still a correlation, just the same.

IRVING: I am not sure there is among the different caribou; the smallest of all is also the most northern. You find many exceptions to that; and as Scholander says, if this were a matter of a law of heat you should not find any exceptions. Thus, one exception would invalidate the significance of such a law. It may be true that many birds as they go north get longer tails, larger bodies, or bigger claws. On the other hand, some do just the opposite. I do not think it has ever been shown that any of these differences in body dimensions are significant to the heat economy of the animal. I will go farther and say that the surface of an animal has no relation to its heat exposure; there is no relation that you or I can define, because in the first place there is no geometrician who can define the surface of such an irregular object as an animal. It is indescribable, mathematically. If it were describable, it would not be worth the time or the effort, and further, attributing the heat loss simply to the surface disregards practically all that we know that is interesting and important with regard to the conservation and dissipation of heat. In other words, it is not a matter strictly of surfaces. For example, the circulation through the skin of the fingers is one hundred times what it is through the skin on the forearm or on the rest of the body. The variability in the amount of circulation, the amount of heat exchange, and the temperature of blood passing through the extremities are far more important factors than is the extent of the skin surface. And those are the variable factors in heat economy, while surface, if there be such a thing, is an invariable function unless the animal chooses to alter his posture, as he does in sleep.

PROSSER: But still there is a general correlation between size and distribution; it may have no relation to temperature regulation at all, but it remains as a correlation.

IRVING: That may be, but it is not of any great interest or importance to physiology.

PROSSER: I am not willing to say that. It may have some meaning which we do not know.

MORRISON: Do you think it is fair to say that a factor has no significance simply because there are other factors which are more significant?

IRVING: Yes, it has less significance, because it conceals or disregards the physiologically important and interesting things, which are the variability in temperature and circulation of the different areas.

MORRISON: Well, would you then say that the high levels of hemoglobin in a diving animal are of no significance in the prolongation of diving, because they would not allow anything like the observed increases in diving time and because the circulatory changes are so much more important? Is there not an analogy here?

IRVING: No, I would not say that the oxygen capacity of the blood is unimportant for the seals. It is very important. It is not the large factor in the prolongation of their dives, but presumably if the blood has twice the oxygen capacity it has at least doubled the transport capacity and the rate of recovery. If you get double the oxygen capacity and improve the elasticity of the whole vascular system, then recovery is apparently attributed to those factors. One of the remarkable things about such diving animals, incidentally, is not only the prolonged diving but also the rapidity with which they can recover and take another dive.

MORRISON: But when we have a factor that is advantageous, when are we to say that it no longer has any significance as long as it is in the right direction? Can we not say that it may have selective significance, even if it is only at the 10% or 5% level?

IRVING: Then you get one of these instances of statistical significance. You are talking about imperceptible adaptations which gradually accumulate by some statistical process to become of visible importance.

JOHANSEN: If you go back to heterothermy, the point here is that these extremities provide insulation, and if they are larger they provide more insulation.

MORRISON: If you do not have extremities, insulation (=1/conductance) is better.

JOHANSEN: No, such a situation is unrealistic and has no relevance to the situation.

MORRISON: If you amputate the leg, you are going to lose less heat from it.

PROSSER: Also, there might be differences which would show up in a population analysis that would not be of any measurable advantage to an individual as such. However, they might be of importance to the whole population.

MAXIMAL STEADY STATE METABOLISM AND ORGAN THERMOGENESIS IN MAMMALS

L. Jansky

The studies of basal metabolic rates in mammals and the relation of metabolic rates to body weight have been the subject of many papers and reviews since the middle of the nineteenth century. These studies have not confirmed the validity of the "surface area theory" and have proved that the basal metabolic rates were proportional to $W^{0.75}$ where W is the body weight (Kleiber, 1947).

On the other hand, very few data are available on the upper limits of metabolic rate that can be sustained for long periods in different species. It is known that very high rates of heat production, up to 100 times the basal level, can be measured in man and horse under extreme exercise (Brody, 1945). However, these rates cannot be sustained for long periods and do not result from steady state effort. Methods of estimating steady state effort and a comparison of results in different species varying in body weight will be considered in this paper. In addition, the total cytochrome oxidase activity, which can yield values for metabolism which are theoretically maximal in different species (Jansky, 1961), will also be considered. This method also provides a means for estimating the theoretical maximal values for different organs of the same species and their relative contributions to the metabolic capacity of the whole animal.

Maximal Steady State Metabolism

For the purposes of this paper, the upper limit of metabolism will be called the "maximum steady state metabolism" and will be defined as the highest oxygen consumption compatible with sustained aerobic effort when there is no progressive accumulation of lactic acid in muscles. It is known for man (Wells et al., 1957) rats (Sreter and Friedman, 1958), and deer mice (Hart and Heroux, 1954) that a certain level of exercise can be attained without accumulation of

lactic acid and that this level of exertion can be sustained for long periods. In practice, lactic acid is not usually measured, and maximal steady state metabolism during exercise is determined at the highest running speed, which can be sustained for about 20-40 minutes.

During exposure to cold there is also a marked increase in metabolism which can be maintained for long periods. The question therefore arises as to whether there is a relationship between the maximal working metabolism and the highest level of metabolism that can be obtained in the cold.

Experiments on man have shown that it is possible to attain the maximal steady state metabolic level only under intensive work conditions and that the effect of cold does not add to the metabolic rate during work (substitution theory - Lefevre, 1933, 1934). On the other hand, tests on some small mammals have shown that maximal oxygen consumption is possible with simultaneous application of work and lowered temperatures, so that the working and cold thermogenesis occur at the same time, (addition theory - Chevillard, 1935; Hart, 1950; Hart and Heroux, 1955; Jansky, 1959, a, b, c).

In the tests on small mammals, the measurement of maximal steady state metabolism during work and exposure to cold is very difficult, owing to the rapid development of hypothermia which eventually causes a decline in heat production. Figure 1 shows a distinct drop in the oxygen consumption of white mice which started immediately at the beginning of the work in extreme cold (Jansky, 1959a). Decline of metabolism presumably due to hypothermia was found at the lowest temperatures in most of the species investigated.

Since the values obtained on hypothermic animals could not be considered maximal, it was necessary, therefore, to perform the tests at various temperatures to find the lowest temperature at which working oxygen consumption was maximal and did not decrease during the test period (40 minutes).

Results obtained on various small mammals showed that there were species differences in the effect of work and cold on metabolism. In rabbits and lemmings (Hart and Heroux, 1955) in white mice

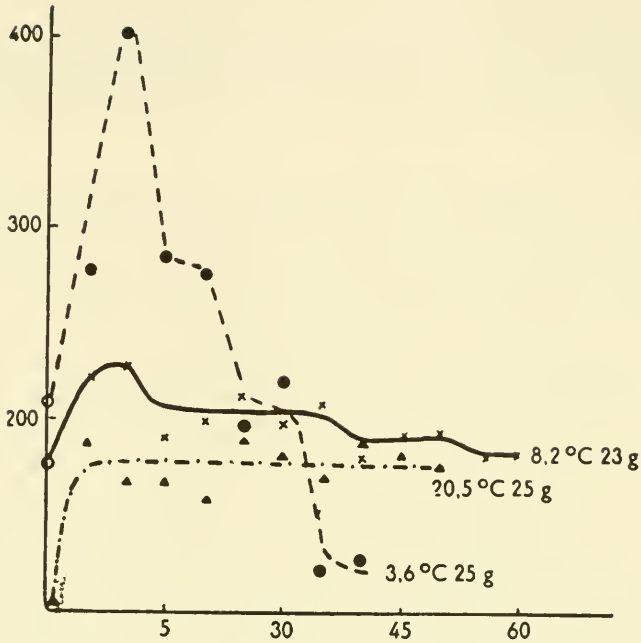


Figure 1. The time course of working oxygen consumption of the mouse at various temperatures. Ordinate: oxygen consumption in ml O_2/hour/animal; Abscissa: time in minutes. (Jansky, 1959a).

(Hart, 1950; Jansky, 1959a), and in golden hamsters (Jansky, 1959c), kept at laboratory constant temperatures, the working oxygen consumption increased with decreasing temperature. Oxygen consumption during work was added directly to the cold thermogenesis, giving two parallel curves (Figure 2). These results confirmed the validity of the addition theory and showed clearly that the highest values of metabolism could be measured only after simultaneous application of cold and work.

Contrasting results have been obtained on two wild rodents, the common vole (Microtus arvalis) and the bank vole (Clethrionomys glareolus) (Jansky, 1959b), kept for a short period at naturally fluctuating temperatures. Both species are closely related and have the same average weight (18 gm). In the common vole, the typical addition relationship between working and resting heat production in the cold was observed. In the bank vole, on the other hand, the metabolism during maximal work below the thermoneutral zone did not increase to the same extent as that during rest with decrease in temperature. Therefore the heat production during work partially substituted for the cold thermogenesis. This was particularly clear when the maximal running speeds of the two species of voles are considered (Figure 3). Although there was a slight increase in running speed with lowering of temperature from 25° C to 5° C, in both species, there was a decrease in the difference between working and resting metabolism in the bank vole but not in the common vole (Figure 2). When the lowest temperature was reached, both the running speed and the difference between working and resting metabolism were greatly reduced. The common vole had a greater range for maximal work than did the bank vole in both heat and cold.

These experiments have shown that the metabolic differences among various species of mammals do not depend on the weight of the animals or on their phylogeny. The only obvious difference between the common vole and the bank vole lies in the ecology of both species and in their acclimatization to various temperatures. Bank voles live in forests in deep burrows and build well-insulated nests and are not, therefore, exposed directly to the effect of low temperatures. Common voles, on the other hand, live in meadows in superficial burrows almost without nesting material and are forced more often to endure extreme temperatures. This is reflected in

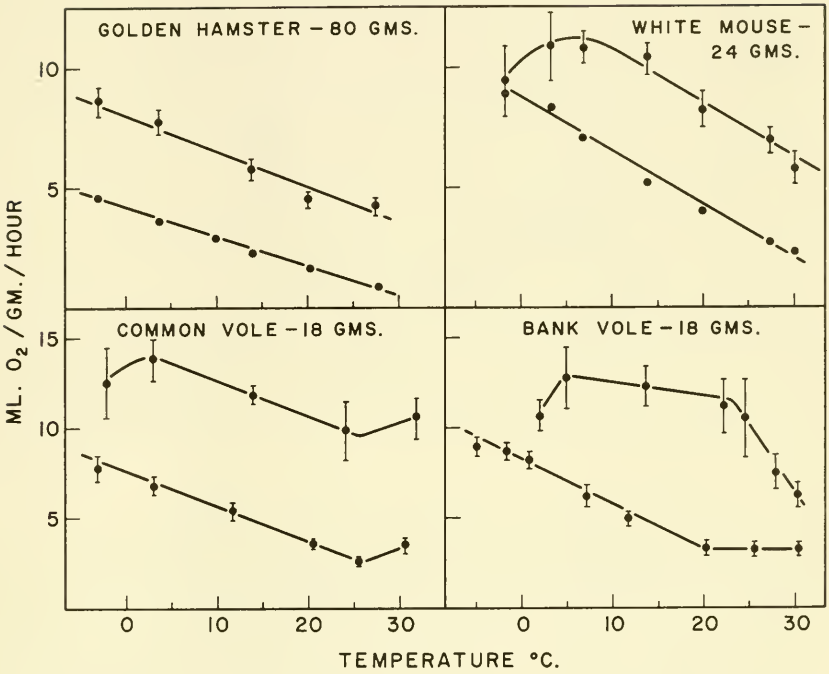


Figure 2. Working and resting oxygen consumption at different temperatures in various mammals.

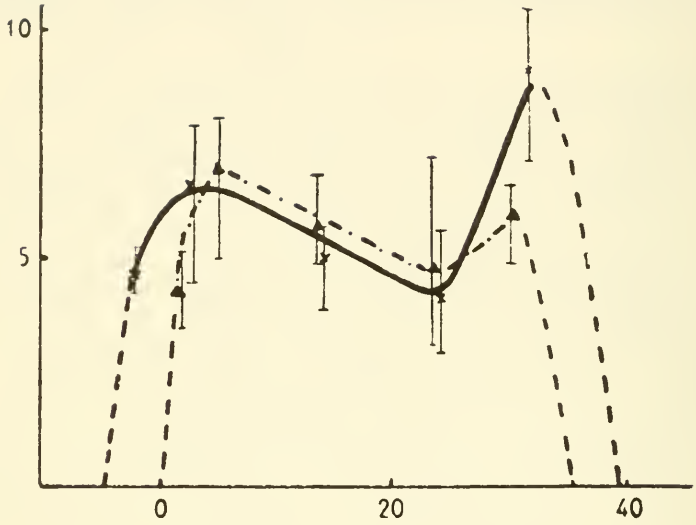


Figure 3. Maximal running speed of the common vole (x___x) and the bank vole (▲- - ▲) at various temperatures. Ordinate: running speed in m/min.; Abscissa: temperature in °C. (Jansky, 1959b).

their greater abilities to run at high and especially at low temperatures.

Recently it has been shown (Hart, 1962, in press) that warm- and cold-acclimated rats behave differently with respect to substitution of exercise for cold thermogenesis. Warm-acclimated rats, having shivering thermogenesis only, substituted heat production from shivering by heat production from exercise. Oxygen consumption during work did not change with decreasing temperature and was identical to the maximal oxygen consumption in rest at the lowest temperatures. This is apparently due to the fact that exercise in cold may reduce or eliminate shivering. This was surmised long ago and recently demonstrated in pigeons during flight (Hart, 1960). On the other hand, in cold-acclimated animals, which can produce heat without shivering (Sellers et al., 1954; Heroux et al., 1956; Cottle and Carlson, 1956), the addition of exercise heat production to cold thermogenesis is made possible (Figure 4). The result is that working oxygen consumption increase with decreasing temperature parallel to resting values and the maximum heat production is greatly increased.

However, at temperatures approaching the peak metabolic rate for cold-acclimated rats, heat production during work did not increase with lowering of temperature. At these low temperatures, shivering was clearly visible in the resting rats, and mechanical work was substituted for shivering as in warm-acclimated rats (Hart, Jansky, unpublished). The values followed closely the broken line shown in Figure 4. As shown for warm-acclimated animals, the resting metabolism was, at very low temperatures, almost as great as the values of working metabolism.

It seems clear, therefore, that the substitution relationship between working and resting heat production exists in these animals only when shivering is replaced by gross physical activity. The additional relationship occurs over a certain range of temperatures in these animals, when non-shivering thermogenesis plays the dominant role in maintaining body temperature.

All these data show that the values of maximal metabolism are obtainable not only after simultaneous application of work and cold,

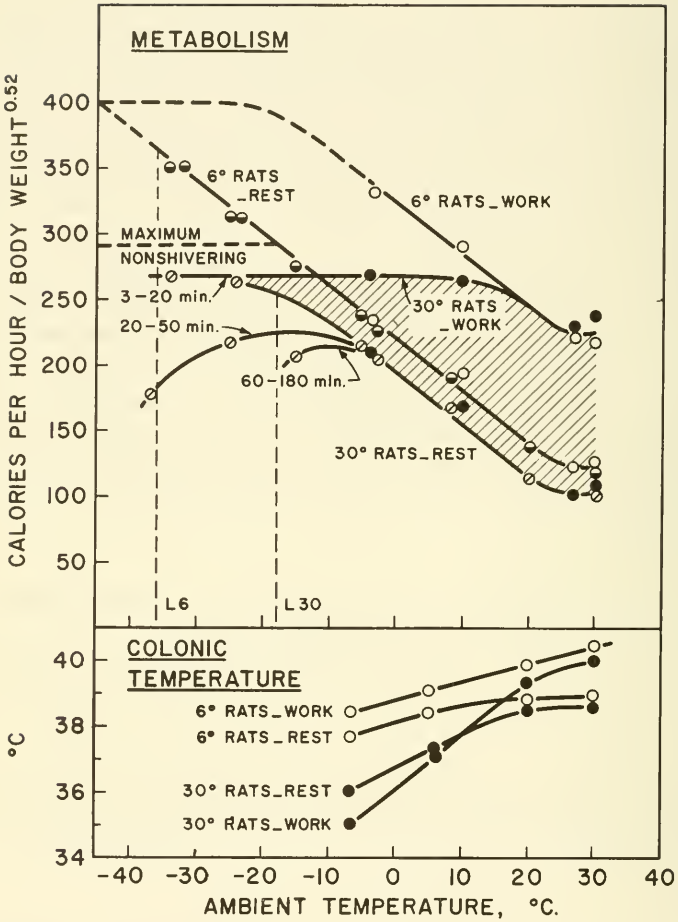


Figure 4. Working and resting oxygen consumption at various temperatures in cold and warm adapted rats. (Hart 1962, in press).

but also in the resting state after exposure to low temperatures approaching the lethal level. Under the latter condition it is necessary to measure the oxygen consumption for a very short period after exposure to cold, because of the substantial drop in body temperature (Figure 4). This period is about 20 minutes long for the rat (Depocas et al., 1957).

Owing to the difficulties described above in measuring maximal steady state metabolism, relatively few values have been published for mammals (Chevillard, 1935; Hart, 1950; Jansky, 1959a for the white mouse; Hart and Heroux, 1955 for the lemming and rabbit; Jansky, 1959b for the bank and common voles; Jansky 1959c for the golden hamster; and most recently by Buskirk and Taylor, 1957, for man). One can expect that rather larger species differences might occur, owing to differences in body size, posture, hair insulation, blood circulation, and air movement, which might be quite different during maximal metabolism than during the resting state and could have a different effect on the amount of heat dissipation.

When all published values of maximal steady state metabolism are plotted against the log body weight of the animals (Figure 5), it was found that maximal steady state metabolism is equal to about six times and basal rate, with a body weight exponent very close to that found for basal metabolism. All the species examined have, therefore, nearly the same capacity to increase energy metabolism from the basal to the maximal steady state level. Species differences in posture, insulation, and other factors that affect heat dissipation have no apparent effect on this capacity to increase heat production.

Total Cytochrome-oxidase Activity

Since the rapid cooling of small animals at low temperatures makes the measurement of maximal steady state metabolism quite difficult, an additional method was sought for measuring the highest metabolic capability of animals and tissues.

It can be assumed that the total oxidative activity of tissues cannot be greater than that of the activity of the only terminal oxidative enzyme, cytochrome oxidase. In other words, it is supposed that the

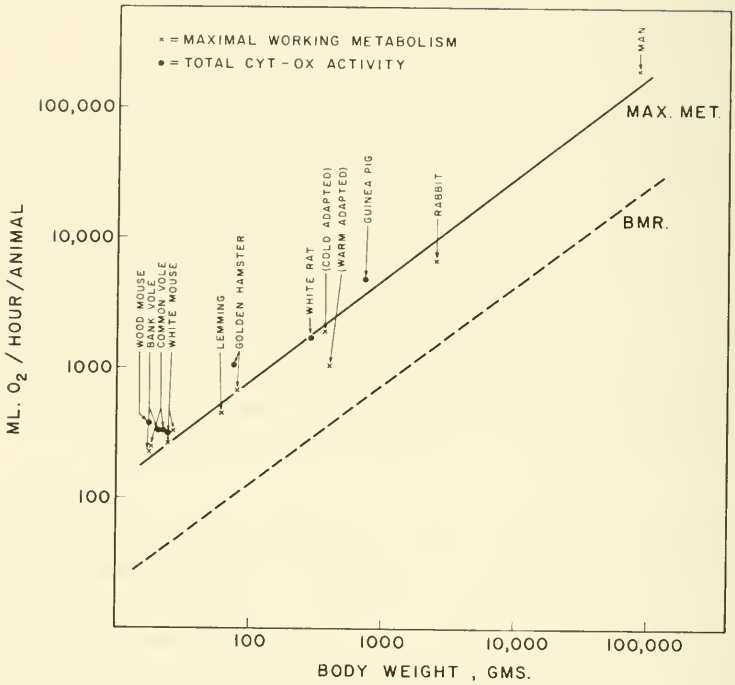


Figure 5. Relationship of maximal steady state metabolism and total cytochrome oxidase activity to body weight in various mammals.

maximal oxidative activity of this enzyme corresponds to the highest tissue oxygen consumption. It can also be assumed that cytochrome oxidase does not occur in excess quantity in tissues, because cytochrome oxidase activity readily becomes adapted to various conditions (Tipton and Nixon, 1946; Hannon, 1960). For these reasons the cytochrome oxidase activities of whole animals and their tissues were examined to find whether the values were related to the maximal steady state oxygen consumption.

The method selected for use in these studies was the classic manometric method of Schneider and Potter (1943), in which cytochrome oxidase activity can be measured in terms of oxygen consumption. The cytochrome oxidase activity was measured in a homogenate of the whole animal for direct comparison with the values of maximal steady state metabolism. Before homogenation in distilled water, the animals were depilated and after removal of their digestive tract, they were ground in a meat grinder. Oxygen consumption of the homogenate was measured at 37° C.

The total cytochrome oxidase activity was determined in seven species of rodents (wood mouse - Apodemus sylvaticus, bank vole - Clethrionomys glareolus, common vole - Microtus arvalis, white mouse, golden hamster, rat, guinea pig) in the range of body weight from 17 to 700 gms. It was found (Figure 5) that the exponent of the relationship between total cytochrome oxidase activity and body weight was very similar to that found for basal and maximal metabolism (Jansky, 1961).

By comparison of the absolute values of oxygen consumption, obtained in vitro, using cytochrome oxidase activity and those in vivo at the level of maximal steady state metabolism, only small differences were found.

In spite of close agreement between in vivo and in vitro values, they are not considered to be identical. Both methods are completely different, and we cannot expect to be able to imitate the same conditions in vitro as in living cells, where the concentration and composition of substrates, pH and various other factors can change during the maximal performance of the organism. In addition there is a possibility that certain organs such as kidney, brain, or gonads are

not performing at maximal capacity when the animal is engaged in maximal steady state effort. This may explain the tendency for cytochrome oxidase values to be higher than maximal working metabolism in the various species.

It is, therefore, suggested that the terms "maximal steady state metabolism," be used for values obtained in vivo and "total cytochrome oxidase activity" be used for values obtained in vitro, which represents the highest theoretical value of oxidative metabolism (metabolic capacity).

Cytochrome Oxidase Activity in Body Organs

The values of total cytochrome oxidase activity are useful for comparative purposes and seem to be especially suitable for estimating the metabolic capacity of different body organs. At present, we do not know of any other method for assessing maximal performance of body organs. The cytochrome oxidase method can provide some information on the relative roles of different organs in the total metabolic capacity of the whole animal.

The cytochrome oxidase activity was measured in 10 of the most important organs (carcass, liver, skin, kidney, brain, lung, heart, diaphragm, spleen, and gonads) in the golden hamster (Svoboda and Jansky, 1959). Some other preliminary experiments were made on the white mouse and on the rat.

In general, the highest cytochrome oxidase activity per mg of dry substance was found in the heart, kidney and brain, the lowest in the carcass and in the skin. The cytochrome oxidase activity per mg dry substance in the same organs of various species seems to decrease in heavier animals.

The most important consideration for our purposes is the ratio of cytochrome oxidase activity in whole organs to the total cytochrome oxidase activity of the whole animal. The results on the golden hamster show very clearly that the muscles play the most important role. At body temperature (37° C), they represent about 76% of

the theoretical total metabolic capacity (Figure 6). The role of other organs is relatively small. The most important are skin (9%), liver (5%), brain (3%), and gonads (3%). Similar observations were also made on the rat.

Organ Thermogenesis in vivo

Owing to the large contribution of the muscles and the minor contribution of visceral organs in the total cytochrome oxidase activity of hamsters and rats, it is important to consider the relative contribution of these organs in vivo to the maximal steady state metabolism. At present only indirect estimation can be made on the role of muscle in intact animals. In warm acclimated rats (Figure 4) the maximal steady state metabolism is approximately 270 Cal/(hour x body weight$^{0.52}$). The increase of metabolism from the basal level (100 Cal/(hour x body weight$^{0.52}$)) is about 170 Cal/(hour x body weight$^{0.52}$), which is 63% of maximal metabolism (270 Cal/hour). Since shivering is the principal source of heat in these rats exposed to cold, it can be assumed that the cold thermogenesis is due to muscles. In addition to the cold thermogenesis, it has to be estimated that the participation of muscles in the basal state amounts to about 30% of the total metabolic rate (Field et al., 1939). This would be approximately 10% of the maximal rate in these tests. The total contribution of the muscles to the maximal metabolism would therefore be 73% (63% + 10%).

In cold acclimated rats the quantitative estimation of the role of the muscles is more complicated. In addition to shivering, the non-shivering thermogenesis is developed (Sellers et al., 1954; Heroux et al., 1956; Cottle and Carlson, 1956), which increases the maximal metabolic rate to about 420 Cal/(hour x body weight) (Figure 4). In order to estimate the contribution of muscles under these conditions, the site of non-shivering thermogenesis must first be ascertained.

The visceral organs have been considered as important sites of non-shivering heat production for many years. Much of the evidence has come from measurements of temperatures near the liver (Grayson and Mendel 1956; Donhoffer et al., 1957). In cold acclimated rats, the elevation of BMR and the elevation QO_2 in vitro give support to

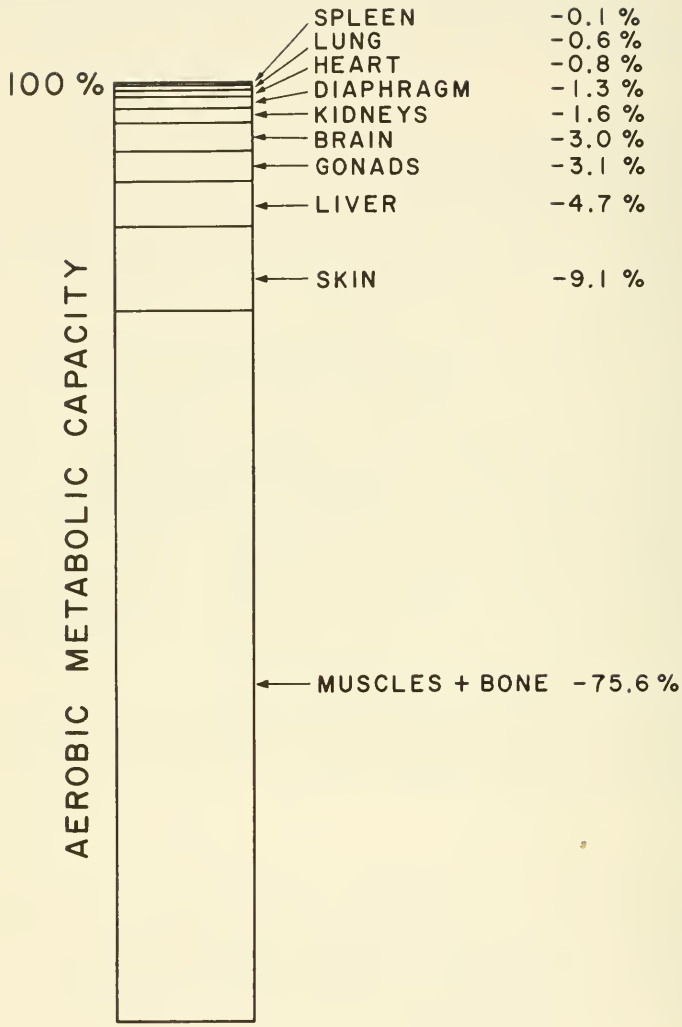


Figure 6. Contribution of various organs to the total metabolic capacity in the golden hamster as measured by cytochrome oxidase activity.

the increased thermogenesis of visceral organs (Weiss, 1954). However, direct evidence on the magnitude of the contribution is lacking.

On the other hand, evidence against the visceral organs as the important site of heat production in non-shivering was provided by Depocas (1958) who found, that the metabolic response to cold in curarized cold acclimated rats was not reduced by functional evisceration. Supporting evidence that the liver did not greatly contribute to increased heat production in cold was provided by Kawahata and Carlson (1959) in cold acclimated rats. Similar observations have recently been obtained for the kidney (Jansky and Hart, unpublished). On the other hand, direct evidence for the participation of muscle in cold thermogenesis was obtained by Jansky and Hart (unpublished) in the leg muscles of cold acclimated curarized rats where elevation in oxygen consumption equal to that in the whole animal were found during exposure to cold.

While thermogenesis from visceral organs still cannot be excluded, it can be concluded that both shivering and non-shivering thermogenesis are dependent to an important extent on the muscles. The total increase in heat production of cold-acclimated rats from the basal level (125 Cal/(hour x body weight$^{0.52}$)) is about 295 Cal /(hour x body weight$^{0.52}$), which is 75% of the maximal rate (420 Cal/hour). If muscle accounts for the entire cold thermogenesis, this would be equivalent to 77% of maximal metabolism, when the contribution of muscle to the basal metabolism is also considered.

The calculations again agree closely with the large proportion of muscle to the total cytochrome oxidase activity in hamsters and rats and show that as an upper limit, muscle could contribute about the same proportion to metabolism in both warm and cold acclimated rats. However, it is clear that the absolute increase in maximal metabolism of cold acclimated rats would require an increase in absolute values of cytochrome oxidase activity in the organs concerned. These observations, which are incomplete and permit only tentative conclusions, will be extended by work now in progress on the cytochrome oxidase activity of the muscles and other organs in warm and cold acclimated rats.

SUMMARY

The measurement of maximal steady state metabolism is complicated by the fact that both cold exposure and exercise may be required to elicit the maximal response and by the fact that the effect of exercise and cold varies with environmental temperature, state of acclimation, and other factors. In most small mammals studied, the metabolic effect of exercise is added directly to the cold thermogenesis, but in the bank vole and in warm acclimated rats, exercise substitutes for shivering and replaces cold thermogenesis. In cold acclimated rats, the metabolic effect of exercise is added to cold thermogenesis, except at the lowest test temperatures where substitution is again observed. The varied responses of different species and of cold- and warm-acclimated rats apparently depend on the extent of participation of non-shivering thermogenesis, which extends the range for activity and increases the maximal steady state metabolism. Maximal steady state metabolism can be determined either by imposing exercise simultaneously with cold or by exposing the subject to cold alone at very low temperatures.

The maximal steady state metabolism of different species was equal to about six times the basal metabolism, and the exponent relating log metabolism to log body weight was not obviously different from that for basal metabolism ($W^{0.75}$) for the species tested. Basal and maximal metabolism, therefore, give two parallel curves.

The total cytochrome oxidase activity was also measured in homogenates of whole animals. It was found that the exponent of the relationship between cytochrome oxidase activity and log of the weight was very similar to that found for basal and maximal metabolism. There was a close similarity between absolute values of maximal metabolism, and the total cytochrome oxidase activity provides a theoretical upper limit to the metabolic capability and is useful for comparative purposes in various species and organs of the same species.

The study of body organ cytochrome oxidase activity in the golden hamster illustrates the importance of the muscles, which comprise about three fourths of the total cytochrome oxidase activity.

This fact agrees with observations on the site of thermogenesis in living animals, where either shivering alone or shivering and non-shivering thermogenesis together are responsible for maintaining body temperature in cold environments.

*Contribution from the Division of Applied Biology, National Research Council, Ottawa, Canada, and Department of Comparative Physiology, Natural Science faculty, Charles University, Prague, Czechoslovakia. Issued as N.R.C. No. 6579. Postdoctoral Fellow, National Research Council, 1960-61.

LITERATURE CITED

1. Brody, S. 1945. Bioenergetics and growth. Reinhold Publishing Corp. New York. p.915.

2. Buskirk, E. and H. L. Taylor. 1957. Maximal oxygen intake and its relation to body composition with special reference to chronic physical activity and obesity. J. Appl. Physiol. 11: 72-78.

3. Chevillard, L. 1935. Contributions a l'etude des echanges respiratorires de la souris blanche adulte. II. Thermogenese et Thermogenese et thermolyse de la souris. Ann. physiol. physicochim. biol. 11:485-532.

4. Cottle, W. H. and L. D. Carlson. 1956. Regulation of heat production in cold adapted rats. Proc. Soc. Exp. Biol. Med., 92:845-849.

5. Depocas, F., J. S. Hart, and O. Heroux. 1957. Energy metabolism of the white rat after acclimation to warm and cold environments. J. Appl. Physiol. 10:393-397.

6. Depocas, F. 1958. Chemical thermogenesis in the functionally eviscerated cold-acclimated rats. Can. J. Biochem. Physiol. 36:691-699.

7. Donhoffer, Sz., Gy. Szevgari, I. Varga-Nagy, and I. Jarai. 1957. Über die Lokalisation der erhöhten Wärmeproduktion bei der chemischen Wärmeregulation. Pflügers Arch. 265:104-111.

8. Field, J., H. S. Belding, and A. W. Martin. 1939. An analysis of the relation between basal metabolism and summated tissue respiration in the rat. I. The post-pubertal albino rat. J. Cell. and Comp. Physiol., 14:143-157.

9. Grayson, J. and D. Mendel. 1956. The distribution and regulation of temperature in the rat. J. Physiol. 133:334-346.

10. Hannon, J. P. 1960. Effect of prolonged cold exposure on components of the electron transport system. Am. J. Physiol. 198: 740-744.

11. Hart, J. S. 1950. Interrelations of daily metabolic cycle, activity, and environmental temperature of mice. Can. J. Research, D, 28:297-307.

12. Hart, J. S. and O. Heroux. 1954. Effect of low temperature and work on blood lactic acid in deer mice. Am. J. Physiol. 176: 452-454.

13. Hart, J. S. and O. Heroux. 1955. Exercise and temperature regulation in lemmings and rabbits. Can. J. Biochem. Physiol. 33:428-435.

14. Hart, J. S. 1960. The problem of equivalence of specific dynamic action: Exercise thermogenesis and cold thermogenesis in Cold Injury, Transactions of the 6th Conference, July, 1958. Josiah Macy, Jr. Foundation, New York.

15. Hart, J.S. 1962. Physiological adjustments to cold in non-hibernating homeotherms. Proc. of the 4th Symposium on Temperature. Am. Inst. of Physics, in press.

16. Heroux, O., J. S. Hart, and F. Depocas. 1956. Metabolism and muscle activity of anesthetized warm and cold acclimated rats on exposure to cold. J. Appl. Physiol. 9:399-403.

17. Jansky, L. 1959a. Oxygen consumption in white mouse during physical exercise. Physiol. Bohemoslov. 8:464-471.

18. Jansky, L. 1959b. Working oxygen consumption in two species of wild rodents (Microtus arvalis, Clethrionomys glareolus). Physiol. Bohemoslov. 8:472-478.

19. Jansky, L. 1959c. Einfluss der Arbeit und der niedrigen Temperaturen auf den Sauerstoffverbrauch des Goldhamsters. Acta Soc. Zool. Bohemoslov. 23:266-274.

20. Jansky, L. 1961. Total cytochrome oxidase activity and its relation to basal and maximal metabolism. Nature 189(4768):921-922.

21. Kawahata, A. and L. D. Carlson. 1959. Role of rat liver in nonshivering thermogenesis. Proc. Soc. Expt. Biol. Med. 101: 303-306.

22. Kleiber, M. 1947. Body size and metabolic rate. Physiol. Rev. 27:511-541.

23. Lefevre, J. and A. Auguet. 1933. La thermoregulation du travail. Rapports de ses courbes avec celles du repos. Ann. physiol. physicochim. biol. 9:1103-1121.

24. Lefevre, J. and A. Auguet. 1934. Les courbes thermogregulatrices et les rendements de la machine vivante dans les grandes puissances de travail. Ann. physiol. physicochim. biol. 10:1116-1134.

25. Schneider, W. C. and V. R. Potter. 1943. The essay of animal tissues for respiratory enzymes. II. Succinic dehydrogenase and cytochromoxidase. J. Biol. Chem. 149:217.

26. Sellers, E. A., J. W. Scott, and N. Thomas. 1954. Electrical activity of skeletal muscle of normal and acclimated rats on exposure to cold. Am. J. Physiol. 177:372-376.

27. Sreter, F. A. and S. M. Friedman. 1958. Sodium, potassium and lactic acid after muscular exercise in the rat. Can. J. Biochem. Physiol. 36:1193.

28. Svoboda, L. and L. Jansky. 1959. Sexual differences in the cytochrome oxidase activity of different organs of the gold hamster. Physiol. Bohemoslov. 8:552-557.

29. Tipton, S. R. and W. L. Nixon. 1946. The effect of thiouracil on the succinoxidase and cytochrome oxidase of rat liver. Endocrinology 39:300-306.

30. Weiss, A. K. 1954. Adaptation of rats to cold air and effects on tissue oxygen consumptions. Am. J. Physiol. 177:201-206.

31. Wells, J. G., B. Balke, and D. D. van Fossan. 1957. Lactic acid accumulation during work. A suggested standardization of work classification. J. Appl. Physiol. 10:51.

DISCUSSION

HANNON: I was particularly interested in your cytochrome oxidase measurements since we have assayed the activity of this enzyme in the liver and muscle of warm and cold acclimatized rats. As you are no doubt aware the manometric technique for measuring cytochrome oxidase leaves a lot to be desired. Despite this, however, we have used the same procedure as you have and have found that cold acclimatization leads to a marked increase in the activity of this enzyme in both liver and muscle tissue. Besides this acclimatization effect, we were also most interested in the fact that our studies showed the liver has about six times more cytochrome oxidase than muscle. Thus, if this enzyme is an index of maximum metabolic capability, as you suggest, the liver would have six times greater metabolic capacity per gram of tissue than muscle. And, to speculate a bit further, if we assume that the level of cytochrome oxidase reflects the capacity of a tissue to produce heat and if we take into account the fractions of the total body mass represented by liver and muscle, then the theoretical ratio of total muscle heat production to total liver heat production would be about 2:1. It will be most interesting to see whether or not this theoretical ratio will be verified by future experiments where organ heat production is directly measured.

JANSKY: In our own recent experiments concerning the cytochrome oxidase activity in various organs of cold acclimated rats we have found a liver:muscle ratio of 2.5:1 for cytochrome oxidase activity. These values of organ cytochrome oxidase correspond to the values of maximal metabolism, which can be measured in working animals or animals exposed to extreme cold. At present it is practically impossible to measure organ heat production in moving animals or on animals in extreme cold. The body temperature of small laboratory animals falls very rapidly under these same conditions.

HANNON: In your data on mice and rats I noticed a convergence of the curves for work metabolism with the curves for metabolism in the cold. In the golden hamster, on the other hand, such a convergence was not apparent. If you had carried the temperature lower, do you feel the same convergence might have occurred in the hamster?

JANSKY: Yes, I think this does look like incomplete results but I have good evidence that the metabolism in the golden hamster will fall at lower temperatures. When I measured the highest running speed the values fell very rapidly at low temperatures; therefore I expect it will also happen in the white mouse, the common vole, and the bank vole.

HANNON: Did you ever compare the absolute amounts of running, say over a period of a day, for animals living in a cold environment and animals living in a warm environment?

JANSKY: No, we measured activity only during the short-time experiment. It was the forced activity or, better to say, running at the highest level which could be obtained at a certain temperature. The animals were not adapted to definite conditions.

HANNON: We have conducted a few experiments on voluntary running of rats living in both warm and cold environments and have observed a tendency for cold to reduce such activity. This would seem to agree with a prediction made some time ago by Dr. Hart that running is an inefficient method for augmenting heat production in the cold. I would like to ask Dr. Hart if he has ever confirmed this prediction experimentally.

HART: Yes, but I have not published it. I did some measurements on rats a few years ago, and there seems to be a range of decreasing temperatures over which running speed actually increases in the cold, reaches a peak, and then falls off again. I think Melvin Fregley has also done this type of work.

HANNON: At certain low temperatures they do increase their running speed?

HART: The activity depends upon the temperature and on the acclimation conditions. In cold acclimated rats it increases with fall in temperature to about 5° C below which it declines as shown in Figure 7.

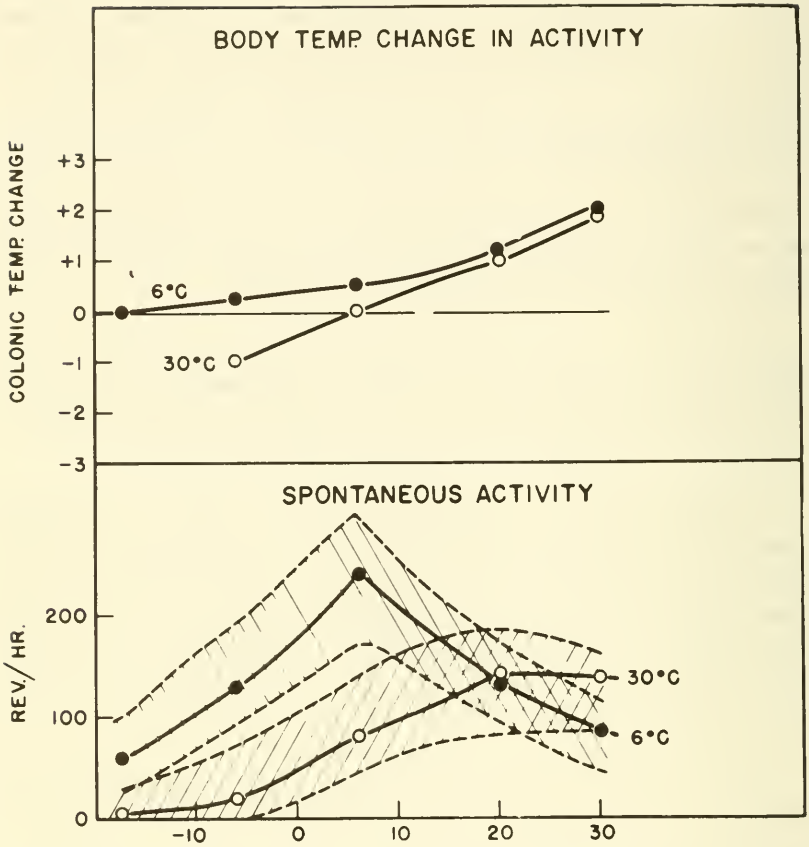


Figure 7. Upper panel: change in colonic temperature from initial resting state in rats running at 1400 cm/min in a treadmill for 30 minutes at various temperatures. Symbols are for groups of 8 rats acclimated for 4 to 8 weeks to 6° C, (●) and to 30° C (0). The rats were exposed to each temperature for 10 min before start of run. Lower panel: mean spontaneous wheel activity of 4 rats acclimated to 6° C (●) and 8 rats acclimated to 30° (0) tested twice at each temperature for one hour periods. Total range of variation shown by shaded areas. Same rats used in both tests show lowering of spontaneous activity at both high and low temperatures, especially those which cause hypotherma during forced exercise. Presented by J. S. Hart.

FOLK: The temperature of the running wheel may be a factor here. If the feet are well protected, some species of animals might make out all right, especially the white rat running on the cold metal. The colder it gets, the more this factor might influence the animal.

HANNON: How did you force your animals to work? We tried this and had all sorts of problems.

JANSKY: All animals were running in a wheel made from plastic. I attempted to get really maximal values of running and to avoid having them change their position; they could not turn back, for instance. In the axis of the wheel was a load, which could touch and excite the animals forcing them to run.

HANNON: Did you have any trouble? Dr. Drury in our laboratory has done similar forced-exercise experiments with the rat in a motor driven screen drum. Other people have tried to make their animals run on a treadmill. We, as well as the individuals to whom I have talked, have encountered a lot of foot and tail injury.

JANSKY: It depends upon which animal we use for the experiments. Some animals are better runners than others. The white rat for example is not a good runner. Many small animals run very nicely, since it is something like a natural movement for them. The species we used really did not need too much force.

FOLK: We have had a great deal of difficulty forcing exercise, and I did not quite understand how you got maximum running. You stimulated them, and I would like to hear more about that.

JANSKY: We used the wheel, and as I said, the wheel was narrow enough to prevent the animals from turning around. The animals, of course, were not restrained. On the axis of the wheel we suspended a load which was freely movable. This load was located behind the animal and would touch him if he ran slower. It was heavy enough to excite the animals. Another improvement

is a net to avoid gliding or riding the axle. Running speed was controlled with a Variac to prevent the animals from being carried by the wheel and we were thus able to obtain really maximal values.

HART: Did you keep increasing the speed until they could just maintain that position without being forced?

JANSKY: Yes, of course they sometimes stopped, but in this case the load touched them and they started again.

JOHANSEN: When you are comparing metabolic rates in these groups, that is, working and resting animals, it seems to me there will have to be a different insulation in the two. How would this reflect in your curves?

JANSKY: Comparing the values of maximal working metabolism and those of resting metabolism, we can see, that at the same environmental temperature the animals produce more heat at the level of maximal metabolism than in the resting state without a significant change in body temperature. This would suggest a certain decrease in total body insulation. On the other hand the values of maximal working metabolism in all species of animals that we studied form a definite exponent to the body weight. This would mean that there are no changes in total body insulation in working animals of different species.

KLEIBER: This change in insulation makes shivering inefficient because it increases the dissipation of heat.

HART: I am interested to know whether anyone has an opinion on the method of total cyt-ox activity as a measure of the theoretical maximum metabolic capacity.

HANNON: Theoretically, at least, this enzyme should be a good index of maximum metabolic capacity since most of the oxidative processes are eventually channeled through it. The manometric method of assaying it, however, is often open to criticism since you are using ascorbic acid to reduce the cytochrome c substrate. There is always a possibility that the ascorbic

acid itself is being oxidized and at differential rates. A more modern and perhaps more accurate method of assaying cytochrome oxidase involves a spectrophotometric procedure where the cytochrome c substrate is reduced with hydrogen gas and palladium prior to its addition to the reaction system.

JANSKY: Of course there is a certain amount of autoxidation of ascorbic acid in the manometric procedure, but we can avoid it very easily by extrapolating to zero after measuring the oxygen consumption in Warburg flasks containing various concentrations of homogenate. I would say the spectrophotometric method is probably more convenient except that we cannot easily measure the oxygen consumption.

TEMPERATURE REGULATION AND ADAPTATION * TO COLD CLIMATES

J. Sanford Hart

Studies conducted largely during the last 10 years have provided us with a reasonably complete picture of the temperature regulation of mammals in cold climates. It is clear that several types of adjustments to cold are theoretically possible, having been described in previous reports by Scholander et al. (1950a) and Hart (1957). The most economical is structural modification in which insulation of the fur and tissues is increased to such an extent that very low ambient temperatures can be tolerated without increased energy expenditure. The most wasteful are metabolic modifications in which extremes of low temperature that limit survival are extended only by increase in metabolic rate. Behavioural adjustments (huddling, burrowing, etc.) can modify costly metabolic requirements through avoidance of cold.

The metabolic studies conducted on mammals have in general been limited to short term tests which do not provide an integrated picture of 24-hour energetics such as that provided for small birds. Nevertheless, within the limitation of the methodology it has been shown that quite distinct adaptive processes are in part dependent on differences in body size and also in part on broad differences between aquatic and non-aquatic animals. It will be the purpose of this review to describe the temperature regulation and adaptation to climate found in free living mammals. The term "acclimatization" will be used to describe individual physiological modification by climate in nature while the term adaptation will refer to differences between groups brought about through evolution. Other aspects of temperature regulation and acclimation to cold under laboratory conditions will not be considered in this review since they have been treated elsewhere (Carlson, 1954; Burton, 1955; Hart, 1957, 1958, and 1962; and recent symposia, 1955, 1957, and 1960).

*Contribution from the Division of Applied Biology, National Research Council, Ottawa, Canada. Issued as N.R.C. No. 6580.

Non-aquatic Fur Bearers

The large fur-bearing mammals have been investigated by American and Russian investigators. The best known work on this subject was published by Scholander et al. (1950a, b, and c), who were the only workers to demonstrate the existence of true evolutionary climatic adaptation. This demonstration was made by comparing arctic and tropical mammals with respect to metabolic rates at different temperatures and with respect to pelage insulation. It was found that the tropical mammals that were investigated were very sensitive metabolically to lowering of ambient temperatures, as shown by an abrupt increase in oxygen consumption with lowering of temperature. In contrast, the arctic mammals did not begin to increase their metabolism until they experienced much lower temperatures and some could virtually remain in a basal state at temperatures down to -40° C and below. The results for the tropical raccoon (Procyon cancrivorus or lotor), the small arctic lemming, and the Eskimo dog pup (Canis familiaris) (Figure 1) illustrate these distinctions. Using Scholander's terminology, it was observed that the critical temperature and the critical gradient for increase in oxygen consumption was lower in arctic mammals. Since the slopes of the curves were extrapolated to body temperature, the lower critical temperatures were associated with a smaller increase in metabolism for a given drop in temperature.

The distinction between arctic and tropical mammals was not associated with differences in the resting metabolism or in body temperature (Scholander, et al., 1950b), but with differences in body insulation. Arctic mammals were found to have greater pelage insulation (Scholander, et al., 1950c) than tropical mammals (Figure 2).

Some of the northern mammals investigated by Russian workers, for example Ol'nyanskaya and Slonim (1947) whose work is shown in Figure 3, were also relatively insensitive to cold but there was a very large individual variability within each species. The interpretation given to the data by the authors did not distinguish between zones of physical and chemical regulation; hence no apparent critical temperatures were noted. The rabbit (Lepus timidus), which showed an increase in oxygen consumption at temperatures below 20° C, differed from the Alaskan hare (Lepus americanus) studied

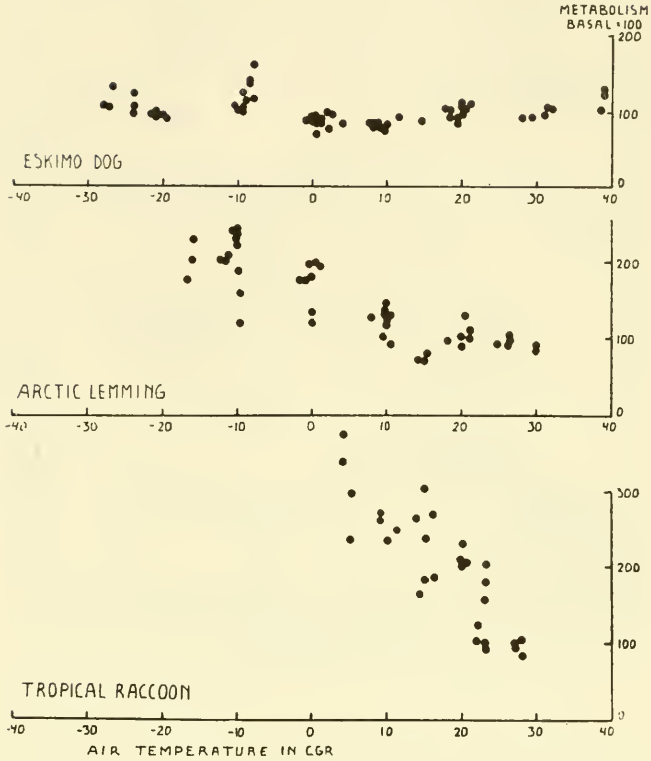


Figure 1. Effect of environmental temperature on the metabolic rates in eskimo dog, arctic lemming, and tropical raccoon, expressed in terms of basal metabolic rate = 100. From Scholander et al 1950.

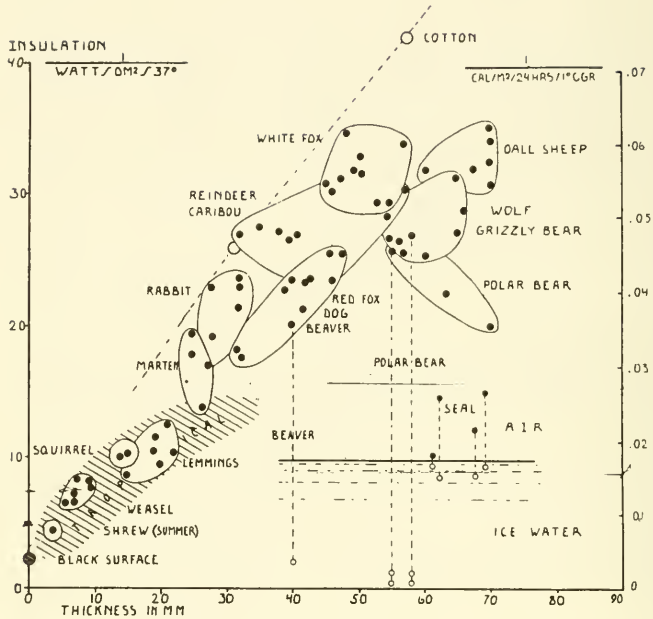


Figure 2. Insulation in relation to winter fur thickness in a series of arctic mammals. The insulation in tropical mammals is indicated by the shaded area. From Scholander et al., 1950.

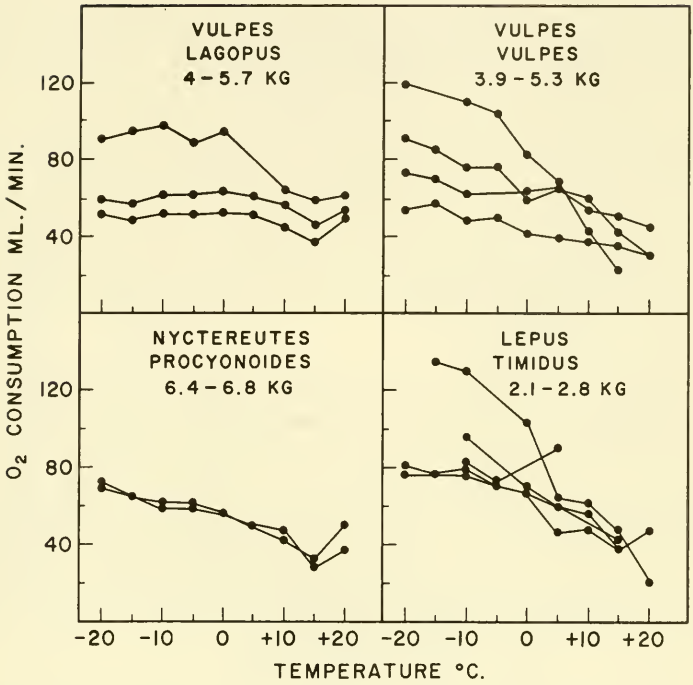


Figure 3. Effect of temperature on metabolism of some Siberian mammals. Redrawn from Ol'nyanskaya and Slonim, 1947.

by Irving et al. (1955), in which metabolism did not increase until the temperature fell below -10° C.

The regulation of body temperature by arctic mammals and birds has been thoroughly investigated by Irving and Krog (1955), who showed that it depended both on thick fur or feathers over the body and on peripheral cooling of the thinly covered legs and other exposed parts. The temperature distribution on the body skin and extremities of various arctic mammals at different temperatures is shown in Figure 4. Warm skin is dependent on a temperature drop through the fur; this phenomena has been described for certain arctic mammals by Griffin et al. (1953). An example of such a temperature gradient measured by thermocouples placed in parallel at various depths is shown in Figure 5.

In thinly fur-covered legs, tissues replace fur as insulators. Heat exchangers are possibly located in the area of the base of the limbs, which show a sharp temperature drop. Such heat exchangers have been demonstrated in tropical sloths (Choloepus hoffmanni and Bradypus griseus) by Scholander (1957) and may occur widely in furred mammals (Scholander, 1955). However, the presence of a marked temperature drop in a limb or appendage does not necessarily signify the presence of a heat exchanger.

The cooling of peripheral tissues, which suggests tolerance to cold not shared by warm tissues, is one of the remarkable properties of homeotherms. The demonstration of functional differences between cool and warm tissues is difficult, although suggestive evidence has been found in the distribution of fats of lower melting point associated with low temperature function. Irving, Schmidt-Nielsen, and Abramsen (1957) have shown that the distribution of low melting point fats in various animals is not related to the climate in which the animals live. Other adaptations to cooling in peripheral tissues have been demonstrated by Chatfield et al. (1953) in the ability of the leg nerve of the herring gull (Larus argentatus) to conduct at lower temperatures in distal than in proximal parts of the nerve, and by Heroux (1959) in a capability of the ears of rats to recover from non-freezing cold injury (Rattus norwegicus) during prolonged cold exposure. Nevertheless, the pronounced retardation

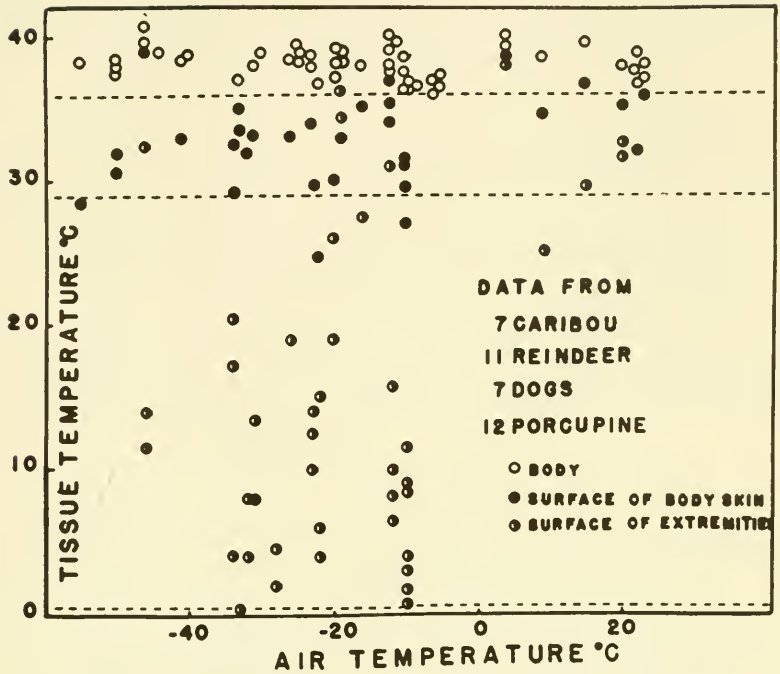


Figure 4. Combined presentation of temperature measurements in 37 individuals of 4 species of mammals adapted to arctic life. From Irving and Krog, 1955.

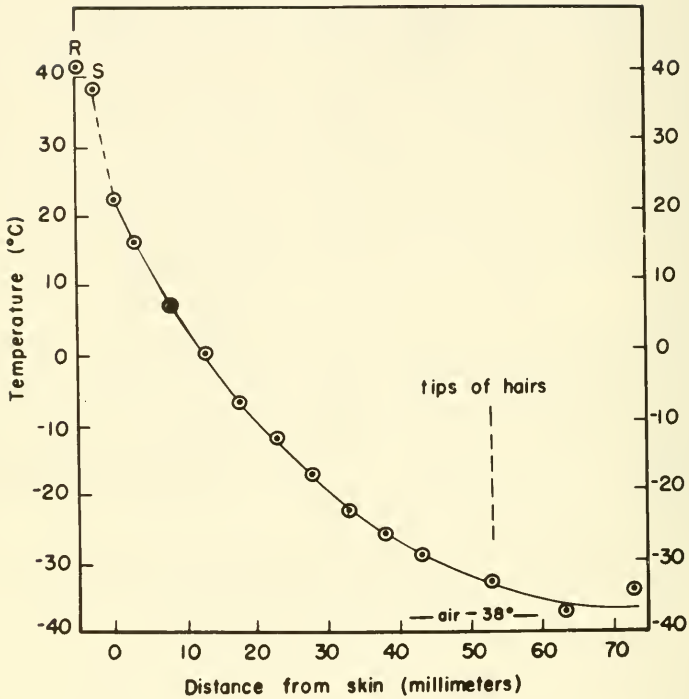


Figure 5. Temperature gradient through fur of a sled dog thoroughly acclimatized to the cold. R and S are rectal and subcutaneous temperatures. Each point is the average of readings 10 to 20 minutes after insertion of gradiometer from Griffin et al., 1953.

of functional activity of cool tissues is one of the puzzling phenomena of homeotherms which must be active at all temperatures. Functional retardation by cold, at least for growth processes, has recently been demonstrated by Heroux (1960), who showed that the mitotic activity decreased about 10-fold for a 10 degree lowering of temperature in the skin of the rat.

While large adult arctic mammals are apparently able to withstand the most severe cold with little or no elevation of metabolic rate, such may not be true for infant animals of the same species. Baby caribou (Rangifer arcticus) born during June in the far north are exposed to cold, wind, and precipitation that may lead to mortality (Hart et al., 1962c). These calves are extremely sensitive to cold, as shown by the marked elevation in metabolism resulting from exposure to the harsh environmental conditions (Figure 6). In contrast, a 9-month calf of the same litter did not show elevation of metabolism at temperatures down to -50° C.

Seasonal changes in some northern mammals have been shown by Irving, Krog, and Monson (1955) for the porcupine (Erethizon dorsatum myops) and red fox (Vulpes vulpes alascensis), but not for the smaller red squirrel (Tamiasciurus hudsonicus preblei). The winter fox and porcupine had lower critical temperatures and would require a much lower temperature than summer animals for the same metabolic response. These comparisons made in a review by Hart (1957) also showed a similar trend for the lemming (Dicrostonyx groenlandicus) when Alaskan (winter) and Ottawa (summer) test animals were considered. It was also pointed out that no changes in the slopes of temperature-metabolism curves were found for the deer mouse (Peromyscus maniculatus gracilis). In this species, winter animals were able to resist lower temperatures (Hart and Heroux, 1953) mainly by metabolic compensation, although some indication of a small increase in insulation of winter animals was observed.

The seasonal changes in these mammals are in line with the seasonal changes in pelage insulation observed by Hart (1956), who demonstrated the obvious fact that smaller mammals with body weights below about 100 gm, unlike the larger ones, fail to achieve significant protection through increased fur thickness during the

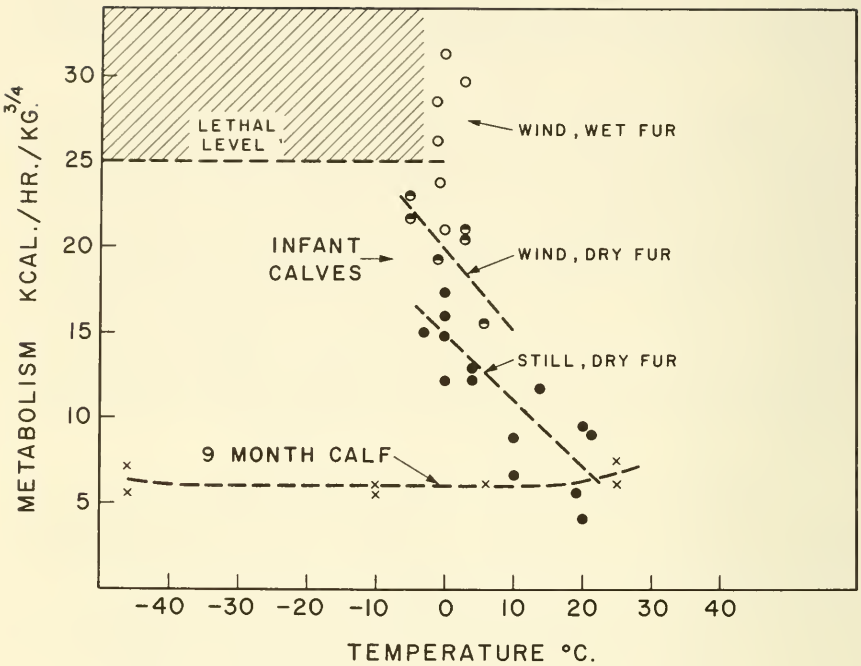


Figure 6. Heat production as a function of environmental temperature in nine-month calf (X) and infant calves in still air with dry fur (●), wind with dry fur (⊖) and wind with wet fur (O). The shaded area and broken line indicate lethal level for prolonged exposure. From Hart 1962c, in press.

winter. Consequently they must rely for protection on nest building, huddling, and other devices as shown by Sealander (1952), Pearson (1960), and Barnett (1956). Microclimatic observations by Pruitt (1957) in Alaska have shown that the environment of the boreal red back voles (Clethrionomys rutilus) 3-9 inches below the moss surface ranges for the most part between -5 and +2° C when the air tempeature falls to -40° C and below. Nevertheless, temperatures in this range are well below the thermoneutral range of most small mammals as shown by Hart (1953), Kalabukhov (1940), Morrison and Ryser (1951), Morrison, Ryser, and Dawe (1959), Pearson (1960), Smirnov (1958), and various other workers, suggesting that metabolic compensation is necessary to maintain homeothermy under these conditions. Evidently the protection afforded to Peromyscus maniculatus during the winter in the Ottawa area is likewise insufficient to prevent cold exposure since metabolic acclimatization to winter conditions was pronounced (Hart and Heroux, 1953). Unpublished observations of Hart and Heroux have likewise shown seasonal metabolic acclimatization in wild dump rats, and similar observations have been made on short tailed shrews. Details of the seasonal metabolic changes in rats reviewed by Hart (1962b) are beyond the scope of this review.

Semi-aquatic Fur Bearers

Certain fur bearing mammals such as beaver, otter, and muskrats are dependent on an aquatic environment for their food and shelter, but spend only a small portion of their total life in the water. These mammals are protected from the cooling effect of the water by a layer of air trapped in the fur. In general, very little is known concerning temperature regulation in this group of mammals. However, observations of the author (Hart, 1962a) on muskrats (Ondatra zibethicus) in air and in water illustrate some of the problems in the temperature regulation of a semi-aquatic mammal.

Muskrats tested in air at various temperatures for about 1 hour showed an increased heat production at temperatures below a critical level of approximately 10° C and a gradual lowering of body temperature which became pronounced below -40° C (Figure 7). No appreciable seasonal changes were observed.

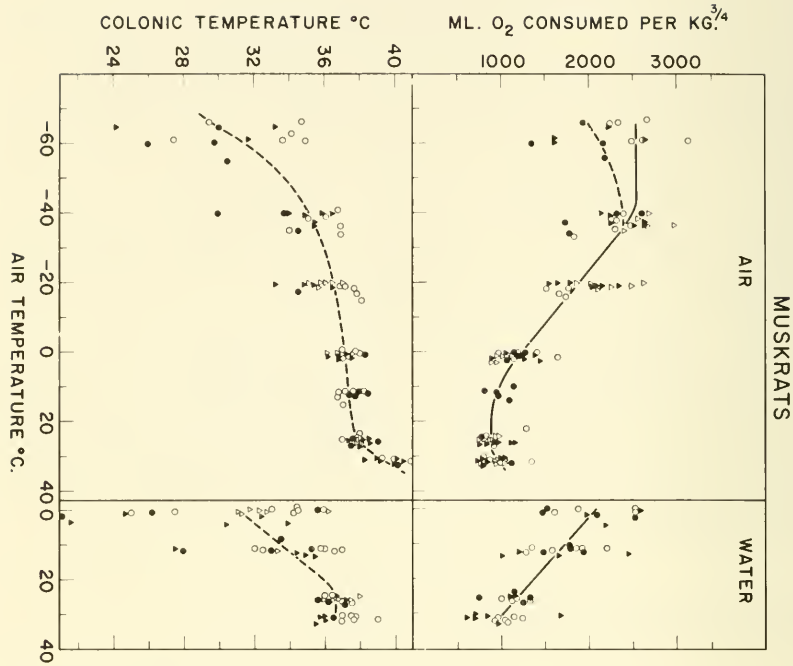


Figure 7. Oxygen consumption and body temperature in muskrats in response to air and water temperatures. Summer animals are indicated by (●) and winter by (○). From Hart, 1962, in press).

Oxygen consumption and body temperatures of animals placed in a small tank of water for about three fourths of an hour increased progressively with lowering of water temperature below a critical level of about 30° C. Colonic temperatures fell after the animals were in water at all temperatures below about 20° C. During both summer and winter, it was apparent that the heat production was inadequate to offset hypothermia for prolonged periods at winter temperatures around 0° C. Skin temperatures measured under the fur confirmed the presence of an air layer, because a gradient of approximately 7° C was maintained in the fur at a water temperature of 0° C. Nevertheless, this air was insufficient to prevent generalized cooling. Since the animals were all healthy, muskrats in nature may tolerate limited hypothermia during winter while under the ice and may limit exposure to cold water to shorter excursions than the test exposures in these experiments.

Bare Skinned and Aquatic Mammals

Metabolic studies have been carried out by Irving and coworkers on swine in Alaska (1956) and on seals of the Atlantic coast (1957, 1959). Swine and aquatic mammals will be considered together in this section because of similarities in problems of temperature regulation associated with the presence of a minimal fur cover and an insulating subcutaneous layer of fat or blubber.

Both the swine at various air temperatures (Figure 8) and the harbor seals (Phoca vitulina) in air and in water (Figure 9) showed marked temperature gradients through the tissues which were characteristic of the insulating layers of fat and the different outside cooling effects. The distributions of surface temperatures on the body surfaces of swine and seals were also rather similar at comparable air temperatures, indicating similarity in physiological insulation by cooling in these two animals. The critical temperatures for increase in metabolic rate (about 0° C) were also comparable in Alaska swine and harbor seals during the summer.

In water, the surface temperatures of harbor seals were, as anticipated, only slightly greater than ambient, and the critical temperature was elevated from approximately 0° C to 20° C (Figure 10).

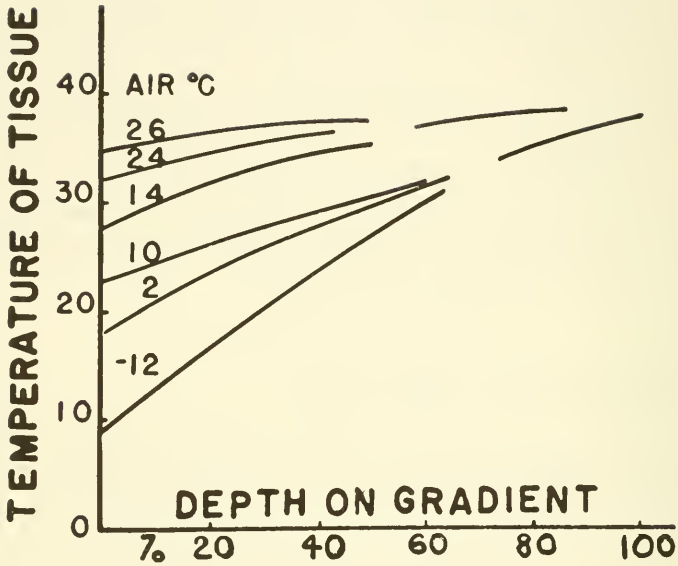


Figure 8. Typical temperature gradients through superficial layers of the swine in air at several temperatures from February to August. Because of seasonal changes in depth of gradient, the scale of the abcissa is observed temperature in tissues/body temperature in ^{o}C x 100. Data from Irving, 1956.

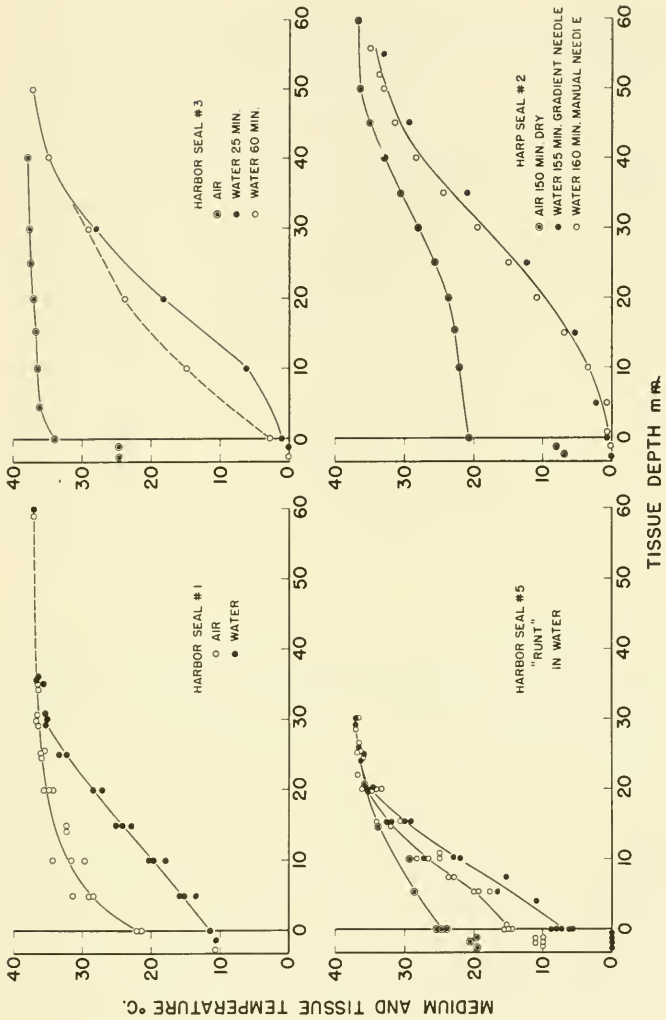


Figure 9. Temperature gradients in the bodies of seals at various air and water temperatures. Ordinates give both medium temperature (outer line) and tissue temperature (inner line). Results from Irving and Hart, 1957.

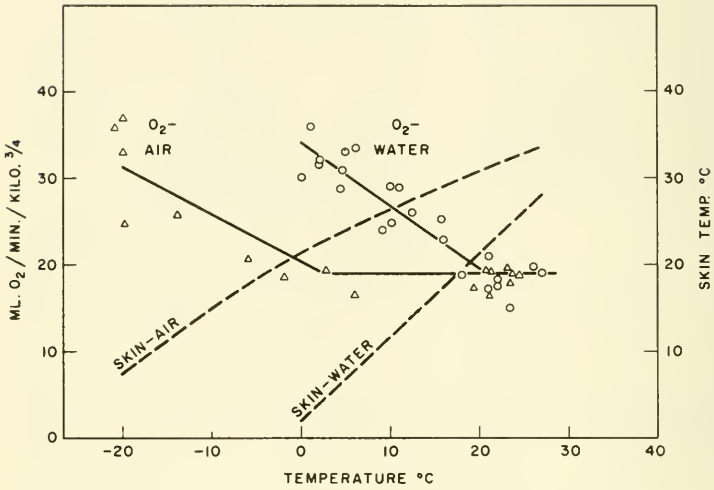


Figure 10. Oxygen consumption of seals in the air (Δ) and in water (O) at different temperatures during the summer. Body skin temperatures as a function of temperature of the medium are also shown. Results from Hart and Irving, 1959.

This represents a difference of about twenty-fold in the cooling effect of air and water, but the total insulation (body + medium) in water was about 50% of its value in air. It can be noted that the metabolic response closely parallels the skin cooling in air and water.

The parallel between peripheral cooling and metabolic response was also seen between different seals and was reflected in the individual variability (Irving and Hart, 1957) (Figure 7). The smallest seal, characterized as the "runt," had a very thin layer of blubber and consequently was unable to maintain a surface temperature lower than 6° C to 8° C when in water at 0° C. The high heat flow resulted in a high oxygen consumption at all temperatures. In other harbor seals with a considerably deeper and less steep gradient through the thicker blubber, there was a much lower surface temperature and a maintenance of resting metabolism down to a critical level of about 10° C. However, a harp seal (Phoca groenlandica), with a still deeper gradient and a lower surface temperature, was able to compensate completely without elevation of metabolism even in ice water. This represents the greatest cooling load experienced by mammals in nature and the harp seal has the greatest physiological insulation known for mammals.

Harbor seals tested in December at St. Andrews, N. B., and at Woods Hole, Massachusetts, during the summer revealed seasonal changes that were comparable to those found by Irving, Krog, and Monson (1955) for the red fox and the porcupine. During the summer there was a greater elevation of oxygen consumption in cold water than during the winter and the critical temperature was raised from about 11° C to 20° C in water. There was, therefore, a greater physiological insulation in winter than in summer; this was associated with changes in peripheral tissues. No anatomical basis for this change was noted. The nature of the seasonal alteration was such that the differences were observed even at the same body skin temperature (Figure 11). This puzzling phenomenon suggests that more heat is lost in summer than in winter at the same body skin temperature. This could be accounted for by a greater evaporative heat loss from the lungs or by a greater heat loss from the appendages, neither of which were measured in this investigation.

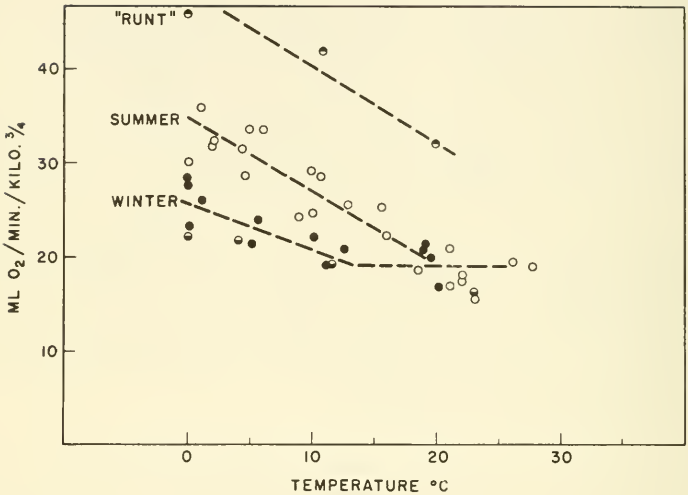


Figure 11. Oxygen consumption as a function of body skin temperature for seals during winter (▲●) and summer (△○) in air (▲△) and in water (●○). Results from Hart and Irving, 1959.

While the temperature of the body skin was uniformly related to the water temperature, temperatures of the appendages showed striking fluctuations, suggesting independent control of heat loss, which might be a basis for seasonal differences. The nature of the fluctuations in temperature of the flippers was consistent with the view that control of peripheral heat loss was affected by the presence of vascular heat exchangers, such as those described by Scholander and Schevill (1955) for porpoises (Lagenorhynchus acutus and Tursiops truncatus).

Comparison of Different Species

Metabolic response to cold versus skin temperature. It is difficult to compare the metabolic responses of species which live in such different media as air and water. One basis is to make the comparisons relative to the actual body skin temperature of the species in question. This has the merit of relating the response to some aspect of the animals' own perception system to which it must be responding rather than to some physical aspect of the environment. The use of skin temperature is disadvantageous because it is highly variable and is known only for a few species. Skin temperatures measured over the mid part of the body on the flank or back of a series of animals are correlated with oxygen consumption in Figure 12, as originally shown by Hart (1962b). The sources of the data are indicated in the legend. Comparisons of the same species relative to air temperature are also shown.

Clearly, the various species are distributed in a series with respect to the sensitivity of the skin as a factor in the metabolic response to cold. All the land mammals tested show increased heat production at relatively high skin temperatures. Next in order is the semi-aquatic muskrat, followed by the swine. The cooling of the muskrat skin for the same metabolic response is not as great as that for the harbor seal, especially during the winter. The least sensitive species was the harp seal, which showed no increase in metabolism even in ice water. The range of responses indicates the very great species differences that exist in toleration of peripheral cooling and in temperature range of peripheral stimuli required to illicit that response. It has also been shown for the harbor seal and for the leg

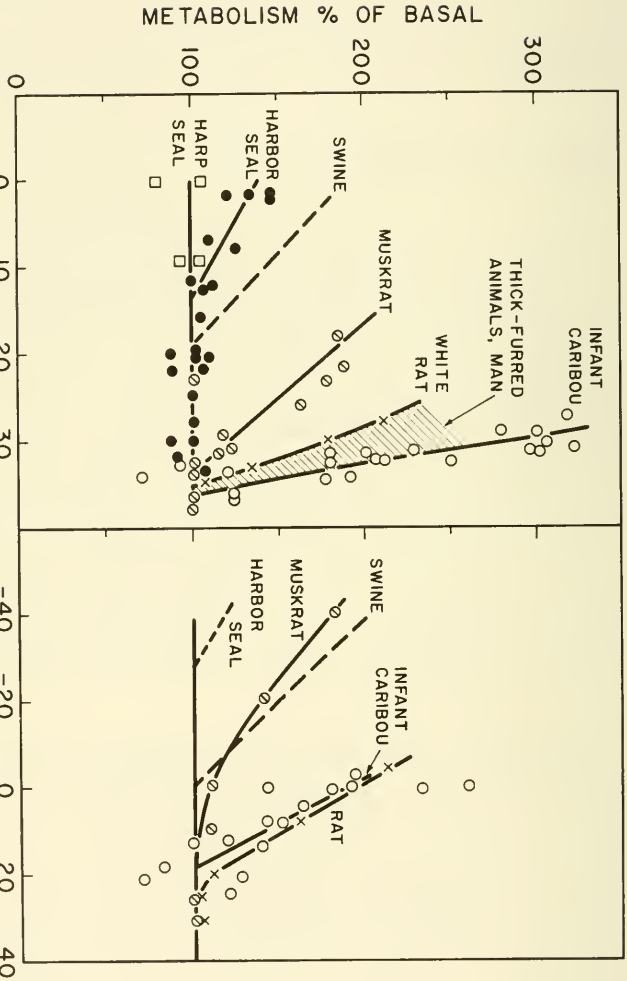


Figure 12. Metabolism, expressed as percentage of increase over the resting or basal value, versus skin temperature (left) and air temperature (right) for harp and harbor seals (Irving and Hart, 1957), swine (Irving, 1956), muskrat (Hart, 1962a), white rat (Heroux, unpublished), and infant caribou (Hart et al., 1962). Individual values given for seals and caribou, group means for muskrat, trend lines (broken curve) given for data on swine. Broken curve for harbor seal in air is an estimate from skin temperatures in water. From Hart, 1962c.

nerve of the herring gull that these responses may be altered by acclimatization in the same species.

The comparisons in Figure 12 also illustrate the fact that the metabolic sensitivity to cold may differ, depending on whether the oxygen consumption is correlated with skin or with air temperature, e. g., swine and muskrat. This is because the fur provides the insulation for the muskrat but not for the swine. Similarly, the thick furred arctic mammals with warm skin may be as sensitive to lowered skin temperatures as the rat, caribou, and man, even though the most severe arctic conditions can be withstood without elevation of resting heat production (Scholander et al., 1950a). Therefore, arctic and tropical mammals may be quite similar with regard to the skin cooling required for a given metabolic response.

Metabolic response to cold in relation to body size and insulation of the fur. A summary of data published in the fourth Temperature Symposium of the American Institute of Physics (Hart 1962b) is illustrated in graphic form in Figure 13. The slope of the temperature-metabolism curve below the critical level is given as the ratio of the temperature drop to the increase in metabolism, which is dimensionally comparable to an insulation rather than a conductivity function. This is done to facilitate comparison of slopes with fur insulation (open circles) for the few species for which data are available.

It may be seen that the slope tends to increase with increase in body weight, but that there is an enormous increase in species variability with increase in weight. This is because the small mammals are all metabolically sensitive to cold while the large mammals may be sensitive or insensitive. The least sensitive are the arctic mammals with thick fur which give the three highest values for slope, e. g., snow-shoe hare in winter, red fox, and white fox. The larger mammals may also have little fur and lower values for slope, e. g., dog, harbor seal in summer, and Brahaman bull.

When slope is related to insulation of the fur (broken line), there appears to be a much closer correlation. However, it is obvious that the same correlation would not be applicable for either bare-skinned or aquatic mammals with subcutaneous fat and a thin fur cover. The

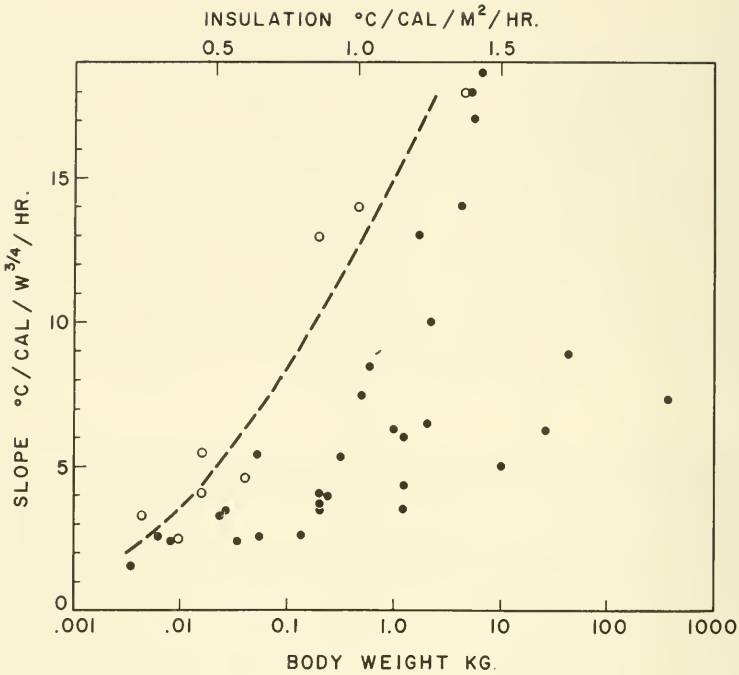


Figure 13. Overall body insulation (●) expressed as the slope of the temperature-metabolism curve below the thermoneutral range (°C/cal/body weight 3/4 /hr) in relation to body weight, and slope (O) as a function of pelage insulation (broken line). Data are replotted from table given by Hart 1962b.

correlation may be applicable to most fur bearers, but information at present is inadequate.

SUMMARY AND CONCLUSIONS

The temperature regulation and adaptation of mammals to cold climates follows different patterns in large and small mammals, and in fur-bearing compared to bare-skinned or aquatic mammals. The large arctic mammals with thick fur have a capability for withstanding the severest climatic conditions without elevation of heat production. This is accomplished by considerable cooling of the peripheral areas and appendages as well as by great insulation of the fur. The combined effect of these insulators provides a variable response graded precisely to the temperature of the environment in a way not yet fully understood. Climatic adaptation to arctic and tropical environments as well as acclimatization to summer and winter environments appears to be related to alteration in insulation of the fur rather than to changes in body temperature or in metabolic rate. However, infant animals of arctic species may be very sensitive to temperature.

In the mammals of small body weight, compensation for cold through changes in insulation is not possible, and when protection is inadequate, an elevation of heat production is necessary. Evidence has been presented that small mammals such as mice and wild rats show an increased cold resistance during the winter that is the result of the development of an increased metabolic capacity. It is therefore apparent for the few species studied that cold exposure and elevation of metabolism must have occurred during the winter to account for the development of the observed seasonal acclimatization.

The only fur-bearing semi-aquatic mammal studied (muskrat) showed no evidence of seasonal change even though exposure to water at 0° C during the winter seems inescapable. The surprising feature of the study was the degree of body cooling observed during short term exposure to cold water and the failure of fur insulation and

metabolism to compensate adequately for the observed cooling. It was suggested that mild hypothermia might be tolerated by muskrats in nature.

In swine and in the true aquatic mammals with an insulating layer of blubber, living tissues replace the fur as the effective insulators, and there is pronounced cooling of peripheral tissues. In harbor seals exposed to ice water, there is a reduction of heat production during the winter, signifying a seasonal change in insulation of the living tissues. Arctic harp seals are superior to harbor seals during the winter since they can tolerate ice water without lowering body temperature or elevating heat production.

When the body skin temperature of various species are compared, very large differences are found in the temperatures corresponding to elevation of heat production. In the fur-bearing land mammals studied, heat production increased with only slight skin cooling whereas in aquatic mammals a pronounced skin cooling was necessary. The swine and muskrat were intermediate. The distinction in the metabolic response to cold between land mammals and aquatic mammals is much more apparent with respect to skin temperature than to air temperature.

The metabolic response to cold in different non-aquatic species is related both to insulation of the fur and to body size. However, while small mammals with thin fur are metabolically sensitive to cold, large mammals may be sensitive or insensitive, depending on the fur insulation. In aquatic mammals so far studied the fur insulation was negligible and hence did not affect the metabolic response to cold. Temperature regulation in aquatic mammals is effected through physical regulation of heat loss in the general body surface and particularly in the appendages.

LITERATURE CITED

1. Barnett, S. A. 1956. Endothermy and ectothermy in mice at -3° C. J. Exp. Biol. 33:124.

2. Burton, A. C. and O. G. Edholm. 1955. Man in a cold environment. Edward Arnold, London.

3. Carlson, L. D. 1954. Man in cold environment, a study in physiology, Alaskan Air Command, Arctic Aeromedical Laboratory. U. S. Dept. Commerce, Office of Technical Services P. B. report 111716, Washington.

4. Chatfield, P. O., C. P. Lyman, and L. Irving. 1953. Physiological adaptation to cold of peripheral nerve in the leg of the herring gull (Larus argentatus). Am. J. Physiol. 172:639.

5. Griffin, D. R., H. T. Hammel, H. M. Johnson, and K. S. Lawson. 1953. The comparative physiology of thermal insulation. Final Rept. Contract 33 (038)-12764 between US Air Force and Cornell University.

6. Hart, J. S. 1953. Energy metabolism of the white footed mouse, Peromyscus leucopus novaboracensis after acclimation at various environmental temperatures. Can. J. Zool. 31:99.

7. Hart, J. S. 1956. Seasonal changes in insulation of the fur. Can. J. Zool. 34:53.

8. Hart, J. S. 1958. Metabolic alterations during chronic exposure to cold. Fed. Proc. 17:1045.

9. Hart, J. S. 1957. Climatic and temperature induced changes in the energetics of homeotherms. Revue Can. de Biol. 18:133.

10. Hart, J. S. 1962a. Seasonal changes in wild rats and muskrats. Can. J. Zool., in press.

11. Hart, J. S. 1962b. Physiological adjustments to cold in non-hibernating homeotherms. Proc. 4th Temp. Symposium. Am. Inst. Physics, Columbus, Ohio, in press.

12. Hart, J. S. 1962c. The influence of climate on metabolic and thermal responses of infant caribou. Can. J. Zool., in press.

13. Hart, J. S. and O. Heroux. 1953. A comparison of some seasonal and temperature-induced changes in Peromyscus: Cold resistance, metabolism and pelage insulation. Can. J. Zool. 31:528.

14. Hart, J. S. and L. Irving. 1959. The energetics of harbor seals in air and in water with special consideration of seasonal changes. Can. J. Zool. 37:447.

15. Heroux, O. 1959. Histological evidence for cellular adaptation to non-freezing cold injury. Can. J. Biochem. Physiol. 37:811.

16. Heroux, O. 1960. Mitotic rate in the epidermis of warm- and cold-acclimated rats. Can. J. Biochem. Physiol. 38:135.

17. Irving, L. 1956. Physiological insulation of swine as bare-skinned mammals. J. Appl. Physiol. 9:414.

18. Irving, L. and J. S. Hart. 1957. The metabolism and insulation of seals as bare-skinned mammals in cold water. Can. J. Zool. 35:497.

19. Irving, L. and J. Krog. 1955. Temperature of skin in the arctic as a regulator of heat. J. Appl. Physiol. 7:355-364.

20. Irving, L., H. Krog, and M. Monson. 1955. The metabolism of some Alaskan animals in winter and summer. Physiol. Zool. 28:173.

21. Irving, L., L. J. Peyton, and M. Monson. 1956. Metabolism and insulation of swine as bare-skinned mammals. J. Appl. Physiol. 9:421.

22. Irving, L., K. Schmidt-Nielsen, and N. S. B. Abramsen. 1957. On the melting point of animal fats in cold climates. Physiol. Zool. 30:93.

23. Kalabukhov, N. I. 1940. Influence of temperature upon oxygen consumption by wood-mouse (Apodemus silvaticus) and yellow-necked mice (Apodemus flavicollis). Compt. rend. (Doklady) de l'acad. Sci. de l'URSS. N. S. 26:89.

24. Morrison, P. R. and F. A. Ryser. 1951. Temperature and metabolism in some Wisconsin mammals. Fed. Proc. 10, No. 1.

25. Morrison, P. R., F. A. Ryser, and A. R. Dawe. 1959. Studies on the physiology of the masked shrew. Physiol. Zool. 32:256.

26. Ol'nyanskaya, R. D. and A. D. Slonim. 1947. On the adaptability of organisms to very low temperatures of the environment. Invest. Acad. Nauk. SSSR. Ser. Biol. 245.

27. Pearson, O. P. 1960. The oxygen consumption and bioenergetics of harvest mice. Physiol. Zool. 33:152.

28. Pruitt, W. O. 1957. Observations on the bioclimate of some taiga mammals. Arctic 10:131.

29. Scholander, P. F. 1955. Evolution of climatic adaptation in homeotherms. Evolution 9:15.

30. Scholander, P. F. 1957. Countercurrent heat exchange and vascular bundles of sloths. J. Appl. Physiol. 10:405.

31. Scholander, P. F., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950a. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull. 99:237.

32. Scholander, P. F., R. Hock, V. Walters, and L. Irving. 1950b. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation and basal metabolic rate. Biol. Bull. 99:259.

33. Scholander, P. F., V. Walters, R. Hock, and L. Irving. 1950c. Body insulation of some arctic and tropical mammals and birds. Biol. Bull. 99:225.

34. Scholander, P. F. and W. E. Schevill. 1955. Countercurrent vascular heat exchange in the fins of whales. J. Appl. Physiol. 8:279.

35. Sealander, J. A. 1952. The relationship of nest protection and huddling to survival of Peromyscus at low temperature. Ecology 33:63.

36. Smirnov, P. K. 1958. Characteristics of heat exchange in the harvest mouse, Micromys minutus. Translation of Doklady Acad. Nauk. SSSR in Doklady Biol. Sci. Section 117(4); 717.

37. Symposium sur l'acclimation au froid. 1957. Rev. Can. de Biol. 16:133.

38. Symposium in Centre Nationale de la Recherche Scientifique. 1955. Arch. Sci. Physiol. 9:C_1-C_{229}.

39. Symposium on cold acclimation. 1960. Fed. Proc. 19:1.

DISCUSSION

MORRISON: I have some data on related species living in the same environment. These show differing thermal sensitivities that can be rather nicely correlated with their habits. I hope this will be of interest because it represents work done with Dr. F. A. Ryser in this laboratory some years ago.

These are simply measurements of the body temperature against the ambient temperature. Figure 14 compares the two common voles taken from the nearby Chena River in February and March. Clethrionomys has excellent regulation. Microtus, on the other hand, falls off badly at low ambient temperatures both in regard to the summer temperature and the higher winter temperature. This correlates with their habits since Microtus stays strictly inside its burrow system when it is cold, whereas Clethrionomys does come out and move around.

Figure 16 compares the two lemmings from the far north. Dicrostonyx regulates well but Lemmus is not so effective. Dicrostonyx is seen above the snow when it is very cold whereas Lemmus carefully restricts himself to his subnivean microclimate. Incidentally, Dr. Hart showed a slide from Dr. Scholander (Hart, Fig. 2) on insulation values in various northern mammals. There the lemmings were grouped, but the two highest values represented Dicrostonyx while the four lower points were for Lemmus, which difference correlates with the physiology and behavior.

HART: How long were the exposures of the Microtus?

MORRISON: These were caged animals living at these low temperatures, so there were a number of hours of exposure, days in some cases.

HART: Continuous exposure?

MORRISON: Yes.

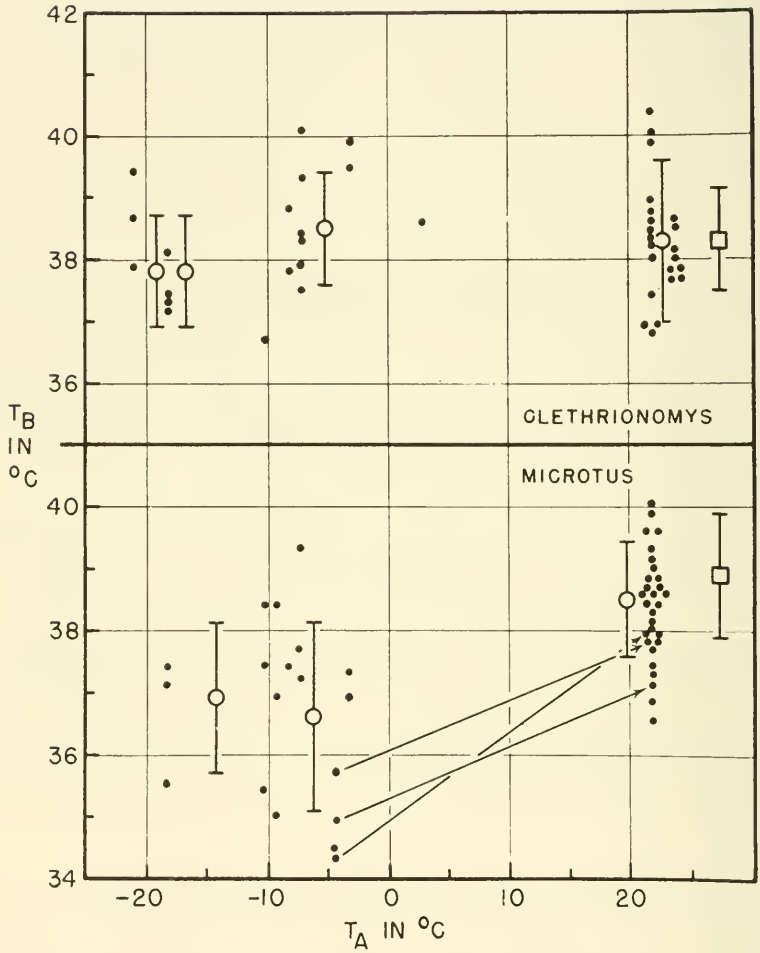


Figure 14. Body temperature in Clethrionomys and in Microtus as a function of ambient temperature. Circles, winter trapped animals from Fairbanks; squares, summer trapped animals.

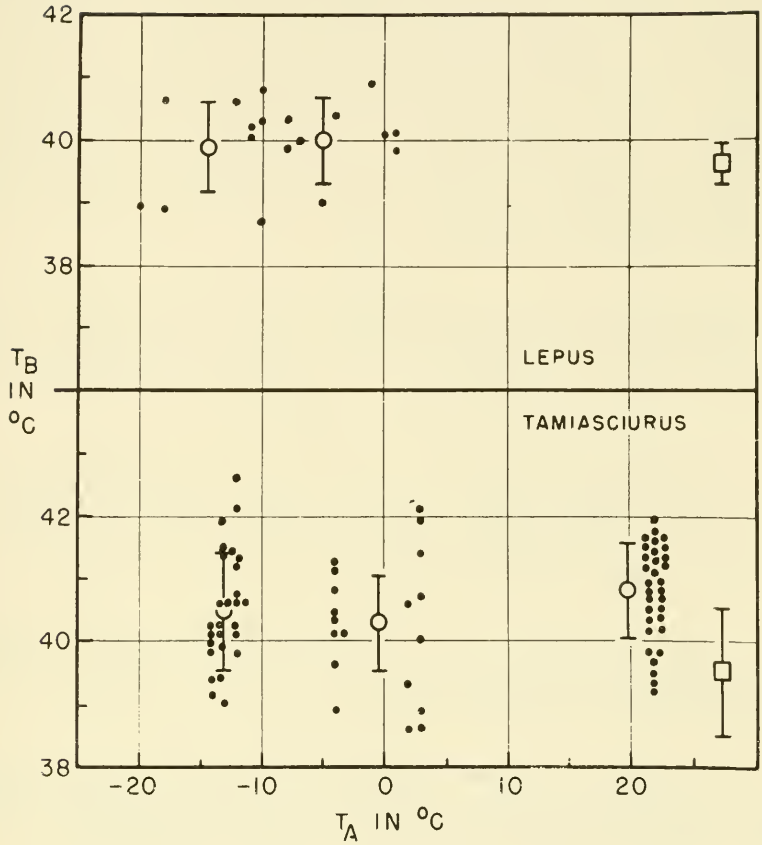


Figure 15. Body temperatures of the snowshoe hare and the red squirrel at various environmental temperatures. Symbols as in Figure 14.

IRVING: They must be able to take quite a lot, because I caught a live Dicrostonyx in March on one of the sand islands off the coast east of Barrow. It was over a mile from shore; we heard him scratching around during the night and he was still alive in the morning. We then traveled about ten miles offshore on the ice and found one Dicrostonyx which had died out there, but it was obviously not killed by, or transported by a predator. I saw the tracks of several others around seven or eight miles from the shore, which must take them quite a long time at their rate of travel.

MORRISON: One of our group tracked a lemming a couple of miles out on the ice off Barter Island. There was no indication of where it was going, but the tracks were in a straight line, not as though it was searching or meandering.

HANNON: With respect to running ability we have observed that the hamster, which is about the same size as the lemming, can run six to eight miles a day--all of this distance being covered entirely during the hours of darkness.

FOLK: The white rat can run 21 miles, so they are capable of running distances, for example one ran 28 miles in 24 hours and another ran 32 miles in 24 hours.

IRVING: But the lemmings were found under conditions where even with their hardiness they were expending metabolic energy at a very rapid rate for maintenance of body temperature.

JOHANSEN: I may perhaps comment on my work on the muskrats. One project was concerned with the fact that the muskrat has a very dense fur and a naked tail, which suggested to me that this tail might have a crucial importance as a heat exchanger; and this turned out to be the case. The tail of the muskrat as it was studied by temperature measurements and plethysmography (where Charles Eagan gave expert help) showed that the tail blood flow can change by a factor more than 400 within a very short

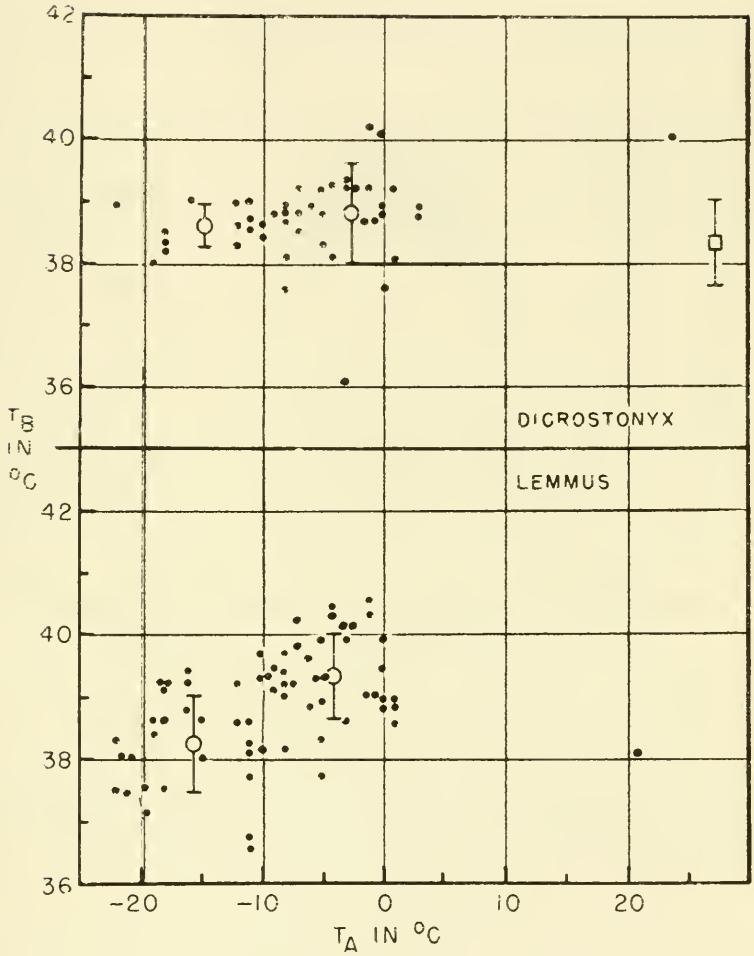


Figure 16. Body temperature in Dicrostonyx and in Lemmus as a function of ambient temperature. Symbols as in Figure 14.

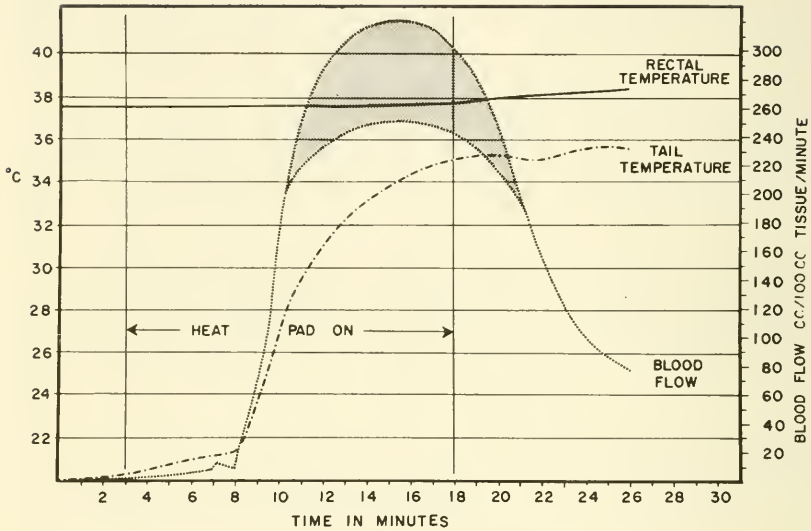


Figure 17. Changes in tail blood flow, rectal and tail temperatures during a vasodilation of the muskrat tail. Note the tremendous increase in tail blood flow.

time (Fig. 18A). If the muskrat is overheated slightly either by exercise or by being exposed to a high environmental temperature, his tail is "flushed" immediately. The skin temperatures are practically as high as the body temperature.

I proceeded by trying to elucidate the mechanisms behind these profound effects and the data acquired from doing nerve blocks of the tail indicate that there exists such a thing as a vasodilator innervation to the skin in the tail of the muskrat. If I nerve-blocked the tail, the animal became hyperthermic in a very short time and in one instance an animal succumbed and died of heat apoplexia when his tail was not intact (Fig 19A).*

In the other project, I tried to assess the importance of the air layer in the fur as an insulator. I compared two groups of animals, one with the air layer intact and one with the air depleted by way of surface active materials, such as detergents. I anesthetized the animals to standardize the condition and to avoid differences in movement. I found that the intact muskrat had a volume of about 800 cc, of which about 200 cc was air. In other words, almost 25% of the volume of the muskrat is air. If these two groups are subjected to water cooling or to air cooling, the temperature drops five times as fast in the one depleted of the air.**

HANNON: There is one question I would like to ask Sandy. In animals such as the muskrat and possibly wild rats living outdoors continuously, do you feel it might be possible for these animals to be continually cold-acclimatized, summer and winter? In the muskrat, for example, in these northern areas, the water is still quite cold in the summer. It may be that they get a level

*Johansen, K. 1962. Heat exchange through the muskrat tail. Evidence for vasodilator nerves to the skin. Acta Physiologica Scandinav. (in press).

**Johansen, K. 1962. Buoyancy and insulation in the muskrat. J. Mammal. (in press).

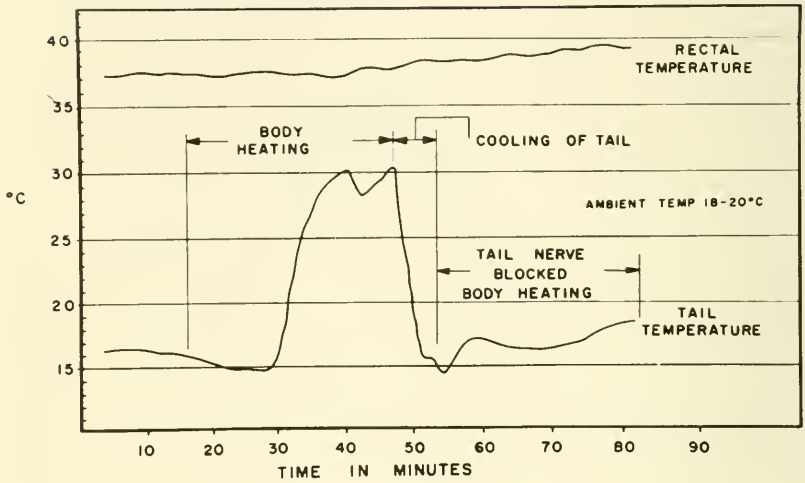


Figure 18. First portion of the figure demonstrates the course of rectal and intracutaneous tail temperature during body heating and consequent vasodilation in a normal undisturbed subject. Subsequently the tail is cooled down, and nerve blocked. Body heating is reapplied but the tail vasodilation and the consequent heat loss is prevented and a rapid increase in rectal temperature is seen.

of acclimatization and just maintain it. And that is why you cannot see the difference between summer and winter.

HART: I always think of it as a matter of degree. The muskrat is probably to a certain extent acclimatized in the summer, too, but you would think that they would be more so in the winter.

JOHANSEN: We did some measurements in the field here and the temperatures in the pushups of the muskrats are rather strikingly high during winter. They are from 5° C to 10° C above freezing in the -40° C weather. We do not really know how much time they spend in the cold water; this is what we should find out.

HANNON: You have essentially 0° C water in the winter time, and maybe it will go as high as 15° C in the summer and maybe a little higher. You still have a pretty big differential, but on the other hand they may be a little more active in the summer time in the water, so they get a longer exposure.

HART: It is possible.

IRVING: Dr. Fay has been making some measurements from time to time in the New York Zoo on the temperature on the body skin and flippers of walrus, both young and old. He has been able to get some measurements of wild walrus around St. Lawrence Island, too, and he finds a fair regularity in the relation between the temperature of the skin of the body in air or water. As Hart and I found in harbor seals, the flippers may be quite different from the body and apparently fluctuate as if for fine adjustment of temperatures. Fluctuations in the extremities are also subject to non-thermal excitation, and in absence of obvious relation to heat, are ascribed to plain nervousness.

PROSSER: In your summary slide, comparing the different mammals, you suggested that there might be differences in the sensory sensitivity.

HART: Do you mean sensitivity to skin temperature?

PROSSER: Yes. Is it possible that there might be differences in the endocrine response mechanism?

HART: You might have the same input and a different response to the input.

PROSSER: Have you any evidence about the response of either the thyroid or adrenal in these different series?

HART: Absolutely none.

PROSSER: It seems to me that endocrine response would be an alternate explanation. Of course this could be explored.

EAGAN: However, this endocrine response could be mediated only through the nervous system.

PROSSER: Yes, but the sensory input might be the same.

HART: Is there any way of assessing sensory input in animals? I do not know of any.

PROSSER: It certainly would be worthwhile to try to record the nerve impulses in response to a given cold stimulus.

KLEIBER: I do not think I would be accused of particularly being in love with body surface or against the three-fourths power of body weight. But when you express the specific insulation, I wonder if it would not be wise, for internal consistency, to express the metabolic rate per unit surface, whatever it might be. I mean that you should use weight to the two-thirds power instead of the three-fourths, because otherwise you might introduce a side effect in this insulation which is actually not present.

HART: This is really a measure of metabolism, though.

KLEIBER: Yes, but the metabolism in this case is related to heat exchange and the metabolism related to heat exchange is a

function of the surface or is related to surface area rather than to metabolic size.

HART: It might not make too much difference because they are rather close anyway.

KLEIBER: That is right, except when you go from one kilogram to a thousand kilograms.

MORRISON: They are close, but there is a difference between the two functions. In our measurements, taking the thermal conductance from the slopes of the metabolism-ambient temperature curves, a rather elegant relation describes some of the smaller mammals (<500 g). Thus, conductance is equal to the square root of the body weight if the weight is expressed in grams and the conductance in $cc0_2$ (gms x hr x $^{o}C)^{-1}$.

HART: If you express metabolism as a square root function of body weight, it should then be independent of weight differences.

MORRISON: The exponent will change depending on whether the expression is per gram or per animal. That would change the exponent.

VIERECK: In your figure comparing skin temperatures of different species at different environmental temperatures, where on the animal's body do you take the skin temperature? Do you have any idea of how to get an average skin temperature for the surface?

HART: It was not an average at all. They were simply representative temperatures taken over the trunk of the body.

VIERECK: But the fur is very thick in the back and thin in the front. Where do you take the temperature?

HART: This is underneath the fur, and in the caribou they were averages of several measurements taken on one side of the fur. In the rat measurements were approximately at the same place.

VIERECK: Do you look for a place where the fur is thickest?

HART: Not necessarily.

FOLK: Possibly some experiments will be able to provide the activity of the animal during oxygen consumption. Benedict has stressed this so much. You find two groups of animals in your series, at very cold temperatures where the metabolism is up high. Some of the animals are quite restless and move around, while others curl up and are quiet with high metabolic rates at these cold temperatures.

HART: In those which I have observed, I find almost invariably that they are huddled up and not moving at all. When the cold is such that the metabolic rate is increased close to its maximum, then these animals are seldom if ever moving in my experiments.

FOLK: Can you give examples of animals that were moving under these circumstances? I think of the tropical raccoon. They might be restless, which would account for part of the high metabolism.

HART: Were there not some measurements by Erikson* on ground squirrels which showed a definite correlation of metabolic rate with activity in the cold? In these animals the activity was greatest at the lowest temperatures which increased the oxygen consumption further.

*Erikson, H. 1956. Observations on the metabolism of arctic ground squirrels (Citellus parryi) at different environmental temperatures. Acta. Physiol. Scandinav. 36:66-74.

TEMPERATURE RESPONSES AND ADAPTATIONS IN DOMESTIC ANIMALS

Max Kleiber

The body temperature of homeotherms is nearly the same as that of man, about 37° C. Consistent changes from the average do occur, but they are not related to body size or to geographic distribution of the animal. Rat and elephant temperatures are about 1° C cooler than those of man; cow, sheep, and swine, about 1° C hotter, rabbit and dog about 2° C* hotter; and the camel lets its body temperature vary from 34° C to 36° C and seems not to mind a temperature of 40° C if this is necessary for saving water.

Figure 1, somewhat schematized from data of Johnson, et al. (1958) shows that below an environmental temperature of 80° F (27° C), cow and man regulate their body temperatures somewhat more accurately than does the rabbit. Man is much more strict in keeping cool in a hot environment than cow or rabbit. The cow's body temperature rises when the environmental temperature is higher than 80° F (27° C). This is also the case for cold adapted rabbits, whereas rabbits adapted to a warm climate do not raise their body temperatures before the air temperature exceeds 90° F (32° C).

I am not aware of any biological theory which would explain why in the evolution of homeotherms that 36° C to 40° C body temperature has been so much more advantageous than other body temperatures. For all conditions under which homeotherms live and for all their sizes, this thermal level has been fixed by natural selection with a very small variation. It is fixed, however, and so is the basal metabolic rate of homeotherms large and small, tropical and arctic. It can be predicted with about 10% accuracy by the equation:

*Rabbit's normal temperature is 39.6° C; its variation is generally not more than 1.8° C. Robert C. Lee (1939).

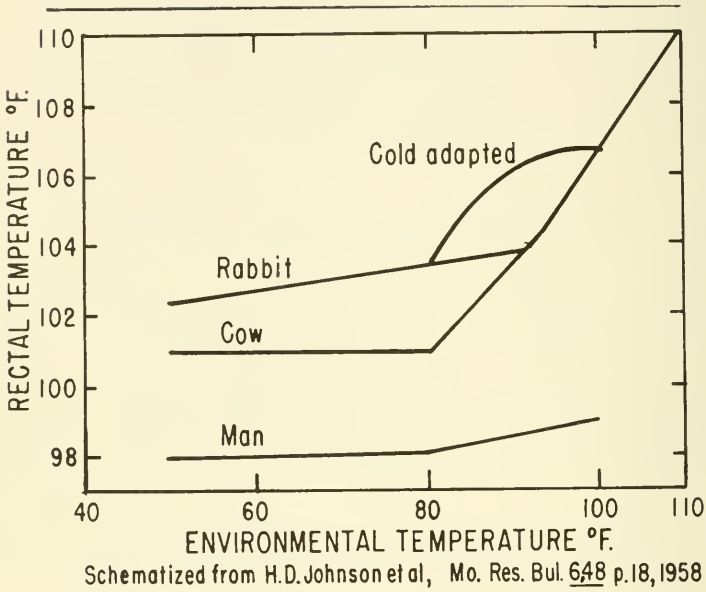


Figure 1. Rectal and environmental temperatures of man, cow, and rabbit (cold-adapted and non-cold-adapted).

$$B = 70 \times W^{3/4}$$

where B = basal metabolic rate per day in kcal
W = body size in kg (Kleiber, 1947)

Scholander (1955) writes as follows:

> The non-adaptability of the resting rate shows that the heat production is not determined by the heat loss as one might infer from the surface law of Rubner (1883) but vice versa. Whatever the surface area happens to be, the heat loss from it must be so regulated by various means that it balances the heat production. In a homeotherm one might say that body temperature plays the first violin, metabolic rate the second, and heat loss the third.

The major, or practically only, adaptation which occurred was the adjustment of the thermal insulation to bring the third violin into harmony with the first and second. This adaptation was accomplished in various ways, and it led to differences in the temperature distribution of various animals.

Figure 2, also schematized from the data of Johnson et al. (1958), shows the skin temperature as a function of the environmental temperature. From 50° F to 90° F (10° C to 32° C) air temperature the rabbit skin maintains an almost constant temperature, whereas the temperature of the skin of cow and man follows the environmental temperature.

This temperature distribution is the result of the high insulating power of the rabbit fur and the fact that man lacks this insulation. The main resistance against heat loss and therefore the greatest temperature gradient in naked man is located in the subcutaneous layer. The cow has a less efficient fur than the rabbit. The difference between rectal temperature and skin temperature, which is an index for the resistance of the subcutaneous layers to heat flow, is shown in Figure 3.

As the environmental temperature rises, the skin temperature of man and cow approaches the rectal temperature but does not reach

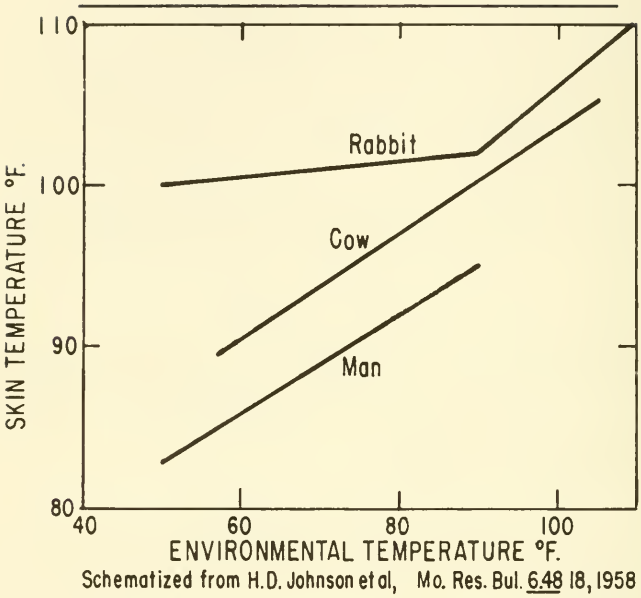


Figure 2. Skin and environmental temperatures of man, cow, and rabbit.

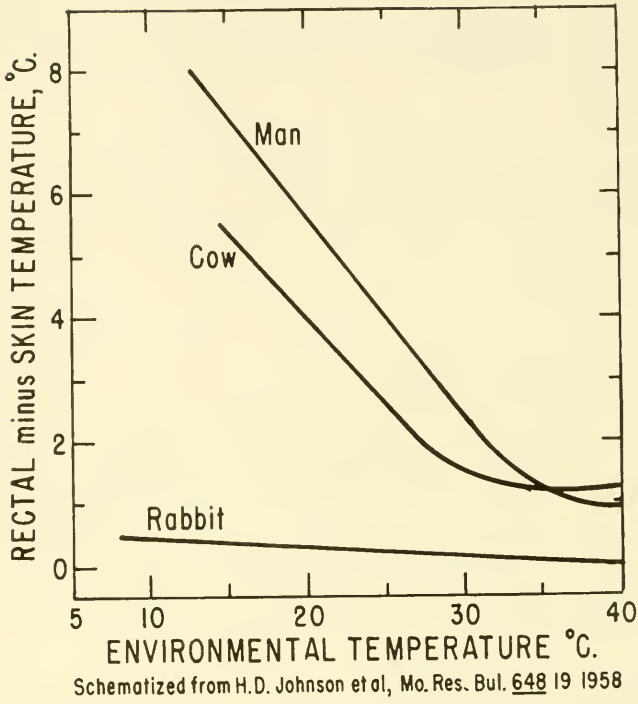


Figure 3. Differences between rectal and skin temperatures in man, cow, and rabbit at various environmental temperatures.

it. When the air temperature rises from 30° C to 40° C, the man and cow maintain an almost constant difference between skin and body temperature. This is mainly the result of evaporative cooling. The rabbit, however, lets his skin temperature almost reach the level of the rectal temperature. Rabbits presumably rely mainly on the evaporative cooling in the respiratory system (or possibly the ear surfaces).

Richet (1889) shaved a rabbit and observed that in this condition the rabbit regulated its body temperature at a lower level. This effect is shown in Figure 4, drawn from data in Richet's book on animal heat.

Diurnal Changes of Body Temperature

Man changes his body temperature during a day in a cyclic fashion, and Kleitman (1951) suggests that differences in this cycle account for differences in the behavior of two types of people, the early risers and the late risers. The late risers are grouchy because their body temperatures are low. They need to be warmed up by a cup of hot coffee to reach a friendly disposition and a positive outlook on life. (See also Kleitman, et al, 1935).

Some domestic animals, such as the donkey and the camel, start their days with a considerably lower body temperature than that of man, and they do not have the benefit of a cup of coffee. They may possibly be endowed with a higher basic level of social grace than man and do not express their grouchy feelings as strongly as some human beings do.

Figure 5 shows the diurnal temperature change of a Holstein cow subjected to an environment simulating the Imperial Valley (Kibler and Brody, 1956). In man, a temperature of 108° F (42° C) would be regarded as a very high fever and the cow's thermostatic capability seems therefore not very impressive; yet comparison of the cow's daily temperature fluctuations with those of the air temperature under actual conditions in the Imperial Valley shows that temperature changes in the body are a small part of those in the

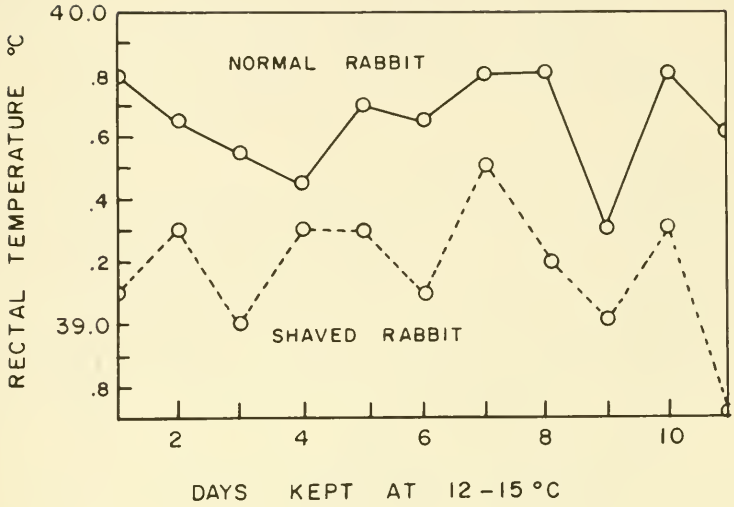


Figure 4. The effect of shaving on the body temperature of rabbits.

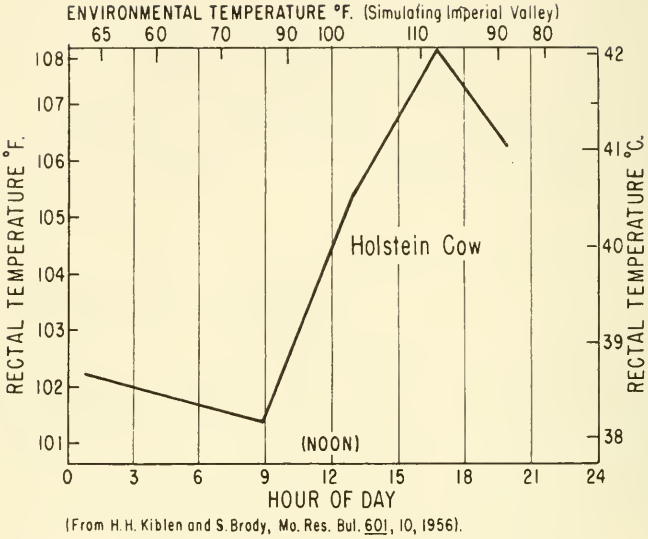


Figure 5. The diurnal change in a cow's body temperature with changes in environmental temperature.

environment (Fig. 6). This is especially true in the relatively cool months of May and June. When it gets extremely hot in July and August, the fluctuations of body temperature become greater.

One may define the effectiveness of temperature regulation as the quotient of the change in the environmental temperature and the changes in the body temperature.

Figure 7 shows this calculation for the cow observed by Ittner (1946) in the Imperial Valley.

As long as the maximum temperature of the environment stays below 40° C, the change in the cow's body temperature is only about one fortieth of the change in the environmental temperature, but when the maximum temperature of the air reaches 44° C, as in July, the cow's regulating efficiency drops to one half. Her temperature fluctuation now becomes one twentieth of that of the environment. The cow is better equipped to maintain her body temperature against a cold than against a hot environment.

Some breeds of Asiatic cattle are better adapted to hot climates than Western breeds. The Zebu cattle may thrive under conditions under which Western cattle suffer. Brody and his coworkers have investigated this difference and McDowell and his coworkers (1953) have studied the inheritance of this adaptation. They crossed Jersey cattle with Sendhi, a breed of Zebus, and exposed Jerseys and crossbreeds to an environmental temperature of 105° F (40° C) for 6 hours. Figure 8 shows some of their results. The crossbreeds maintain a body temperature close to 102° F (39° C), whereas the body temperature of the Jersey cows rises to over 103° F (39° C). The reaction of the Jerseys depends on the season. During the winter months they are least able to cope with a 6 hour exposure to 105° F (40° C), whereas during the summer months this exposure raises their body temperatures to a level not much higher than that of the crossbreeds.

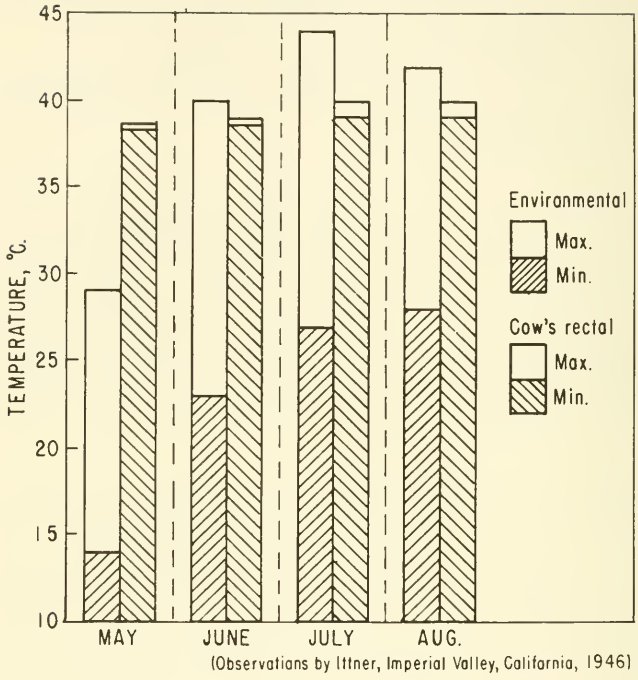
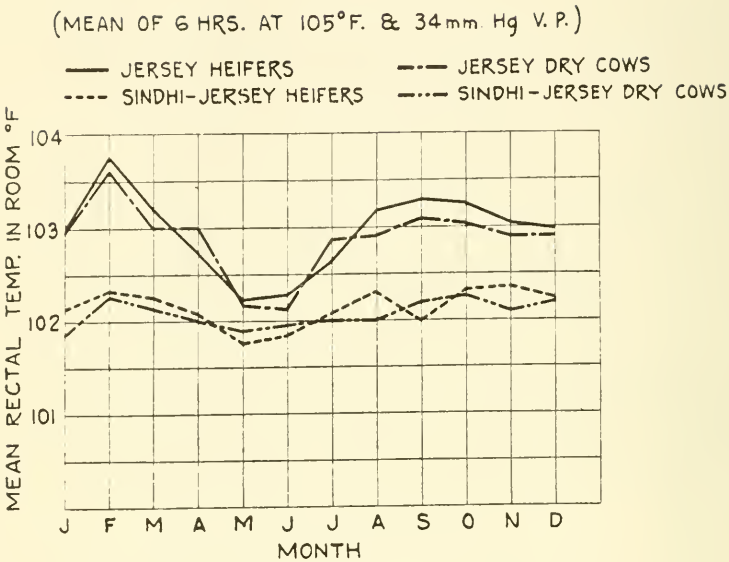


Figure 6. Daily fluctuations of a cow's body temperature compared with those of the environmental temperature.

Month	Environment			Cow (rect.)	Effectiveness $\frac{\Delta \text{ Envir.}}{\Delta \text{ Rect.}}$
	Min. °C.	Max. °C.	Δ Envir. °C.	Δ Rect. °C.	
MAY	14	29	15	0.4	38
JUNE	23	40	17	0.4	42
JULY	27	44	17	0.9	19
AUGUST	28	42	14	0.9	16

Note: Total variation of rectal temperature 38.2 to 40 °C.
Based on observations by Ittner, Imperial Valley, Calif., 1946.

Figure 7. Daily temperature fluctuations and the effectiveness of a cow's thermostat.



Journal of Animal Science, Vol. 12, No. 4, November, 1953

Figure 8. Seasonal effects on body temperature response to heat.

REGULATION AGAINST COOLING

By cooling I mean a decrease in temperature and, to the best of my knowledge, that is what Newton meant by cooling when he formulated his law of cooling which is erroneously applied when one means loss of heat rather than of temperature. Temperature regulation means prevention of cooling but not prevention of heat loss.

The classic example for adaptation to cold has been given by Hoesslin (1888). He set out to test experimentally Rubner's theory that the metabolic rate of homeotherms is proportional to their surface area because their heat loss is proportional to their surface area. Hoesslin argued if the metabolic rate is governed by the heat requirement, then it should be directly proportional to the difference between environmental temperature and body temperature. To test this deduction, Hoesslin raised one dog at 32° C and a twin brother of that dog in the refrigerator at 5° C. From his records of food consumption and his estimate of body substance produced, Hoesslin concluded that the dog raised at 5° C had a metabolic rate only 12% above that of his brother raised at 32° C. The difference between body temperature and environmental temperature of the cold dog was about six times as great as the corresponding difference for the hot dog.

Hoesslin concluded that heat requirement could not be the determining factor in the control of metabolic rate or the explanation for the surface law. He observed that the cold dog's pelt weighed 3.6 times as much as that of the hot dog, indicating an adaptation of insulation to environment. It may be that the adaptation was mainly on the side of the hot dog, that his fur was abnormally light. We now would accept Hoesslin's argument that the metabolic rate of his hot dog was not determined by heat requirement, but we would maintain that the metabolic rate of the cold dog presumably reflected a thermostatic heat requirement. This assumption is justified by the relation of metabolic rates to body temperatures of various animals

obviously reflecting the insulating power of their body covering as shown in Figure 9.

We simplify the situation by the scheme in Figure 10. If the dogs behaved strictly like ordinary thermostats, then the metabolic rate of the hot dog would be on the line between the rate of the hot dog and the rate zero reached when the environmental temperature becomes equal to the body temperature. On the scale of our figure the hot dog would produce about 16% of the "normal" rate marked 100. The hot dog, however, produces almost as much heat as his cold brother and operates special devices to get rid of the excess heat. Obviously, the metabolic rate of the hot dog cannot be explained as a heat requirement. Rubner realized that, and he explained the surface law of animal metabolism as heat requirement proportional to surface area in a cold environment and as necessary cooling power also proportional to surface area in a hot environment.

There is, however, a difference between the two dogs in their immediate reaction to cold. If the hot dog were suddenly brought to the cold living quarters of his brother, he would presumably shiver and produce more heat than the cold-adapted litter mate. If he stayed long enough in the wintery climate and if he had enough youthful adaptability he would gradually grow a fur as thick as that of his brother and quit shivering; then presumably the two dogs would have the same metabolic rates. The rise in metabolic rate is known as "chemical," or metabolic temperature regulation. By that term, Rubner simply meant an increase in the rate of chemical processes, whether or not connected with muscular movement such as shivering. The idea of chemical temperature regulation as contrasted to regulation involving shivering is a later and not too useful complication. The change in the insulation, in contrast to the change in metabolic rate, is known as "physical" temperature regulation, and, if it involves slow processes such as changing one's fur, it is classified as "acclimatization."

Scholander reports that dogs truly acclimatized to the arctic regions have a critical temperature as low as -40° C. This shows that domestication has not led to a degeneration of the dog or at least has left the dog the possibility of overcoming the softening

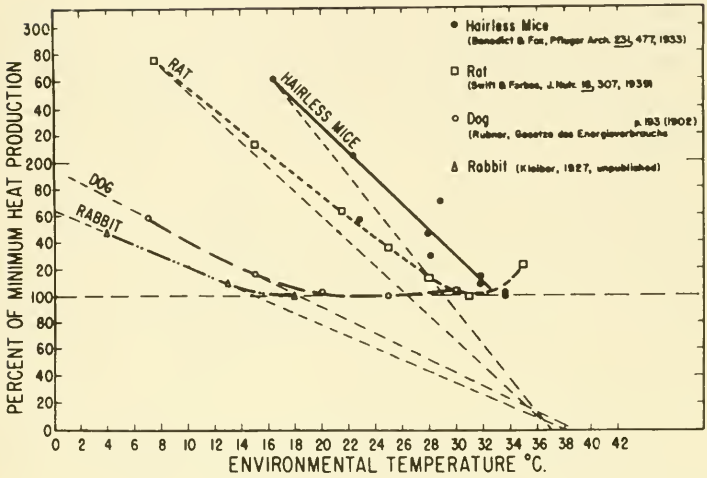


Figure 9. Fasting katabolism in the hairless mouse, the rat, the dog, and the rabbit at various environmental temperatures.

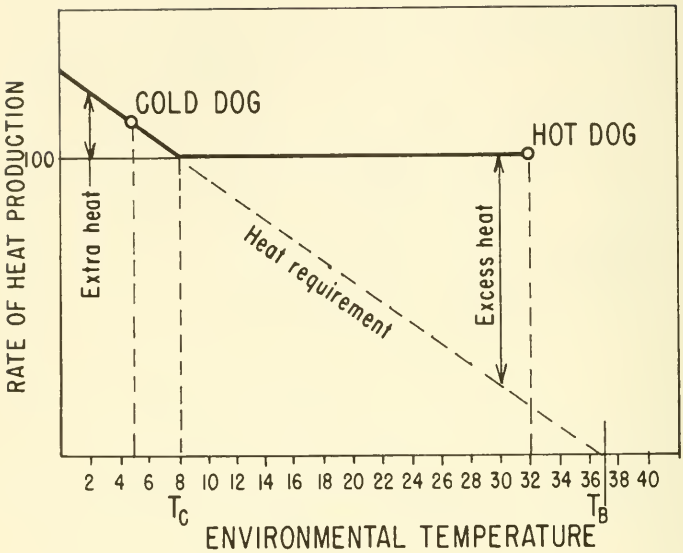


Figure 10. The rates of heat production in Hoesslin's "hot" and "cold" dogs at various environmental temperatures.

effect of civilization and becoming fit to follow "the call of the wild," as Jack London would say.

Between the immediate response of shivering and the long term acclimatization of growing a thicker fur, there is an intermediary adaptation. For some time the dog brought from the hot to the cold environment would presumably respond with "insulative cooling." He would let the temperature, especially of the outer layers of his body, drop. Scholander (1958) discovered this temporary answer to cold exposure in the Australian aborigines. This adaptation is especially advantageous in climates with great diurnal temperature changes.

I remember Nansen's account of his polar expedition, especially his description of Johansen's sleeping peacefully with his bare foot stuck out from the tent into the subzero polar air. This observation indicates that the Norwegian polar explorers may also have acquired some ability to utilize insulative cooling.

Social Temperature Regulation

My account of adaptations to prevent a fall of body temperature in a cold environment would not be complete without mentioning social temperature regulation. Animals have learned to conserve heat by "togetherness," also called "huddling." That this method is effective has been shown in baby chicks, some of which were denied fulfillment of their social instinct and were forced to burn up more fuel to keep warm, while involuntarily practicing rugged individualism (Fig. 11).

REGULATION AGAINST OVERHEATING

An old method to get relief from too much heat is the use of a fan. I am told that ladies used this instrument not only to increase

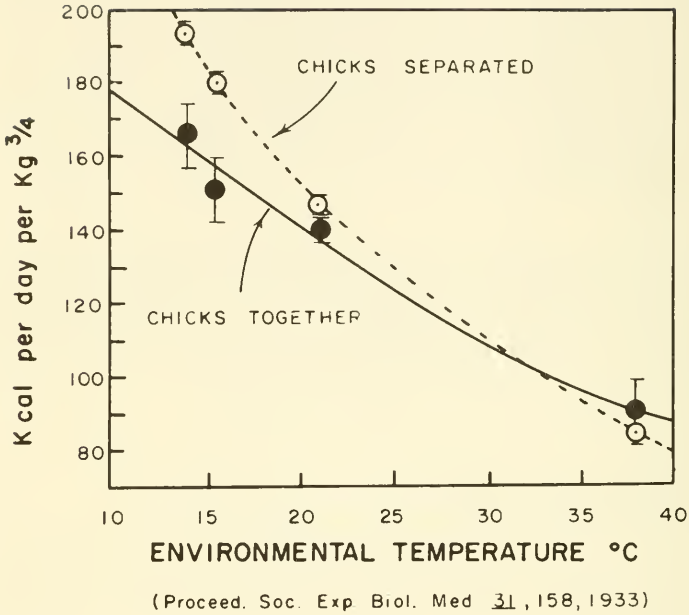


Figure 11. Social temperature regulation in chicks 20 days old.

cooling but also to hide blushing and even to hide non-blushing. Steers do not worry about blushing but they get relief against overheating from fans, as shown on Figure 12, which was constructed from a table giving observations by Ittner, Bond, and Kelly (1955), in the Imperial Valley of California. The fan could keep the body temperature one degree lower than it would have been without the fan. This type of relief, of course, is given the animal by his keeper. The animal itself, however, also has methods for preventing overheating. The first reaction of an animal exposed to a high environmental temperature is to increase the blood flow to the skin, which increases the heat flux from skin to environment. This type of physical temperature regulation is effective only when the skin temperature is higher than the environmental temperature. When the air temperature and the temperature of the objects toward which an animal radiates are equal to, or higher than body temperature, more drastic means of cooling have to be taken. The last resort is water evaporation. Men and horses perspire. Dogs and cattle have discovered a flaw in this method. When the surface is wet and evaporative cooling takes place, there is not only the welcome temperature difference for the flux of heat from the interior to the surface, but also an increase in the flux from the hot environment to the animal surface. The animal therefore spends water to cool its environment. To overcome that disadvantage, cattle and dogs operate an internal evaporative cooler which leaves the surface temperature higher and keeps the heat influx lower. Dogs and cattle increase the evaporative cooling by panting. Increased respiratory ventilation, however, involves the danger of depleting the blood of CO_2, a condition known as acapnia which causes unpleasant disturbances in the operation of the breathing reflexes. The answer to this danger is shallow breathing, increasing the ventilation rate in the upper parts of the respiratory system only, this provides the desirable increase in evaporation, with little change of the CO_2 washout from the alveoli.

Figure 13 shows the type of breathing in heat exposed cows compared with that at a low (for the cow's taste comfortable) temperature. A threefold increase in respiratory frequency produces a twofold increase in ventilation rate because the volume for each breath is reduced. Cows do not start panting at a certain

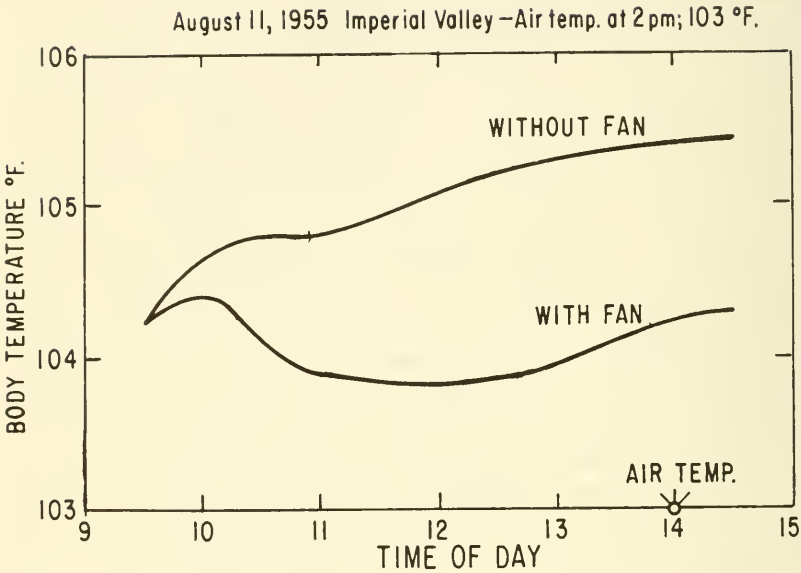


Figure 12. The effect of a fan on a steer's body temperature.

	Environmental 7°C.	Temperature 32°C.
Breaths per minute	15.5 ± 0.3	46.0 ± 3.8
Respired air per minute, liters	52 ± 3	105 ± 5
Respired air per breath, liters	3.4 ± 0.2	2.2 ± 0.04

(Proceed. Soc. Exp. Biol. Med. 33, 10-14, 1935).

Figure 13. Physical temperature regulation in cows. The adaptation of breathing at various environmental temperatures.

environmental temperature. As they get warmer, their breath rate increases rather gradually, so that the relation between respiratory frequency and the environmental temperature can well be expressed by the Arrhenius equation.

Figure 14 shows the logarithm of respiratory frequency plotted against the reciprocal of the environmental temperature in degrees Kelvin.

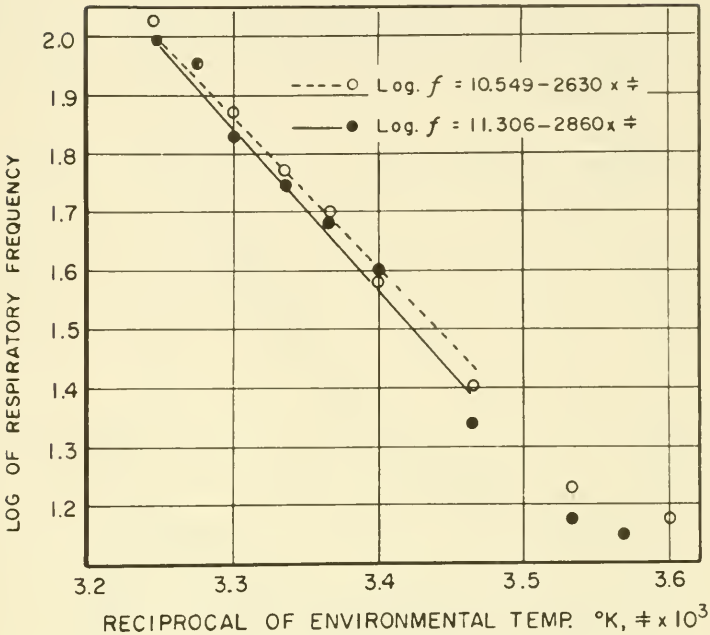
The idea that cows do not perspire at all through their body surface has been proven erroneous. Figure 15 summarizes the results of Kibler and Brody (1952), which indicate that indeed a great part of the heat given off by cows, especially in a hot environment, is accounted for by surface evaporation, and the evaporation in the respiratory system amounts to only one-third of the total evaporation.

Kibler and Yeck (1959) later observed that the greater heat tolerance of Brahman cattle compared with shorthorns is related to a greater evaporative capacity and that in particular the ratio of skin evaporation to respiratory evaporation is greater in the heat tolerant Brahmans. The major advantage of the Brahmans, however, in combating overheating, according to Kibler and Brody (1954), is their relatively low metabolic rate, about 80 kcal/(m^2 x hr) as compared with 150 kcal/(m^2 x hr) in Jerseys and Holsteins.

The Method of the Camel

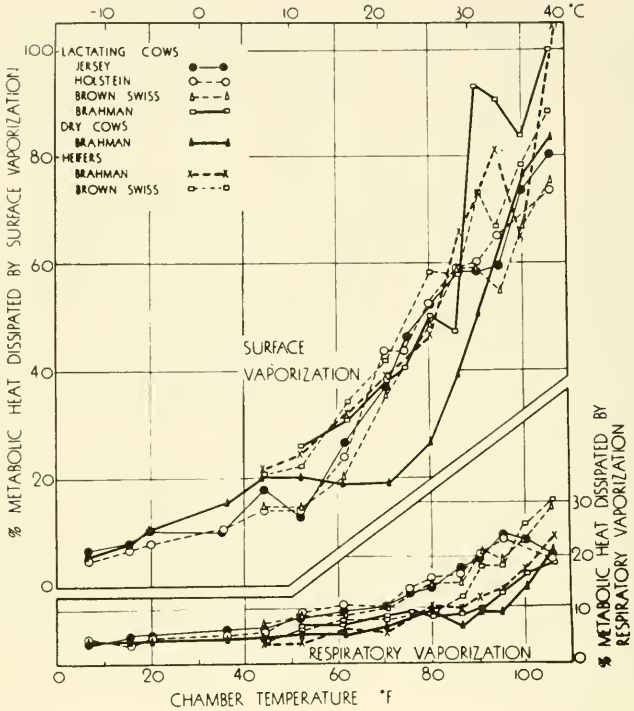
The most ingenious system of keeping cool has been developed by the camel, also known as the ship of the desert. The U. S. Navy has a perfectly good reason, therefore, for supporting research on this animal by Knut and Bodil Schmidt-Nielsen, a team of extraordinarily keen observers.

The camel apparently realizes the advantage of inside cooling as opposed to surface cooling. It also is very much interested in the most economic use of water and can hardly afford to have sweat drop to the ground unevaporated, as it does in human athletes and in



Proc. Soc. Exp. Biol. Med. 33: 11 (1935)

Figure 14. The Arrhenius equation for cow's respiratory frequency.



Kibler & Brody

Mo. Research Bulletin 497 (1952)

Figure 15. Percentage of metabolic heat dissipated by surface vaporization.

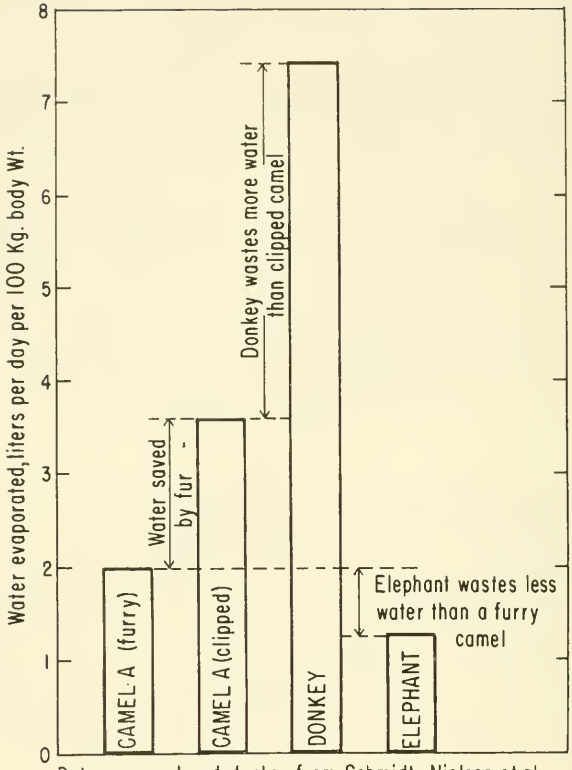
horses. Yet the camel apparently does not think much of panting and, having observed panting cows and dogs, I cannot blame the camel for disliking that method. The ship of the desert solves the problem by making the skin surface an inside surface insulated by an effective fur. This leaves the outer surface of the hair hot and dry, minimizing the heat influx from the environment and reserves the entire cooling effect of the evaporation for the benefit of the animal.

The Schmidt-Nielsens and their coworkers (1957) demonstrated the importance of the fur in water economy by clipping a camel's hair. The result is shown in Figure 16 which is redrawn from Figure 1 in Schmidt-Nielsen's paper. Under given conditions, the furry camel uses 2 liters of water per day per 100 kg body weight. Clipping of the hair increases the water loss to 3.7 liters daily per 100 kg body weight.*

Schmidt-Nielsen et al. also measured the water expenditure of a donkey (presumably under the same conditions as the camel), and they state that the donkey wastes more water even than the clipped camel. As a good Democrat I am bothered by this wastefulness of the donkey and I think the accusation is unjustified. For a fair comparison of wastefulness, the rates of evaporation should be expressed per unit surface area instead of body weight, and when rates are expressed that way, the donkey is just as economical in the use of water as the clipped camel. To demonstrate the fallacy of the comparison per unit body weight for this discussion, I have added the probable rate of water loss of a 4000 kg elephant, and the result shows that by Schmidt-Nielsen's comparison the elephant is much more economical with water than even the furry camel. I must warn my Republican colleagues not to get too excited about this result. It is just a matter of body size, and the fact that elephants are bulkier than donkeys has no political significance. I hasten to mention that in fact my calculation is based on the strictly bipartisan assumption that the evaporation rate per unit surface area is the same for donkey and elephant.

Figure 17 shows the calculations which show the same water loss for the camel and the donkey per unit surface area.

*Some water may be used for the excretion of metabolic products in urine, but under the circumstances, evaporation presumably accounts for most of the water used.



Data on camel and donkey from Schmidt-Nielsen et al Amer. J. Physiol. 188 p. 110, 1957. Elephant calculated with equal evaporation rate per m^2 surface area as donkey.

Figure 16. The effect of clipping and of body size on rate of water evaporation per unit body weight in camel, donkey, and elephant.

	Camel	Donkey
Body weight	206 Kg	81 Kg
Surface area $W^{2/3}$	34.9 $Kg^{2/3}$	18.7 $Kg^{2/3}$
Daily water used per 100 Kg (Schmidt-Nielsen 1957*)	3.5 lit.	7.3 lit.
∴ " " " " animal	7.2 "	5.9 "
" " " " $Kg^{2/3}$	0.206 "	0.206 "
" " " " $Kg^{3/4}$	0.133 "	0.218 "

*Amer. J. Physiol. 188, pg 110 Fig. 7, 1957

Figure 17. Rate of water evaporation in the camel and the donkey.

The water loss per interspecific unit of body size is kg 3/4 (Kleiber, 1947). This interspecific unit is a unit of probable metabolic rate and it shows that the donkey had a higher rate of water loss than the clipped camel.

The comparison of rate of water loss between donkey and camel leads not to one but to several different conclusions, and no one is absolutely superior to the others. Assuming isometric composition of the two animals, the conclusion based on loss per unit body weight indicates that the donkey loses a given percentage of its body water twice as fast as the camel. For an estimate of the daily water requirement of a caravan, it may be of interest to know the water loss per animal--7.2 liters per camel, 5.9 liters per donkey. For a comparison of mechanisms of heat transfer it is noteworthy to know that both camel and donkey lose daily 2.1 liters H_2O per m^2 of surface area. For comparisons of the rates of water loss with metabolic rates, the loss per interspecific unit of metabolic body size is the most useful.

Daily Heat Load and Body Size

In many regions, especially deserts, it is very hot during a period of the day and cold during the night. Under those circumstances the larger animal has an advantage over the smaller one because heat load is proportional to body surface and heat capacity proportional to body weight. The rise in body temperature for a given period of excessive temperature during the day is therefore inversely proportional to the cube root of body weight. Figure 18 illustrates this relation.

It is assumed that during a 6 hour period every day the influx of heat exceeds the animal rate of heat loss so that during this 6 hour hot period 2.5 kcal of heat are stored in the animal per dm^2 of its body surface. This would be a rate of influx of 250 kcal per m^2 in 6 hours and would equal the basal metabolic rate which, according to Rubner, is 1000 kcal per day per m^2.* What is the rise in body temperature at the end of the 6 hour period resulting from this storage?

*This is approximately correct for an animal of 100 kg body weight, whereas smaller animals produce less, larger ones more heat per m^2 per day.

Body Weight	$\frac{\text{Surface}}{\text{Heat cap.}}$	Change in Body Temp.
W	$= 12.5 \times W^{-\frac{1}{3}}$	$= 2.5 \frac{\text{Surface}}{\text{Heat cap.}}$
Kg.	$\frac{dm^2}{kcal / °C.}$	°C.
1	12.5	31.4
10	5.81	14.5
100	2.70	6.7
1000	1.25	3.1
10000	0.58	1.4

Figure 18. Periodic heat load, body size, and body temperature for a periodic heat storage of 2.5 kcal per dm^2. For a 6-hour period the rate of this storage would be equal to the daily metabolic rate of one megacal per m^2 (Rubner).

The surface area in square decimeters may be estimated to be 10 x $W^{2/3}$, where W is the body weight in kg. The heat capacity of the animal may be estimated as kg water x 0.4 x kg dry matter in the animal (Kleiber, 1961). Assuming a water content of 68%, the heat capacity of the animal would therefore amount to 0.81 kcal/^{o} C per kg body weight. The ratio of surface area to heat capacity then would amount to

$$\frac{10 \times W^{2/3}}{0.81W} \text{ or } 12.5\ W^{-1/3} \quad \text{(second column in Figure 18)}$$

The increase in body temperature from the storage of 2.5 kcal/dm^2 then amounts to 2.5 x 12.5 $W^{-1/3}$. This rise would be 31.4^{o} C for an animal weighting 1 kg and 1.4^{o} C for a 10 ton super elephant. A large animal, therefore, may comfortably survive discontinuous daily heat loads which are fatal for smaller animals. When, however, the heat load is continued, the advantage of size is lost.

Professor Regan at Davis noted that a cow can stand a good deal of heat during the day when she cools off during the night, whereas a constant rather moderately high temperature in an air conditioned room may be fatal.

The camel can take advantage of cool nights by letting its body temperature decrease to 34° C (see Schmidt-Nielsen). A human being could hardly stand this, nor could he let his body temperature rise to 41° C when water is short and the day hot.

Schmidt-Nielsen feels that this relatively large change in body temperature should not be regarded as a failure regulation, but rather as an adaptation which conserves water. It may be more cautious to say that in this case the water economy at the cost of an accurate temperature regulation proves advantageous for survival.

The difference between controlled and run away increase in body temperature, the latter resulting from positive feedback, is clearly shown in a plot of pigs' body temperature against time of exposure to various environmental temperatures, observed by Robinson and Lee (1942).

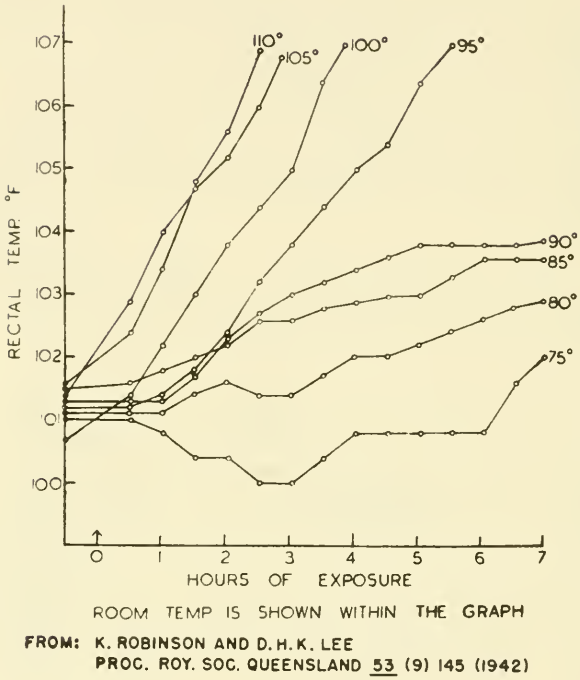


Figure 19. A pig's body temperature in 75° F to 110° F air.

TEMPERATURE AND FOOD UTILIZATION

An animal that is producing flesh or other forms of animal product invariably has a higher metabolic rate than a non-producing and especially a fasting animal would have. The difference in heat production between the fed and the fasting animal is called the "heat increment", or the calorigenic effect of food, or the specific dynamic effect of food, an intriguing name considering the fact that the effect is neither specific nor dynamic.

This calorigenic effect of food intake means a relief to the animal in its fight against a cold environment and an extra burden in the regulation against overheating.

The situation is illustrated in Figure 20. At a low environmental temperature the metabolic rate, being determined by the heat requirement, will be the same for fed and fasting animals. There is thus no calorigenic effect of the food. At this low environmental temperature the extra heat for thermostatic control is now less because the minimum heat production of the fed animal is higher than that of the fasting animal, and the calorigenic effect of the food helps to heat the animal. The critical temperature of the fed animal (Tcf) for that reason is lower than that of the fasting animal (Tco). Between these two temperatures the calorigenic effect of the food increases from zero to C_m in proportion to the increase in environmental temperature. Rubner called the description of this effect his compensation theory. The calorigenic effect compensates for the thermostatic rise in heat production of the fasting animal.

Above the critical temperature of the fasting animal, the calorigenic effect of the food is independent of changes in environmental temperature. The excess heat of the fed animal is greater than that of the fasting animal. This means an extra burden in the fight against overheating. If this burden becomes significant, it affects the food intake. At a sufficiently high environmental

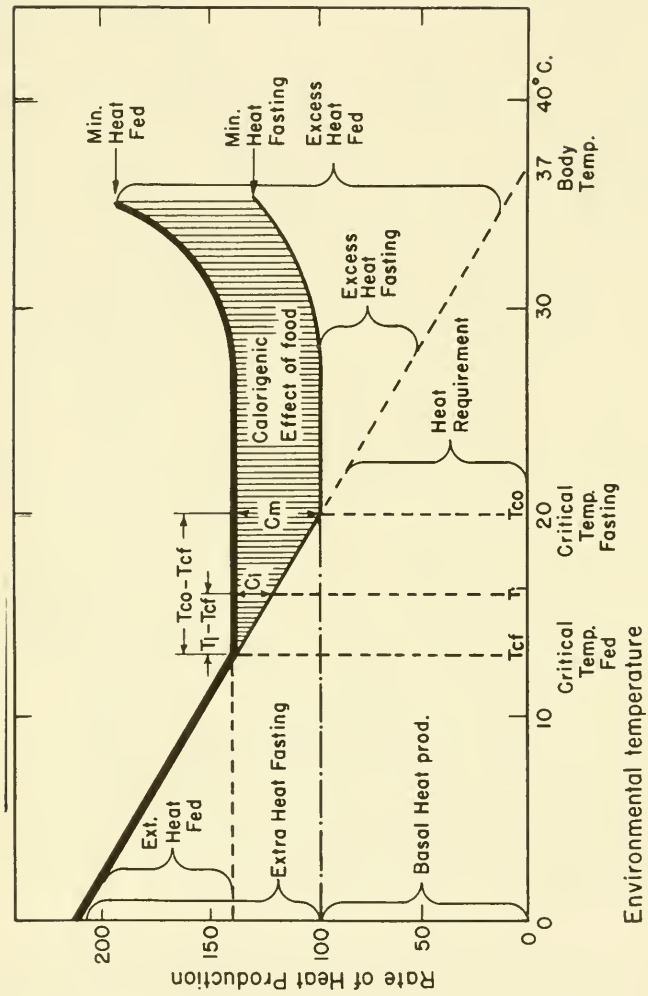


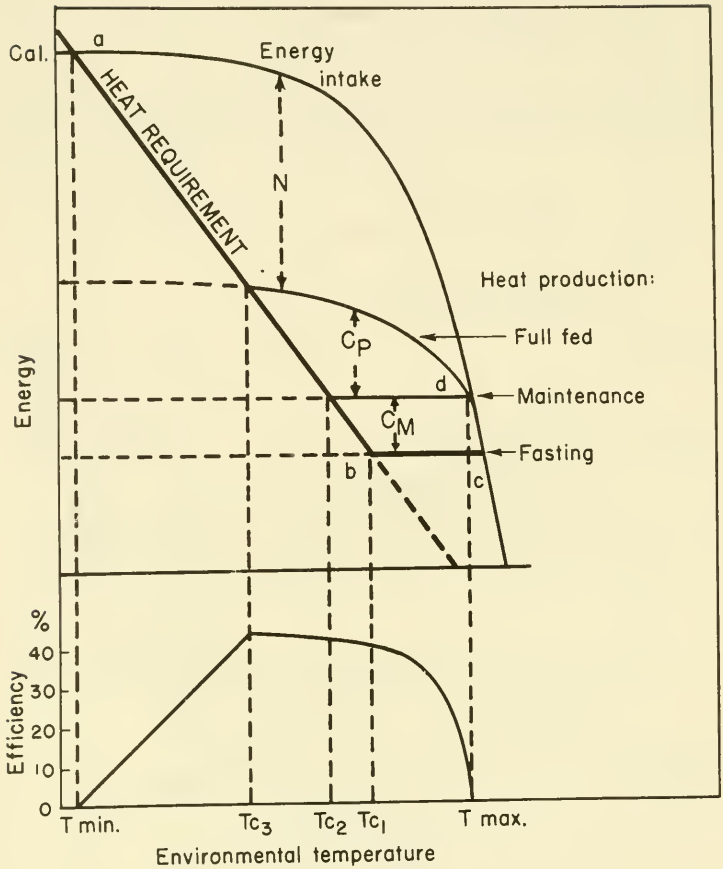
Figure 20. Metabolic rates of a fed animal at various environmental temperatures.

temperature , the animal may eat only enough for maintenance, as illustrated in Figure 21 (Kleiber and Dougherty, 1934).

This temperature (T max) is the highest environmental temperature for animal production. As the environmental temperature is decreased, the animal will eat more, and the net energy, appearing in the animal product, N, will rise. Below the critical temperature of the full fed animal, Tc_3, the heat production will be determined by the thermostatic heat requirement. Since the capacity for food intake is limited, whereas the heat requirement continues to increase with decreasing environmental temperature, less and less energy is available for production, and at the temperature, T_{min}, the maximum food intake of the animal provides just enough heat for maintaining the animal's body temperature. Below this temperature the animal will eat all it can and yet starve to death because it will have to burn up its own body substance in addition to all the food it can eat in order to maintain its body temperature. This situation may be less significant for practical purposes than the lack of food in a cold environment which calls for human action such as operation "Hay Lift". Between the low temperature, at which the animal eats a lot but needs most of the food for fuel for keeping warm, and a high temperature at which it loses appetite to such an extent that it burns up all it takes in for maintenance, there should be an optimal environmental temperature at which the efficiency of animal production is at a maximum. This is illustrated on the lower part of Figure 21.

An indication, though not too obvious, of such a temperature optimum has been obtained in respiration trials with lactating cows fed to capacity with alfalfa hay, beet pulp, and grain, and kept alternately for weekly periods at 7° C, 18° C, and 30° C (Kleiber, 1961). Total carbon and nitrogen balance was determined over a three day period during each week.

The results are shown in Figure 22. The decline in food intake at a high environmental temperature is most conspicuous. The milk production was little affected, but the loss of body substance was greater at the low and at the high temperature, than at 18° C where the net energy was at a maximum.



J. Gen. Physiol. 17: 703 (1934)

Figure 21. Scheme of influence of environmental temperature on food utilization.

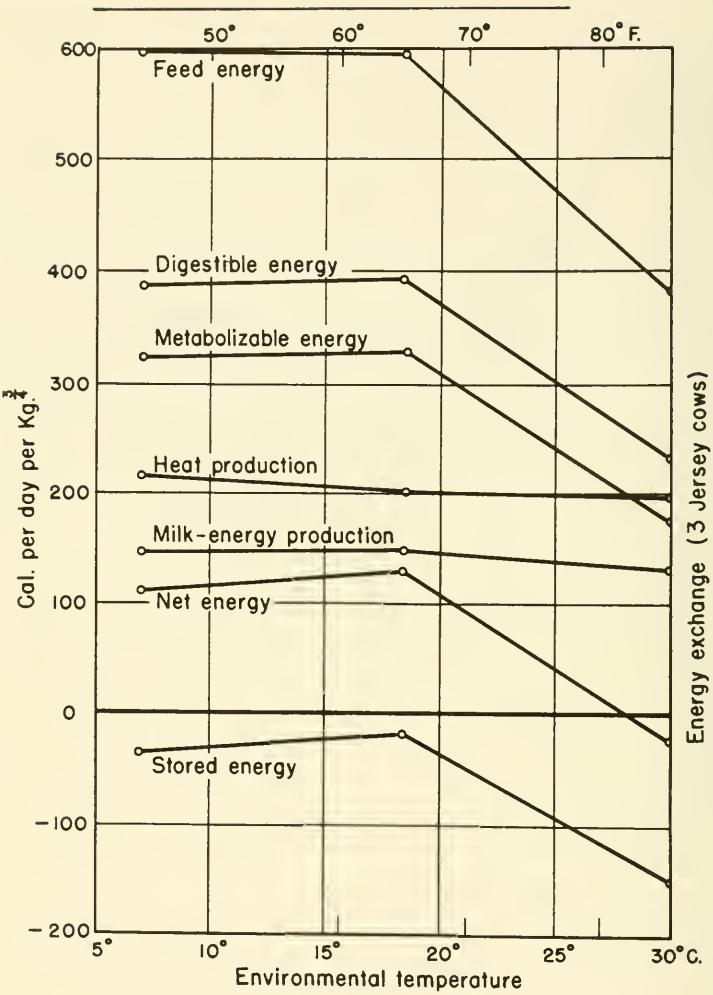


Figure 22. Food utilization of dairy cows at various environmental temperatures.

Figure 23 shows a hydraulic model as an analog of animal energy utilization in which the effect of cooling power is coordinated with other effects such as stimulus for milk production and for growth on the regulation of food intake. This was an early suggestion (Kleiber, 1936) of the two great regulators of food intake, a chemostatic principle now worked out especially convincingly by J. Mayer (1953) and the thermostatic principle represented especially by Strominger and Brobeck (1953).

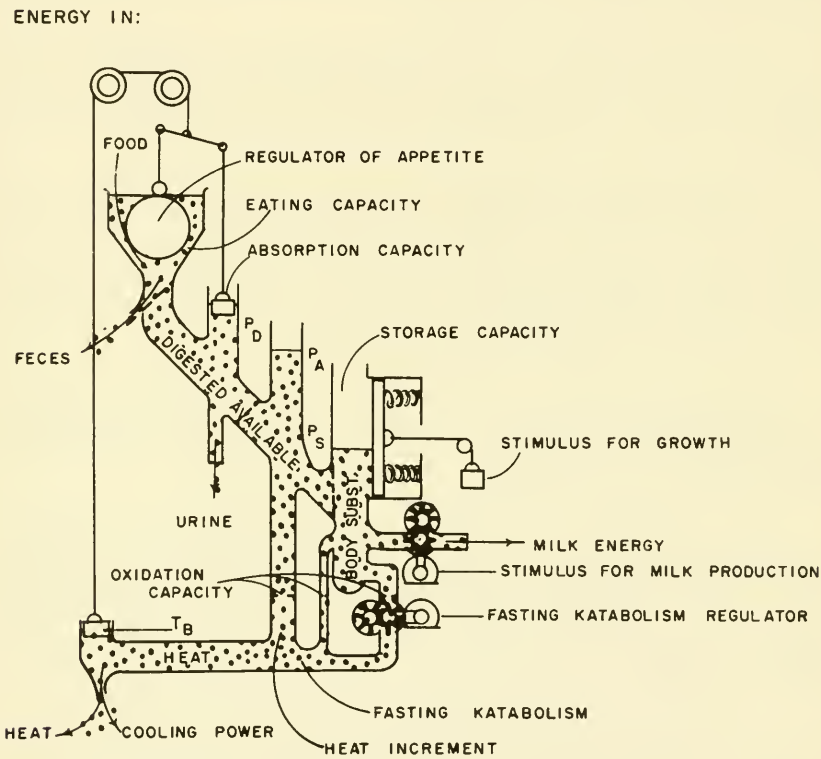


Figure 23. Scheme of energy-utilization.

SUMMARY

Domestication has not essentially changed the basic responses of animals to challenges from cold or hot environments.

A reaction to cold exposure, common to man and other homeotherms, is an increase in metabolic rate called chemical temperature regulation. A more economical response, known as insulative cooling, has been lost by civilized man, but operates in domestic animals and Australian aborigines.

In order to adapt to continued cold exposure, animals increase their insulation mainly by growing a thicker fur. Man has replaced this adaptation by technical control of the microclimate.

Overheating is prevented mainly by evaporative cooling at the body surface or in the respiratory system. Contrary to older belief, cattle evaporate more water from the skin than by respiration, even though respiratory frequency increases consistently with increase in environmental temperature.

Evaporation from a wet body surface in a hot environment is uneconomical because it allows an influx of heat from the environment to the surface.

The camel's fur maintains its outer surface dry and hot, minimizing the influx of heat to the skin which is kept cool by evaporation. Clipping of the fur increases the camel's water loss in a hot environment to a rate per unit area similar to that of a donkey.

Excessive but time-limited daily heat loads producing heat storage in the body can be endured better the larger the animal because heat load is proportional to body surface area and heat capacity is proportional to body weight. Increase in body temperature for given loads, therefore, is proportional to the reciprocal of the cube root of body weight.

Animal production increases metabolic rate and consequently the problem of overheating. The breeds of cattle which are best adapted to endure hot climates are usually low producers with relatively low rates of heat production.

LITERATURE CITED

1. Hoesslin, H. V. 1888. Ueber die ursache der scheinbscheinbaren Abhängigkeit des Umsatzes von der Grösse der Körperoberfläche. Arch. Physiol. 11:323-379.

2. Ittner, N. R. 1946. A progress report on livestock investigations in the Imperial Valley. College of Agr., Univ. of Calif., Davis. Table 1, p. 3.

3. Ittner, N. R., T. E. Bond, and C. F. Kelly. 1955. Methods of increasing beef production in hot climates. Cal. Exp. Sta. Bul. 761, Table 13.

4. Johnson, H. D., C. S. Cheng, and A. C. Ragsdale. 1958. Comparison of the effect of environmental temperature on rabbits and cattle. Missouri Res. Bul. 648:1-27.

5. Kibler, H. H. and S. Brody. 1952. Relative efficiency of surface evaporative, respiratory evaporative, and non-evaporative cooling in relation to heat production in Jersey, Holstein, Brown Swiss and Brahman cattle, 5° to 105° F. Missouri Res. Bul. 497:19.

6. Kibler, H. H. 1954. Influence of radiation intensity on evaporative cooling, heat production and cardiorespiratory activities in Jersey, Holstein and Brahman cows. Missouri Res. Bul. 574:20.

7. Kibler, H. H. and S. Brody. 1956. Influence of diurnal temperature cycles on heat production and cardio-respiratory activities in Holstein and Jersey cows. Missouri Res. Bul. 601:10.

8. Kibler, H. H. and R. G. Yeck. 1959. Vaporization rates and heat tolerance in growing Shorthorn, Brahman, and Santa Gertrudis calves raised at constant 50° and 80° F temperatures. Missouri Res. Bul. 701.

9. Kleiber, M. 1947. Body size and metabolic rate. Physiol. Rev. 27:538.

10. Kleiber, M. 1936. Problems involved in breeding for efficiency of food utilization. Am. Soc. Animal Prod. Proc. p. 247-258.

11. Kleiber, M. 1961. The Fire of Life, and introduction to animal energetics. Wiley and Sons, New York, p. 102.

12. Kleiber, M. and J. E. Dougherty. 1934. The influence of environmental temperature on the utilization of food energy in baby chicks. J. Gen. Physiol. 17:701-726.

13. Kleitman, N. 1951. When your temperature goes up. San Francisco Chronicle "This Week", March, p. 18-19.

14. Kleitman, N. , S. Titelbaum and P. Feievson. 1935. Diurnal variation in reaction time and its relation to body temperature. Am. J. Physiol. 113:82.

15. Lee, R. C. 1939. The rectal temperature of the normal rabbit. Am. J. Physiol. 125:521-529.

16. McDowell, R. E., C. A. Matthews, D. H. K. Lee and M. H. Fohrman. 1953. Repeatability of an experimental heat tolerance test and the influence of season. J. Animal Sci. 12:757-776.

17. Mayer, J. 1953. Genetic, traumatic and environmental factors in the etiology of obesity. Physiol. Rev. 33:472-508.

18. Richet, Ch. 1889. La Chaleur Animale. Felix Alcan, Paris, p.23.

19. Robinson, K. W. and D. H. K. Lee. 1942. Reaction of the Pig to Hot Atmospheres. Proc. Roy. Soc. Queensland 53:145-158.

20. Schmidt-Nielsen, K., B. Schmidt-Nielsen, S. A. Jarnum and T. R. Houpt. 1957. Body temperature of the camel and its relation to water economy. Am. J. Physiol. 188:103-122.

21. Scholander, P. F. 1955. Evolution of climatic adaptation in homeotherms. Evolution 9:15-20.

22. Scholander, P. F. 1958. Studies on man exposed to cold. Fed. Proc. 17:1054-1057.

23. Strominger, J. L. and J. R. Brobeck. 1953. A mechanism of regulation of food intake. Yale J. Biol. Med. 25:383.

DISCUSSION

EAGAN: There are three minor points I should like to make. First, Figure 1 showed that the rectal temperature of the rabbit decreased in response to a moderate decrease in environmental temperature. I know that this has been shown by some people, for instance by Carlson (1955).* but we have not seen this--not even in rabbits that were exposed to -25° C. There is no change in rectal temperature in mature animals exposed at -25° C for several hours (Eagan, 1961).**

Secondly, Burton presented a theory on why the body temperature is regulated at about 37° C. This theory is presented in the first chapter of Man in a Cold Environment (Burton and Edholm, 1955)*** to support the suggestion that the level of body temperature adopted by the homeotherms has something to do with the stability of temperature regulation. It is a matter of choosing a temperature which favors economy in physiological function over the widest range of environments.

KLEIBER: What is that theory?

EAGAN: I would refer the listeners to the original work cited above. Briefly, the regulated body temperature is that one from which a deviation will cause the change in heat production (Arrhenius' law) to be balanced by the change in heat loss (Newton's law of cooling), at the 25° C annual isotherm where homeothermic animals are believed to have originated.

*Carlson, L. D. 1955. Interrelationship of circulatory and metabolic factors. pp 13-51 in Ferrer, M. Irene, Ed., Cold injury (Trans. Third Conf.). Josiah Macy, Jr. Foundation, New York.

**Eagan, C. J. 1961. Reactive error in the measurement of rectal temperature in the cold. AAL TN 59-20, USAF Arctic Aeromed. Lab., APO 731, Seattle, Wash.

***Burton, A. C. and O. G. Edholm. 1955. Man in a cold environment. Edward Arnold (Publishers) Ltd., London.

The third point is that heat loss in the rabbit exposed to high temperatures is certainly accomplished through panting. I did some experiments wherein rabbits were exposed at 50° C (Eagan, 1961).* In spite of vigorous panting by each animal, rectal temperature rose steadily (after a transient slight decrease) and ear temperature ran between 1° C and 2° C higher than rectal temperature.

FOLK: Is there a histological difference in the skin of the Brahman cattle and the American domestic breeds? Are there sweat glands in any of the cattle?

KLEIBER: Apparently the histologists agree that there are sweat glands in both breeds.

WEST: I was interested in the caloric intake of the cows; you have quite a nice curve of caloric intake as temperature falls. Is this something that they just do without any forcing or do they just eat this much so they can produce milk or something?

KLEIBER: This was a theoretical, not an empirical curve. I was attempting to figure out what we have to look for.

WEST: I see, because I was wondering how you were able to get cows to do this. We are trying to do this with birds.

KLEIBER: It was just an arbitrary expression, that there must be some limit where the temperature is too high for food intake, and there must be some low temperature limit where the food intake must be increased. I drew a curve against these two limits.

WEST: In other words, you think of it as a curve, not as a straight line more or less paralleling the resting metabolism or heat requirement?

KLEIBER: Well, it could be a straight line, perhaps, but I do not see how.

*Eagan, C. J. 1961. Topical adaptation to cold in the rabbit ear. Fed. Proc. 20, No. 1, Part I:210.

WEST: It seems as though it were the same as maximal activity.

KLEIBER: The only reason I am not particularly happy with the straight line is that usually these things do not stop all at once.

WEST: I was thinking of the work that Dr. Jansky showed, where all the maximal rates were nearly parallel; this would be a similar situation.

KLEIBER: It may be that within a certain range it might be parallel with the other curve for resting metabolism, and then smooth out.

JOHANSEN: I found it very peculiar that you could apply "Arrhenius" so beautifully on the breathing rate of your cows. This is very much different from what I found in the armadillo. They increase their breathing rate suddenly; some marsupials do, too.

PROSSER: I would also question that Arrhenius plot, because you are plotting the breathing rate against external temperature. What does this mean? One would think if you are going to extrapolate to a chemically determined rhythm, you should do this against body temperature instead of environmental temperature.

KLEIBER: Well, the body temperature remains essentially constant; that is, within a small range.

PROSSER: In that case I am wondering what is the meaning of the Arrhenius coefficient.

KLEIBER: Here you embarrass me, because the meaning is completely unknown to me. It just happens to be so and the only thing which I can deduce is that the breathing rate of the cow is not the same function of environmental temperature as that of the armadillo.

HANNON: This brings up a question that we have wondered about for a long time. That is, why do small animals lose weight when you first put them in the cold? Is it due to a lack of appetite,

to a lack of capacity in their G. I. tract for the extra food that is needed, or is it due to some other factor? I would like to hear Dr. Hart's opinion on this eventually, but from the data that Dr. Vaughan and I have accumulated with diets of a high caloric density, it would seem that the capacity of the G. I. tract is not the limiting factor. You can give them plenty of calories but they will still not eat enough to gain weight at the same rate as their controls. Eventually, however, they will be able to increase their food consumption, so that they can gain weight. It has been my feeling that the reason it takes a while for the cold-exposed animal to acquire the capacity to utilize more food and thus to gain weight is that he is not initially able to metabolize food material at a fast enough rate to supply all of his energy needs. Until he builds up an enzyme capacity to do this, his growth is going to lag behind the control animal.

HART: I would be very surprised if you could, by overfeeding an animal, increase its capacity to oxidize the material. In other words, the appetite would be regulated by internal mechanisms adjusted to the oxidative capacity of the animal, and by pushing food in you are not going to change this.

HANNON: In our studies we compared the food consumption and growth of rats that were maintained on a high carbohydrate diet with rats that were maintained on a high fat diet. It was found that the group subsisting on carbohydrate consumed much greater bulk of food but the same number of calories as the group subsisting on fat.

Apparently their ability to utilize the calories was the limiting factor, not the ability to get calories into the digestive system.

HART: Did the carbohydrate or the fat diet have any particular advantage?

HANNON: Not as far as we could see.

KLEIBER: Yes, I think the limiting capacity is not the capacity of the volume. Adolph showed this when he diluted diets with clay and other kinds of inert matter. His rats took in and digested as

much energy with the bulky diet as with the other. This is in line with Jean Mayer's* idea of the regulation of the food intake, which is a hemostatic principle. It may have been slightly premature to suggest in my scheme of 1926** that these two regulators of food intake, namely the hemostatic principle (which is affected by concentrations of material in the blood stream) and the thermostatic principle, proposed by Brobeck according to which food intake is affected by the possibility of getting rid of heat.***

EAGAN: Limitation in oxidative capacity is not the only factor, for in rabbits which are moved to a cold (5° C) environment, food intake will often be less than normal for the first week or so, whereas a 50% to 100% increase would be required if body weight were to be maintained. It can hardly be thought that oxidative capacity is reduced when the animal is moved into the cold. An explanation must be sought for its change in behavior--a failure to eat sufficiently even though food is continuously available. This must represent an effect of cold stress upon the organism as a whole.

HANNON: I think this is possible in some animals, anyway. I do not think it appears in rats.

VAUGHAN: Rats will increase their food intake within a couple of days after you put them in the cold--the delay is probably partially due to the shock of putting them into the cold environment, but it is also probably due to just moving them into different surroundings. If they are accustomed to a certain diet, we have found, especially with synthetic diets, that they will increase their food intake very rapidly in the cold within a few days, e. g., up to 50% over their normal rate of intake.

*Mayer, J. 1953. Genetic traumatic and environmental factors in the etiology of obesity. Physiol. Rev. 33:472-508.

**Kleiber, M. 1926. Problems involved in breeding for efficiency of food utilization. Amer. Soc. Animal Prod. Proceed. pp 249.

***Kleiber, M. 1961. The Fire of Life. An Introduction to Animal Energetics. New York, Wiley and Sons, Inc. pp 282 ff.

***Brobeck, J. R. 1946. Regulation of Energy Exchange. Howell's Textbook of Physiology. (J. F. Fulton, ed.) Philadelphia, Saunders.