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# Environmental Physiology

## With Special Reference to Domestic Animals

## I. Physiological Backgrounds

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*Dairy Department, Missouri Agricultural Experiment Station and the Bureau of Plant Industry, Soils, and Agricultural Engineering United States Department of Agriculture Cooperating*

COLUMBIA, MISSOURI

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## With Special Reference to Domestic Animals

## I. Physiological Backgrounds

SAMUEL BRODY

This discussion[1] outlines several principles in climatic or environmental physiology and presents tentative plans for the cooperative[2] investigation on the influence of temperature factors on dairy cattle in the Psychroenergetic, or Climatic, Laboratory in Columbia, Missouri. As climate in relation to living things is a rather complex, often confusing, constellation of variables, it seems desirable, for purposes of simplification, to subdivide its discussion into sections.

### I. REASONS FOR UNDERTAKING THIS PROJECT

The major agricultural reason for undertaking this project is that the climatic conditions in America are different from those in Europe where our livestock evolved, and we have the problem of adapting, by biologic (breeding) and engineering (housing) methods, the "old country" animals to their "new country". Moreover, elimination of distance by modern transportation facilities places the selection of breeding stock on a global scale. Breeders think nothing of transporting by plane valuable animals thousands of miles, perhaps across oceans and mountains, often into climates quite unlike those in which the impressive production records were made. How do the changed climatic conditions affect the productivity, health, and longevity of the animals? How wise is it to import animals from different climatic regions?

A second, economic, reason is that the farmer wishes to know before he spends his money on farm shelters the most desirable and economical hot- and cold-weather shelter. Such knowledge must take for its foundation a study of the responses of animals to various environmental factors.

[1]Presented mostly at the "Psychroenergetic Laboratory" Open House Meeting at Columbia, Missouri, March 11, 1948. Portions of this address were also presented at: the February 1948 meeting of the Office of Naval Research, Bethesda, Md.; the September 1947 Conference of the American Council on Education, Gatlinburg, Tenn.; the June 1947 meeting of the American Home Economics Association, St. Louis, Mo.; the December 1946 meeting of the American Society of Agricultural Engineers, Chicago, Ill.

[2]A cooperative investigation between the University of Missouri and the United States Department of Agriculture, Bureau of Plant Industry, Soils and Agricultural Engineering (generally known as BPISAE). Credit is given to all the collaborators on this project, especially to Dean Trowbridge and Professor Ragsdale for inviting the author to prepare this paper and also to Dorothy M. Worstell (of the BPISAE) for her assistance in the preparation of the MS, including charting and typing. Acknowledgment is made to the Office of Naval Research for assistance in this project under Contract N7onr-292, Task Order IV.

A broader reason for undertaking this research is that our war and peace efforts are now global in scope, embracing weather extremes which strain man and machine to the limits of endurance, and there is need for general knowledge on the relations between organism and environment and need for developing methods for the control of the "private climates" of man and animal. The peace aspect of this problem relates to the fact that three-fourths of the human population live outside the temperate regions. Much of America has tropical climates during most of the year in which the superior European livestock do not thrive. There is need for gaining insight into the facts and mechanisms relating climate to productivity and to devise methods for overcoming environmental disadvantages.

Finally, physioclimatology, bioclimatology, or environmental physiology, a rather neglected subject, is worthy of cultivation in its own right to furnish an intellectual basis for understanding and controlling the world.

## II. RATIONALIZATION OF THIS RESEARCH

Many scientists like to formulate a rationalization, hypothesis, or theory, to guide and inspire them in their research. The following is the author's rationalization of the problem.

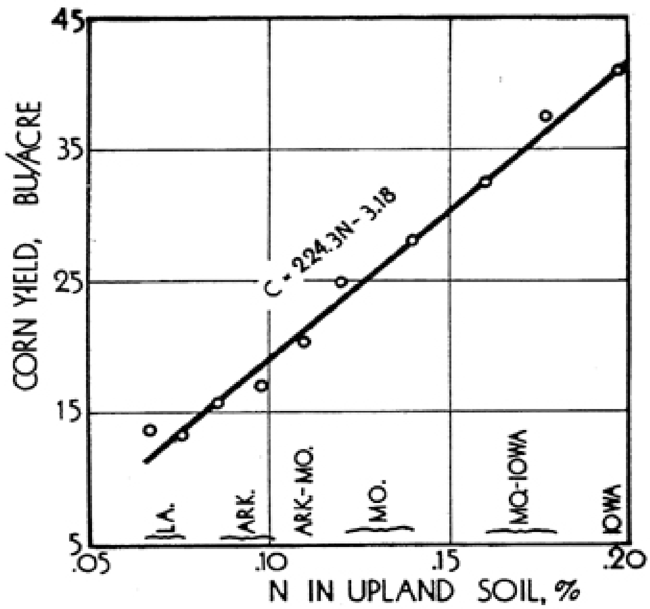


Fig. 1.—Corn yield increases with increasing latitude in the Mississippi Valley, from Louisiana to Iowa, presumably because of increasing soil fertility; the corn yield declines at the still higher latitudes (Minnesota and the Dakotas), despite increasing soil nitrogen, presumably because of declining temperature or reduced growing season. The corn yield is seen to increase by 22.4 bushels per acre for a soil nitrogen increase of 0.1 per cent. From data by Hans Jenny, Missouri Agriculture Experiment Station Research Bulletin 152, 1930.

1. One of its aspects concerns the apparent *chain reaction relating climate, successively, to soils, to crops, to animals and to man.* For instance, in the Mississippi Valley the gradient in temperature from Louisiana-Mississippi through Arkansas-Tennessee, Missouri-Kentucky, and Iowa-Illinois-Wisconsin is paralleled by a gradient in soil fertility, crop productivity, and general agricultural prosperity. Fig. 1 shows how the corn yield parallels the soil nitrogen level from Louisiana to Iowa. With further rise in latitude and nitrogen level the corn yield declines because the temperature falls below the optimal requirements of the corn plant. This generalization, with reference to the influence of climate on corn production by way of effect on plant nutrients, is substantiated by Figs. 2 to 4 which depict rising soil fertility with rising latitude and declining environmental temperature.

**Other Variables and Relationships.**—There are factors other than soil fertility that influence crop yield, for example, temperature, rainfall, and cultural methods; and there are factors other than climate that influence soil fertility, for example, geological history. The high corn production in the corn belt may be due—in part—to the rich soil brought there by the glaciers as well as the temperature and cultural factors; the high cotton, rice, and sugar cane yield in the Gulf Coast

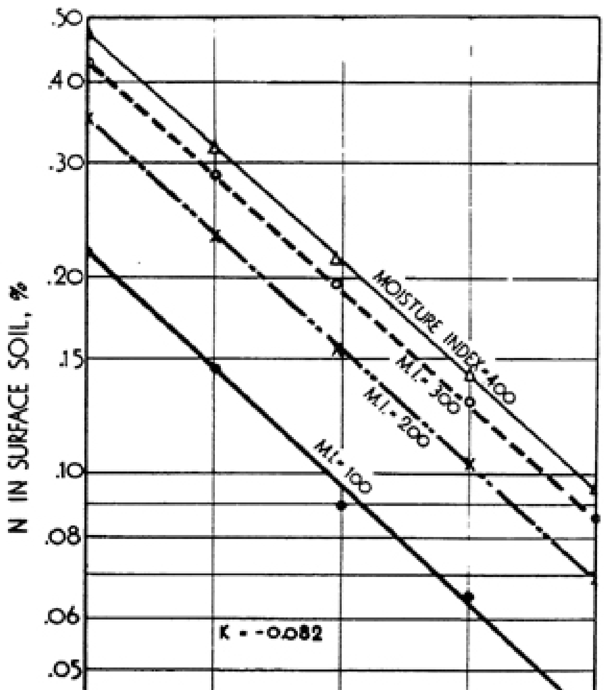


Fig. 2.—Nitrogen is a prime soil fertility factor and the slope, *k*, of the curve on this arithlog grid shows that soil nitrogen declines at the rate of 8.2 per cent (of itself) for a temperature increase of 1° C, which harmonizes with the van't Hoff-Arrhenius rule. Data on surface soil nitrogen (of the Great Plains Area) by Hans Jenny.

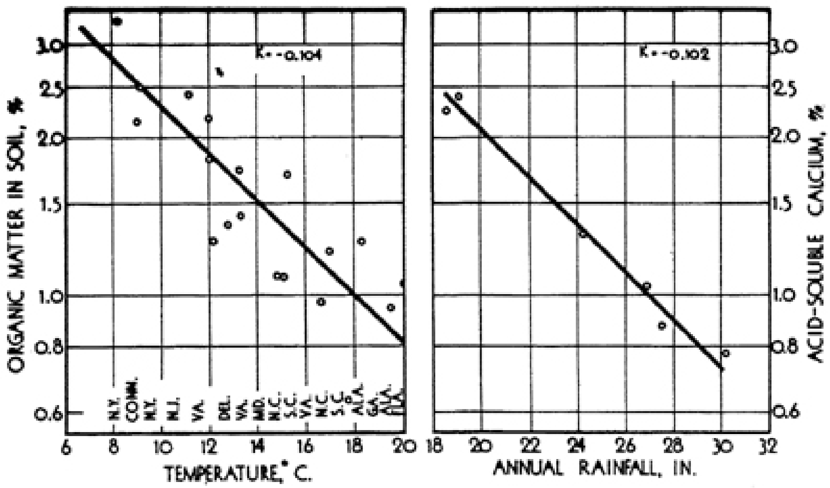


Fig. 3.—The organic matter in the soil (Glaciated Region, Coastal Plain, Piedmont Region) declines with rising temperature (declining latitude) from New York to Florida at the rate of 10.4 per cent per 1° rise in environmental temperature, which accords with the van't Hoff-Arrhenius rule. From data by Hans Jenny, Missouri Agricultural Experiment Station Research Bulletin 152, 1930. The chart on the right shows that the soil lime declines at 10.2 per cent per inch rise in rainfall. From data by D. F. Alway, "Soil Science," 1916.

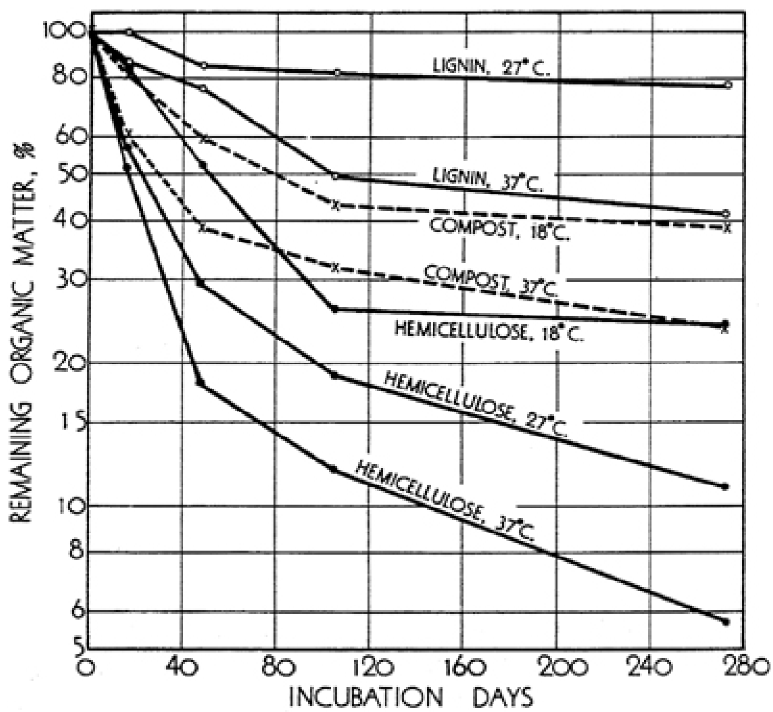


Fig. 4.—The influence of temperature on the decline (due mostly to microbiological decomposition) of three categories of organic matter under laboratory conditions. Plotted on an arithlog grid. Note especially the rate of disappearance of hemicellulose at 18°, 27° and 37° C. From data by S. A. Waksman and F. C. Gerresten, Ecology, *12*, 33, 1931.

Region may be due to its long growing season needed by these crops. Productivity is a function of many interrelated factors not easily generalized by one theory.

Soil is a mixture of decomposing rock and organic matter; the rates of its formation (from its parent materials), and of its loss (by micro-biological decomposition, oxidation, erosion, and leaching), increase with increasing temperature and rainfall. The resultant effect of the two opposing processes on soil fertility and crop production therefore follows a rising and declining course with increasing latitude or decreasing temperature. It is significant that the influence of temperature on the soil processes, within the limits shown in these charts, tends to follow the van't Hoff-Arrhenius equation, which states that the rates of chemical reactions tend to double for an increase in 10° C (k in Figs. 2 and 3). A generalization formulated on the basis of laboratory test tube experiments is here extended to the complex soil system, and therefore to plants, animals and the economic and social life of man.

There is also, within limits, a causal relation between soil fertility and nutritional value per unit weight of crop. For instance, K. C. Beeson reported that, depending on the soil composition, the calcium content of alfalfa ranged from 0.5 to 5.0 per cent and the iron content of cabbage from 1 to 10 parts per million. J. B. Orr reported that, depending on soil composition and fertilization, the calcium content in the dry matter of pasture grass ranged from 0.2 to 1.0 per cent (as CaO), phosphorus ($P_2O_5$) from 0.2 to 0.8 per cent, and protein from 6.6 to 17.7 per cent. The caloric value of the pasture grasses examined—about 2.65 kg-calories per gram dry matter—was approximately the same on all pastures. Gross caloric values do not always, however, indicate nutritional values, since the gross caloric value per unit weight of nutritionally unavailable lignin is the same as that of available starch or sugar, and hot climates seem to accelerate the rate of lignification. The protein content of plants seems to be more affected by soil fertility than the vitamin content, which is apparently related to sunshine rather than to soil fertility. In brief, the poorer the soil the poorer the crops in protein and minerals, although, depending on length of growing season and other climatic factors, they may produce great bulks of carbohydrates, such as cotton, rice, and sugar cane.

The yield and composition of the crop is reflected in the well-being and productivity of the animal and man that consume it. W. A. Albrecht of the Missouri Station reported that the growth efficiency and health of rabbits that were fed hay varied with the fertilizer applied to the soil on which the hay was grown. The nutritional anemias in the "salt sick" regions of Florida, Australia and New Zealand reflects iron, copper, and (for ruminants) cobalt deficiencies of their soils. Livestock malnutrition, in some parts of Minnesota and Texas, reflect soil phosphorous deficiency, and in Florida and Louisiana calcium deficiency. Thyroid abnormalities in parts of Switzerland, North and South America, Asia, Australia, and New Zealand reflect iodine deficiency. The correlation between soil mineral deficiencies and dietary mineral deficiencies in man and animals is substantiated by their prevention and cure by either feeding these minerals to the animals or by fertilizing the soil.

We thus have the chain reaction relating climate, successively, to soil, plant, domestic animal. and man, as illustrated in the Mississippi Valley in which the Missouri Agricultural Experiment Station is located. The associated gradient in general prosperity and cultural and technological levels is accentuated—and confused—by prevalence of disease-producing organisms; by historical factors, some of which may have been fortuitous while others, such as the over-specialized cotton type of farming, were brought about by climatic factors because of their suitability for producing abundant lignified types of carbohydrates; by physiological effects, such as reduction of thyroid activity in hot weather with consequent depression of the "rate of living", which means reducing the progressiveness characterizing the more stimulating cooler temperature regions.

General progressiveness undoubtedly tends to be conditioned by climate although we are confused by the multiplicity of involved factors and mechanisms. This confusion is further accentuated by the physician's and novelist's use of such semantic ambiguities as "tropical deterioration", "tropical neurasthenia", "tropical paradise", "tropics are places of pleasantly morbid putrefaction of body and soul", and so on. The tropics seem alternately to fascinate and to repel. We need the facts uncolored by fiction. And the facts are not easily ascertained in an area in which such a bewildering variety of biological and cultural factors (genetic, physiological, historical) are affected by such a confusing variety of changeable meteorological factors (temperature and sunlight with their seasonal and diurnal rhythms, barometric pressure, humidity, air movement, rainfall) and geological factors, especially the phase contributing to soil fertility.

2. Another aspect of this rationalization concerns the *chain reaction relating climate, successively, to the nervous system, to the endocrine system, to the enzyme system, to metabolic levels, to metabolic rates and, therefore, to the rates of all productive processes.*

This chain reaction may be illustrated by the *seasonal rhythms* in fur growth, energy metabolism, reproductive activity, including egg and milk production as illustrated in Figs. 5 to 7.

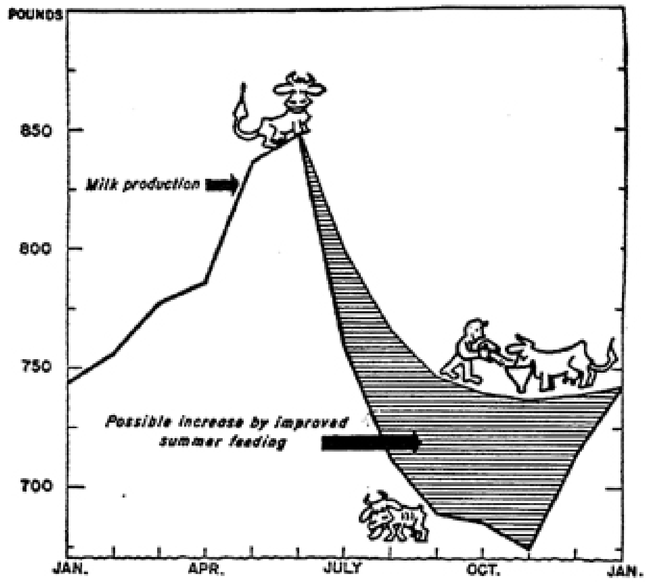


Fig. 5.—Milk yield declines during the late summer mostly as result of the high temperature but also in part because of the deterioration of the food supply, including the lignification of the herbage. Courtesy U. S. Department of Agriculture.

The seasonal reproductive rhythm is known to be under the control of the neuro-endocrine system which is affected by the seasonal meteorological rhythms, such as length of day and temperature; and seasonal reproductive rhythm is also influenced by food supply, which is, in turn, controlled by meteorological factors directly and by way of soil fertility. The effect of meteorological factors on animals is thus often by way of many consecutive-simultaneous, or chain, reactions, involving hormones, enzymes, and nutrients.

The effect of temperature on endocrine activity is illustrated quantitatively by the increased thyroid activity with decreasing environmental temperature. E. W. Dempsey and E. B. Astwood reported in 1943 that 100-gram rats produce about five times as much thyroxine at 1°C as at 35°C (9.5 $\mu$g vs 1.7 $\mu$g). C. W. Turner

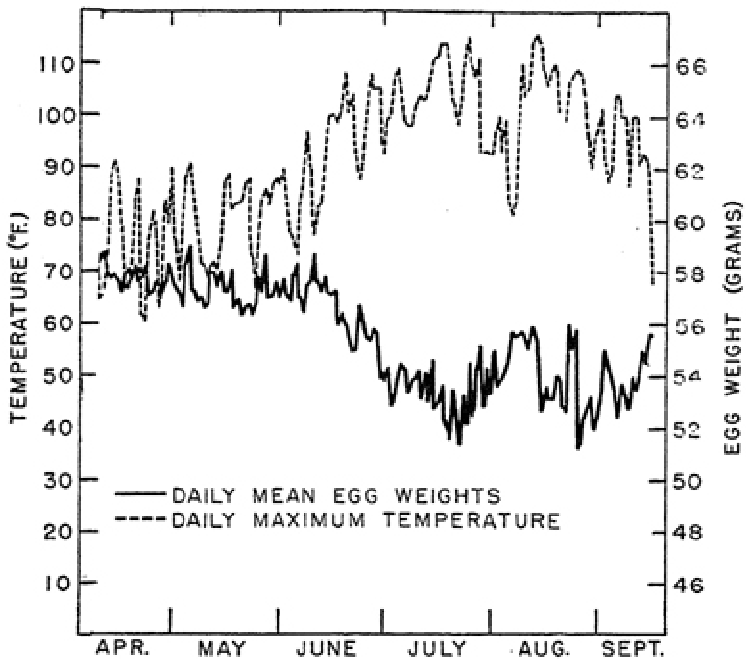


Fig. 6.—Environmental temperature and egg size. Courtesy D. C. Warren, J. Agr. Res., *59*, 443, 1939, and Poultry Sc., *19*, 67, 1940.

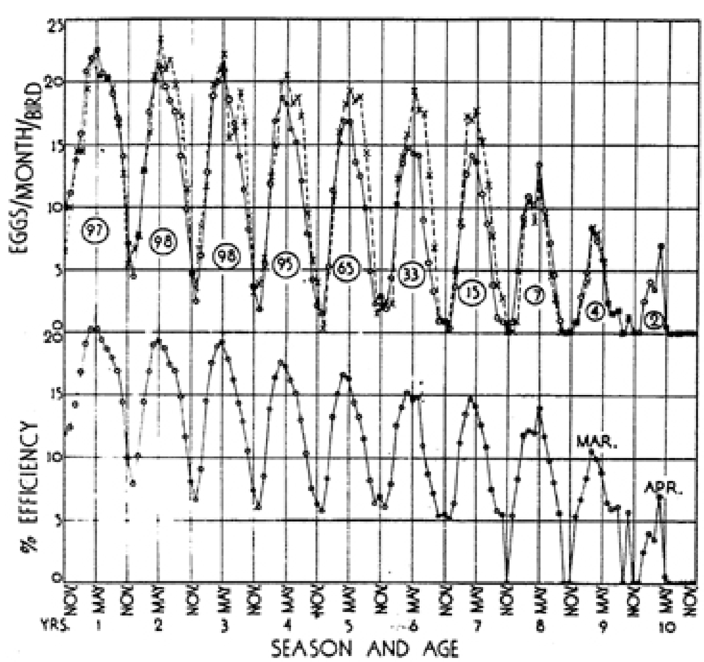


Fig. 7a.—Seasonal rhythms in egg production of chickens with increasing age (Brody, Kempster and Funk, Missouri Agricultural Experiment Station Research Bulletin 278, 1938). The x's represent the same seven birds that survived 9 years; the circles and corresponding numbers, the number that survived in successive years.

reported that domestic fowls produce over twice as much thyroxine in the Missouri winter as in summer and, as might be expected from the widespread metabolic effects of thyroxine, there was parallelism between thyroxine production and egg production. Thyroxine is also known to influence the rates of milk production and of growth and, indeed, of virtually all metabolic processes. In general, man and animals may not do as well in hot regions possibly because they tend to be hypothyroid. We thus have here an illustration of one endocrine mechanism, thyroid activity, through which the environment affects productive processes.

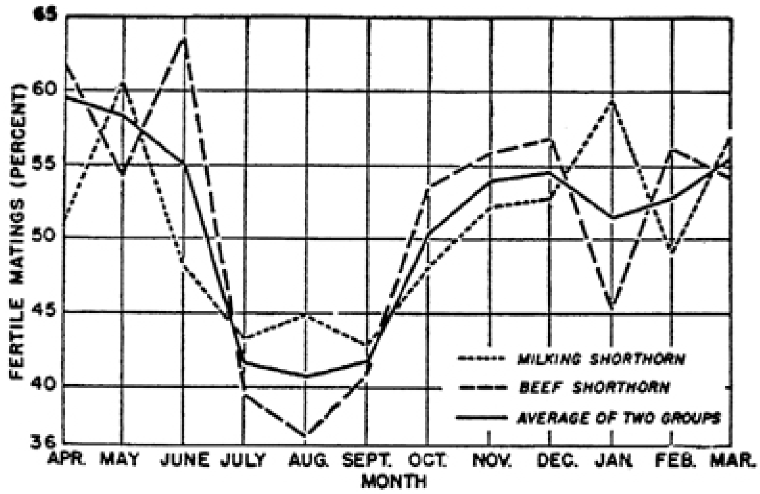


Fig. 7b.—Fertility in cattle as function of season (ratio of length of day to night), and/or environmental temperature. Courtesy R. W. Phillips, B. Knapp, Jr., L. C. Heemstra, and O. N. Eaton, Am. J. Vet. Res., *4*, 115, 1943.

Thyroid activity is, however, under the direct control of the pituitary so that temperature can control the thyroid activity only by way of the pituitary. The pituitary controls not only the thyroid but also most other endocrines. The pituitary activity must, then, be influenced by meteorological factors and so must all other glands that are under the influence of the pituitary. Climate, especially temperature and light, thus appears to control, by way of the pituitary, most endocrine activities.

There is evidence, illustrated by Cori on the regulative effects of hormones on the enzyme hexokinase, that hormones regulate the activities of enzymes. But enzymes regulate the metabolic rates and hence the levels of the metabolites. Therefore, meteorological or climatic factors exert regulative effects on the levels of hormones, enzymes, metabolites, metabolic rates, and, consequently, on the entire physiology, chemistry, and economy of the animal, including its agriculturally productive processes. We thus have a species of chain reaction relating climate, by way of the neuro-endocrine-enzyme system, to most agriculturally productive processes. The aim of our Climatic Project is to investigate some of these processes.

The depressing effects of hot weather on bodily activities, a species of hotweather laziness, in animals—and perhaps in man—is, homeostatically viewed, a biological mechanism for preventing overheating the body. But this "laziness" affects food supply, the cultural tone of the region, its habits and outlook on life, that is, its psychology, philosophy and religion, its politics, mores and morals, and indeed the entire course of its history. Parts of this could, perhaps, be changed by discovering the involved regulating mechanisms and by developing methods for the control of the "private climates" on man, his animals and perhaps plants, and thus, to a degree, emancipate man from climatic restraints and change his mode of life.

## III. WEATHER, CLIMATE, AND THEIR CONSTITUENT METEOROLOGICAL FACTORS

The meteorological components of *weather* include air temperature; air humidity; air movement (wind); radiations from the sun, earth, and other objects; barometric pressure; rainfall; and, very importantly, quantitative *changeability* in these factors because change itself stimulates (or depresses) the body, its nerves, glands, and temperature-regulating mechanisms.

Missouri, for example, has a changeable and therefore stimulating weather. This April day the sun is shining brightly, the breeze is gentle, the temperature is in the seventies; yesterday it was cloudy, windy, chilly, the temperature was in the forties. Clouds are always drifting in and out, smiling or frowning, covering or exposing the face of the sun and moon and thereby changing the mood of man, of the birds in the trees and of the cattle in the fields. The weather is almost certain to be different tomorrow. This is *weather*.

In addition, we have weather *rhythms*: spring, summer, autumn, winter, and all the transitional shades.

The long-range regional weather pattern is *climate* (Greek *klima*, meaning slope or tilt). The polar axis of the earth tilts some 23½ degrees from the perpendicular. The seasonal weather rhythm in a given region, therefore, depends on its position on the earth (latitude), its inclination to the vertical sun's rays, and to the rotating movement of the earth around the sun.

But climate also depends on topography, distribution of vegetation, especially forests, and of large bodies of water (71 per cent of the earth's surface is covered with water, six miles deep in places). Water distribution profoundly influences climate because water is very mobile and has remarkable thermostatic properties. Water has the highest specific heat of any substance (1.0—it takes one kg.-calorie, about 4 Btu, to heat one kg. of water 1° C—as contrasted to 0.015 for soil or 0.241 for air); it has a very high heat of fusion (it takes 80 Calories, about 300 Btu, to melt or freeze one kilogram water); it has an especially high latent heat of vaporization (it takes 580 Calories[1], over 2300 Btu[1], to vaporize one kilogram, or 2.2 pounds, of moisture from the skin). Water is an excellent heat conductor (about 27 times that of air). Moreover, while water vapor (up to 5 per cent in warm humid air) is transparent to light, it traps and holds about 20,000 times as much heat as air. The remarkable mobility (of the vapor and liquid phases) and thermostatic properties of water make it a basic stabilizing factor of world climate, and of body temperature because water is the medium in which the body machinery functions (over three-fourths of the body weight is water). Water is a prime *physical* factor in regulating the weather and climate of the world and a prime *physiological* factor in regulating the internal environment, especially temperature, of the body.

## IV. HEAT PRODUCTION AND HEAT LOSSES BY ANIMALS

Animals, even when non-productive and nonactive, have a huge "maintenance cost" to supply the energy for such obvious processes as circulation, respiration, excretion, muscle tension, and for many other processes not so obvious (Ref. 1, pp. 1, 4, 40, 98, 352). The maintenance energy expense is eventually given off as heat.

The heat thus produced may be measured by the rate of oxygen consumption since, normally, all energy in higher animals is derived from oxidation of body fuels. In this way it was observed that non-lactating, resting, dairy cows produce heat at the rate of 400 to 500 Calories per hour and about double this amount when lactating (Fig. 8). Resting men were similarly observed to produce heat at the rate of 75 to 100 Calories per hour and estimated to produce heat about 100-fold rest at peak effort (such as in a 100-yard sprint). Horses were similarly estimated to produce heat, when engaged in peak effort (4- to 11-second) pulling contests, at rates of about 100-fold that expended at rest (Ref. 1, pp. 910-15). Even food consumption—a necessary prerequisite for productive processes—increases heat production (Figs. 9 and 10).

This heat must be dissipated as soon as it is produced, else the body temperature rises above the normal level for the species, which warm-blooded animals cannot endure. A rise in body temperature

[1]A kg.-calorie, or Calorie, is the heat required to raise the temperature of one kilogram water 1°C at 15°C: a Btu is the heat required to raise the temperature of one pound water 1°F at 60°F. One Calorie, therefore, equals 3.968 Btu and one Btu equals 0.252 Calorie.

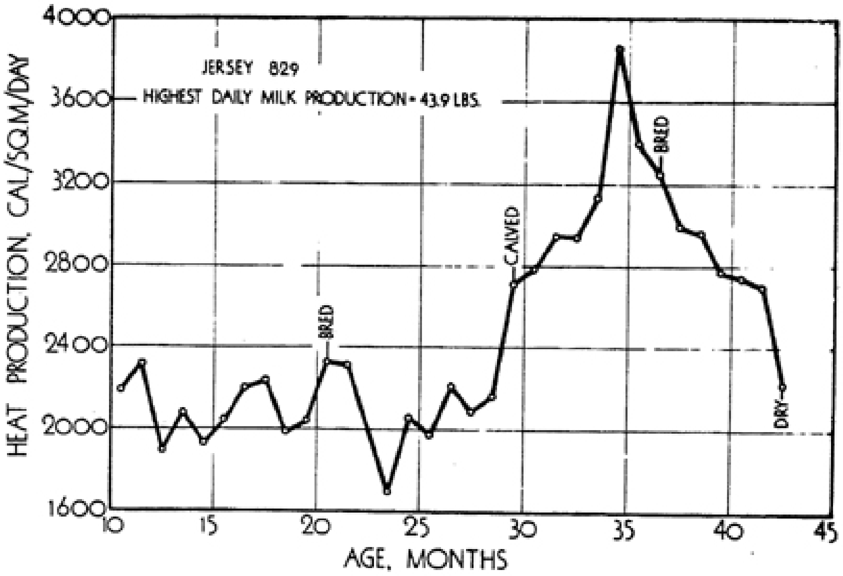


Fig. 8.—Heavily milking dairy cows produce about twice as much heat as dry cows; hence, the depression of milk production in hot weather by various homeothermic mechanisms so as to avoid overheating the animal.

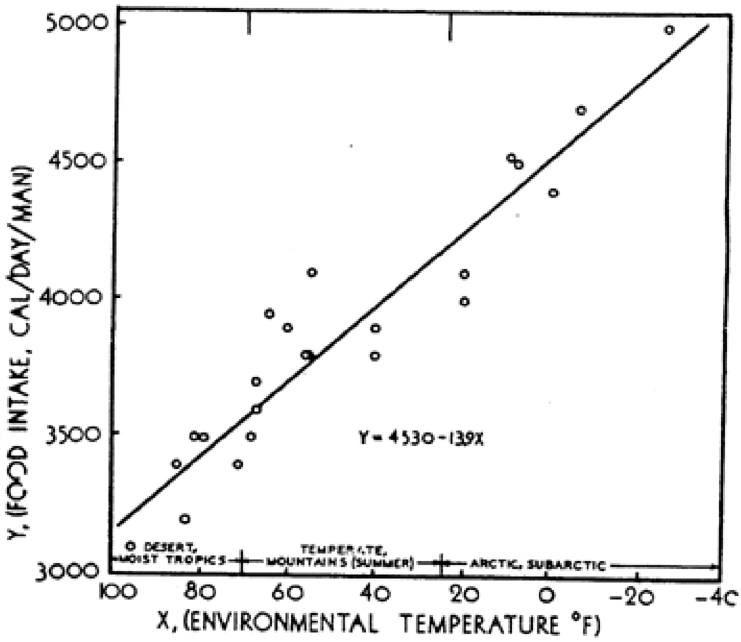


Fig. 9.—Increasing cold increases food consumption (American Army experience) with decreasing environmental temperature. (Protein supplied 11 to 13 per cent of the calories; fat, 33 to 43 per cent; carbohydrates, 44 to 54 per cent.) Since only about 400 Calories of the difference in food intake can be explained by the known changes in basal metabolic rate, this difference is probably due in large part to the greater amount of heat required to warm and humidify the inspired air. The equation (by us) is given on the curve by R. E. Johnson and R. M. Marks, Science, 105, 378, 1947.

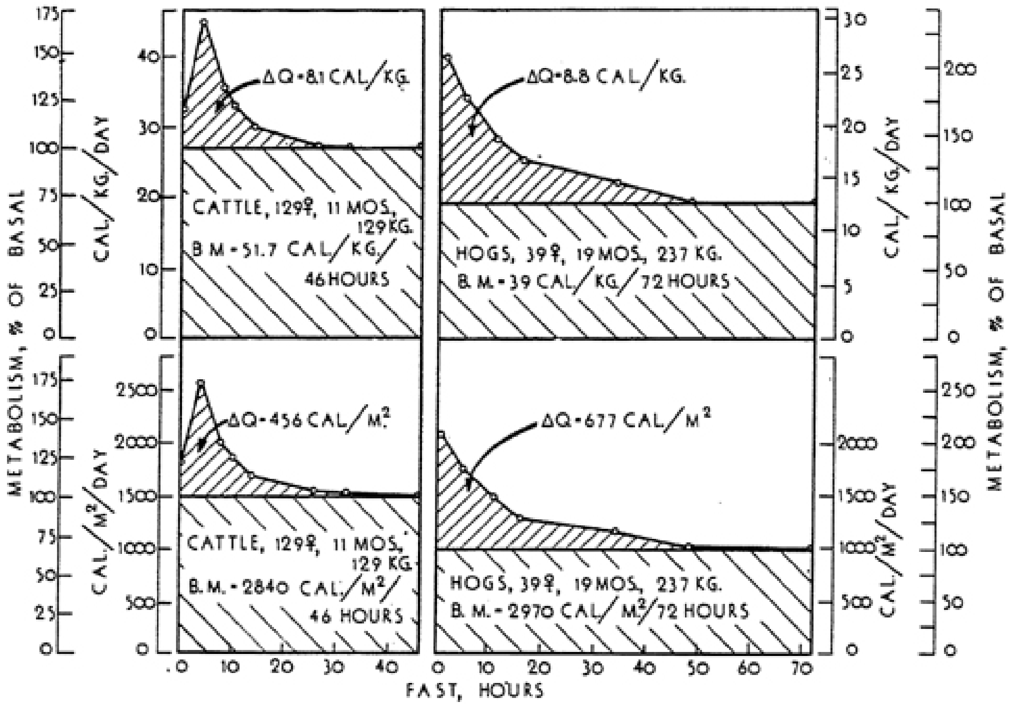


Fig. 10.—The heat increment of feeding in farm livestock (useful for warmth in cold weather but unpleasantly heating in hot weather); hence the reduction of feed consumption (and therefore reduction in productivity) in hot weather.

by only 8°F above normal is often quickly fatal, and the efficiency of the body machine deteriorates rapidly even with slight increases in body temperature.

When the environmental temperature is considerably below that of the body, the rate of heat loss in standing animals is mostly by *radiation* and *convection,* which may, together, be estimated with the aid of Newton's Law of cooling. This law may be written in several forms, such as

$$q = kA\ (t_1 - t_2)$$

in which $q$ is the rate of heat flow between the body surface and the environment; $A$ is the surface area of the body; $t_1$ and $t_2$ are, respectively, the temperature of the body surface and of the environment; $k$ is the coefficient of heat transfer defined by the equation and determined experimentally; its numerical value depending on the units employed.

Newton's Law of cooling indicates that the larger the surface area of a given body the greater the rate of heat transfer. The same holds for heat transfer by vaporization, convection, conduction and radiation. Since, from geometrical considerations, the larger the body the smaller the surface area *per unit volume* (or per unit weight), heat dissipation becomes more difficult as the body size of the animal increases. Conversely in hot regions, where heat dissipation is difficult, the adaptational evolutionary trend must be for the body to be small and lean giving it a large surface per unit volume, so as to have the largest possible rate of heat dissipation (Fig. 11). Pre-

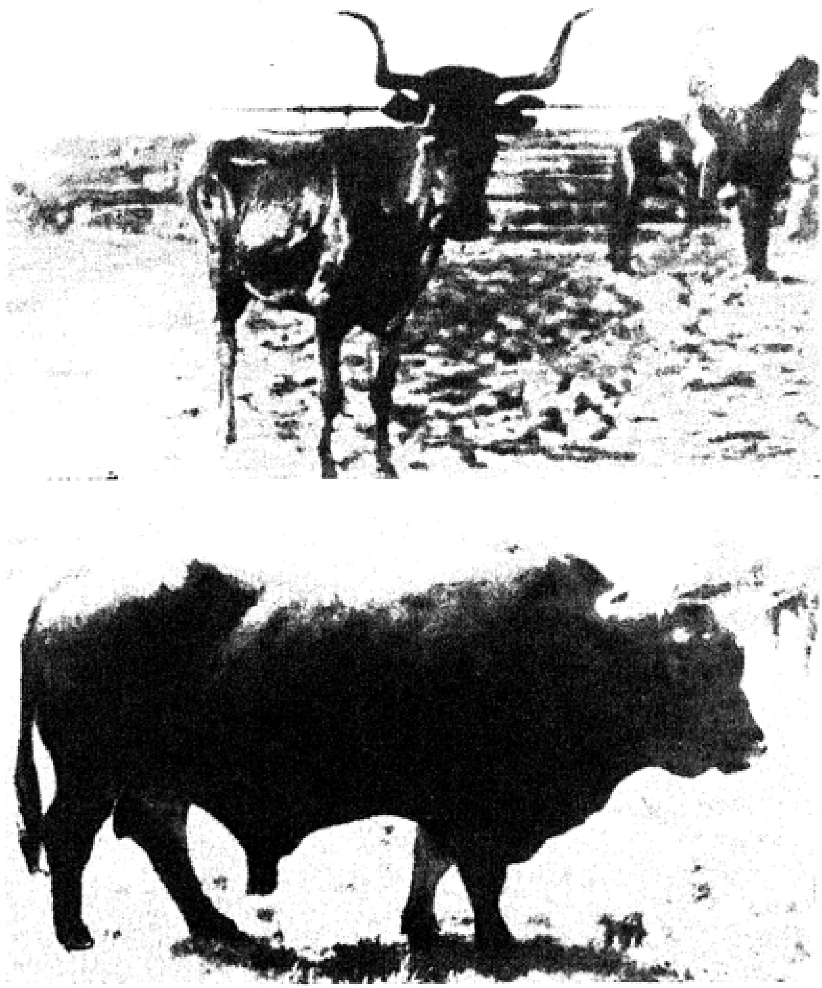

Fig. 11.—Evolution of body size and climate. The large, fleshy, cattle (*small* surface area per unit weight) evolved in cool England; the small, lean cattle (*large* surface area per unit weight) evolved in warm Spain and South America. Courtesy of Dr. Ralph W. Phillips (see Reference 2), from photos by Robert J. Kleberg, Jr., who used these animals for developing the Santa Gertrudis beef cattle of the King Ranch, Southern Texas.

liminary observation in our Climatic Laboratory indicate that smaller cows stand high temperatures better than larger ones. There are, of course, factors other than temperature involved in body size determination, but it is probable that other conditions being equal, animals tend to be smaller and leaner in hot than in moderately cool regions where our best and largest breeds of cattle evolved.

Newton's law of cooling was formulated for non-living bodies. But warm-blooded animals have uniquely organismic or homeothermic methods of heat dissipation, the most important of which is moisture vaporization from the respiratory tract and skin. The rate of heat dissipation by *vaporization* is dependent on: 1) the surface area of the animal; 2) difference in vapor pressure between surface and of surrounding air (humidity); 3) rate of air movement which removes the humid air from the surface; 4) extent of respiratory activity—amount of air exhaled per unit time—since the exhaled air is nearly saturated with moisture—and absolute amount of moisture in the inhaled air (as contrasted to relative humidity).

The rate of heat dissipation by *convection*, that is hot air near the skin replaced by cooler air which is in turn heated and moved away, is also proportional to the surface area of the animal, as indicated by the equation

$$C = kA\sqrt{v}\ (t_1 - t_2)$$

in which $C$ is the convection rate; $A$, surface area; $v$, velocity of air; $t_1$ and $t_2$ are, respectively, the temperatures of the body surface and environment; $k$ is the "unit convection conductance" or "film coefficient". The convection rate is, of course, accelerated by breeze, that is, by increasing the air velocity, $v$. But the convection (cooling) rate is increased only by the square root, or the 0.5 power, of the velocity; so that increasing the velocity, $v$, by 100 per cent increases the convection rate by only 50 per cent (41 per cent computed by the arithmetic method).

The rate of heat dissipation by *conduction*, that is, by physical contact, as for example, when an animal lies on a cold floor, is also proportional to the area through which the heat flows at right angles and to the temperature gradient (Fourier's Law).

The physiological feature of heat transfer from the body by conduction is that still air has an extremely low conductivity and that hair (especially the fur-like downy kind), and feathers (especially eiderdown), and also wool garments contain much air and are, therefore, excellent non-conductors or insulators. Fat (or blubber in whales) is also non-conducting. Hence the evolution of long downy hair in species evolved in cold regions (Fig. 12a), and the almost hairless skin of species evolved in hot regions (Fig. 12b), and also the difference in the amount of subcutaneous fat (including blubber in some marine animals) in cold and hot environments. J. C. Bonsma (*Farming in South Africa,* Feb. 1943) contrasted the 505 gm winter hair coats in Shorthorn heifers with 129-gm winter hair coats in Afrikander heifers of equal weight (600 lbs.); or 303-gm summer

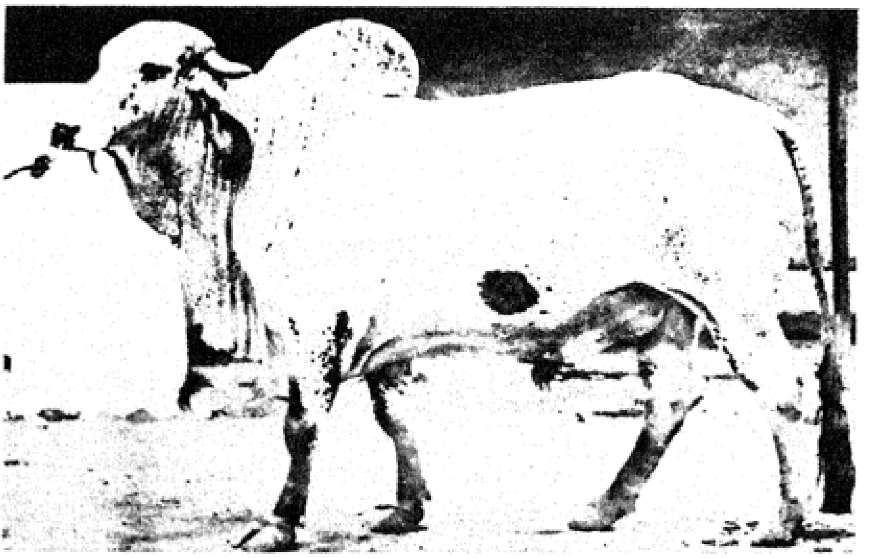

Fig. 12.—Contrasting adaptation of cattle. Fig. 12a (courtesy of Dr. Ralph W. Phillips, see Ref. 2) shows the hairy Yak type of cattle evolved in the cold, windy, high altitudes of Central Asia. Fig. 12b (courtesy F. Ware, Misc. Bull. 54, Imp. Council Agric. Res. New Delhi, 1942) shows the almost hairless Brahman or Zebu type of cattle evolved in hot India, characterized by enormous heat radiating surfaces (dewlap, sheath, navel flap) and sweating ability.

hair in the Shorthorn and 30-gm summer hair in the Afrikander heifers (see also Ref. 2).

The lower the environmental temperature and the longer the protective hair coat, the greater the temperature difference between the skin surfaces and of the hair coat, that is, the greater the insulating capacity of the hair. This was fully confirmed by the preliminary observations in our Climatic Laboratory.

The rate of heat loss (or gain) by *radiation* is also proportional to the surface area of the animal but modified by a "configurational factor" (Lambert's Law) since there is no heat loss by radiation between surfaces facing each other. In man, this modified *profile* surface area, or "Bohnenkamp surface", is 80 per cent to 85 per cent of the anatomical surface area.

The computation of the profile surface area is complicated when observing groups of adjoining animals as in our climatic chamber where six cows are stanchioned in a row. The end cows are obviously cooler than the other cows if the wall temperature is below the cow skin temperature. If the wall is below 94° F, one side of the end cow radiates heat to the wall whereas both sides of the other cows face the surfaces of the neighboring cows of the same temperature and so can not lose heat by radiation from the side. There may, however, be some compensatory convective cooling in the middle cows. The rate of heat dissipation should probably, in such case, be computed with the aid of Newton's Law of cooling, which includes heat loss by both, convection and radiation.

When discussing heat loss by *radiation* within a building, it should be remembered that "environmental temperature" means not ambient *air* temperature but *wall surface* temperature, including adjoining animal *surface* temperatures, since heat loss (or gain) by radiation is not to (or from) the *air* but solid surfaces.

The heat loss by radiation from the animal body is given by the expression

$$A \sigma (e_1 T_1^4 - e_2 T_2^4),$$

in which A is the effective, or profile, surface area of the animal; $T_1^4$ and $T_2^4$ the fourth powers, respectively, of the absolute temperatures of the surfaces of the animal and of the surrounding objects; $\sigma$ is the proportionality factor (dimensional constant in the Stefan-Boltzman Law which states that the emissive power is proportional to the fourth power of the absolute temperature); e is the emissivity, which is virtually one or perhaps slightly lower, 0.95, for the human or animal skin as explained below.

**Significance of Radiation:** The sun is, of course, the source of our energy, including the energy of photochemical reactions in the production of our food crops, and of the warmth of the earth. The sun transfers its energy by radiation. Radiation is also a very important method in heat loss from the animal to cooler objects and heat gain by the animal from warmer objects.

Like a fire, the sun radiates with the speed of light its energy in straight lines by electromagnetic waves of various lengths. Radiant energy does not heat the air directly, but by heating solid surfaces such as soil, water, buildings, trees, clouds, animals etc., where the radiant energy is changed to thermal energy, which, in turn, heats the air by conduction and convection; also solid objects are heated by reflected radiation.

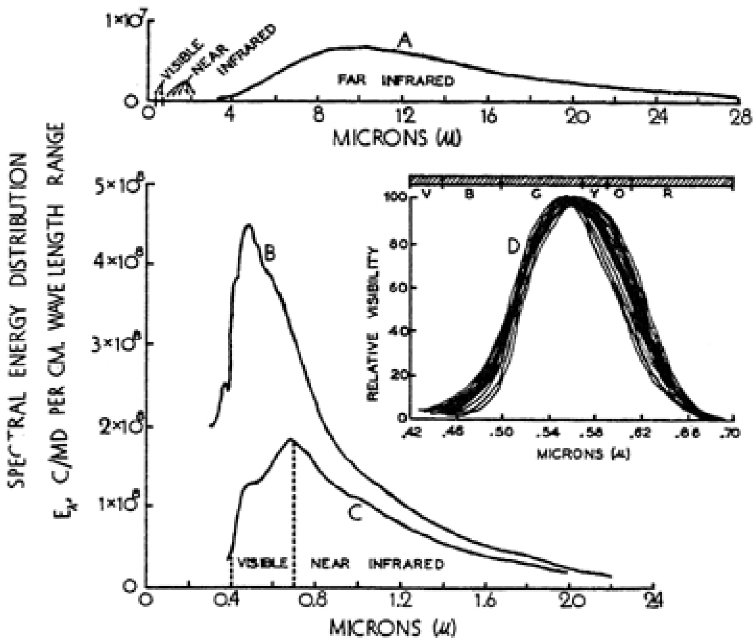


Fig. 13.—The insert (Curve D) shows the light wave lengths in the *visible* spectrum (from Coblentz and Emerson, Bull. Bureau Standards, *14*, 167, 1918). Curves A, B, and C are presented by courtesy of A. D. Moore in a book manuscript on "Comparative Animal Energy". Curve A represents Far infrared radiation at 27°C and includes the energy interchange between animal and ground, grass, trees, water, snow, etc. But if the solar radiation strikes the animal, it is mostly in the visible and in the Near infrared spectrum, 0.4 to 2$\mu$; Curve B, solar radiation before entering atmosphere; Curve C, transmitted solar radiation (normal incidence) for a clear sky, with the sun at 70.7° from zenith when the atmosphere path length is 3 atmospheres. C/MD represents kg.-cal. per square meter per day.

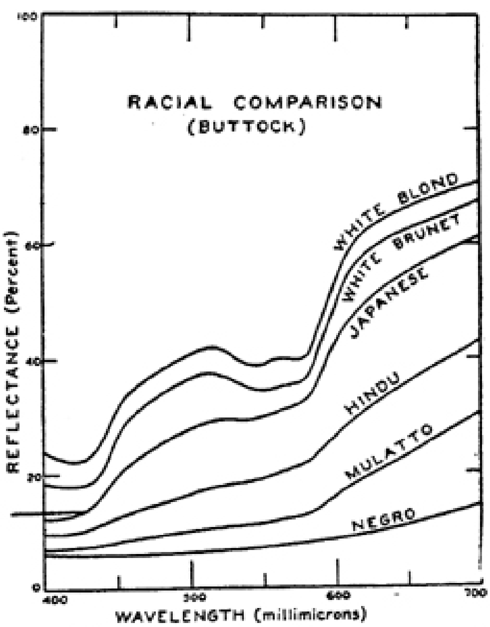


Fig. 14.—Percentages of light reflected between wave lengths 0.4 and 0.7 microns, from the buttocks of males of different "color". See the insert in Fig. 13 for the color of the light of each wave length. Courtesy E. A. Edwards and S. Q. Duntley, Am. J. Anat., *65*, 1, 1939.

If a body does not reflect or transmit, but absorbs 100 per cent of the incident radiant energy from warmer objects, or radiates 100 per cent of its energy to cooler objects, it is called a *perfect blackbody*, or simply "blackbody". A blackbody is thus a perfect emitter or absorber of radiant energy. *Emissivity* (or absorptivity) is the ratio of the rate of emission (or absorption) of radiant energy per unit area by the given body to the rate of emission (or absorption) from a blackbody at the same temperature. (At thermal equilibrium the emissivity and absorptivity are the same—this is Kirchoff's Law.) *Reflectivity* is the ratio of the rate of reflection of radiant energy from the given surface to the rate of incidence of radiant energy upon it. The value of each, reflectivity and absorptivity, is less than unity and the sum of these two is unity. Total emissivity refers to radiation of all wave lengths, and monochromatic emissivity to radiation of a particular wave length.

The solar spectrum (Fig. 13) ranges from short ultraviolet waves, 0.1 to $0.4\mu$ in length (bactericidal, injurious to nerve and skin, vitamin D forming), through the visible spectrum, 0.4 to $0.7\mu$ long; to the Near infrared, 0.7 to $2\mu$ (temperature of body near 1000° F). Very little of the solar radiations that reach the earth are above $2\mu$. Bodies having a temperature below 900° F (no visible glow), such as animals, plants, clouds, soil, houses, etc. radiate in the Far infrared region, from 2 to $100\mu$. According to J. D. Hardy and D. F. Du Bois (J. Nutr., *15*, 464, 1938), human body radiates its heat in the 5 to $20\mu$ region, with a summit at about $9\mu$; and the human skin, white or black, is (within 1 to 2 per cent) a perfect blackbody radiator or emitter. This means that the skin absorbs practically all the infrared radiation (*invisible*, in the 5 to $20\mu$ spectral region) from bodies which have a higher temperature than itself, regardless of skin color and emits to bodies which have a lower temperature than itself. The situation is quite different with regards to the *visible* spectrum, wave lengths 0.4 to $0.7\mu$ (Fig. 13). The relative amounts of the *visible* energy absorbed or reflected from the skin or its covering (clothing, fur, feather) depend on the color and nature of the surface. E. A. Edwards and S. Q. Duntley reported (Am. J. Anat. *65*, 1, 1939) that the reflectance of visible radiant energy, at wave length $0.7\mu$, is about 15 per cent from Negro skin, 30 per cent from Mulatto skin, 50 per cent from the East Indian skin, 60 per cent from brunet skin, and 65 per cent from blond skin (Fig. 14). C. J. Martin (Lancet, 1930) reported that a blond absorbs 57 per cent, brunet 65 per cent, East Indian 78 per cent, Negro 84 per cent of the London summer-noon daylight energy. (See also H. F. Blum, Physiol. Rev., *25*, 483,1945.)

J. C. Bonsma reported (l. c.) on the basis of measurements with a "Weston Model 603 illumination meter" that the percentage of sunlight reflected from the skin of white Afrikander cattle is about four times that from black Aberdeen Angus cattle, that the percentage of sunlight reflected from very light grey fawn Jersey cattle is about three times that from dark coffee colored Jerseys; and that if the *skin* is dark, the lighter the *coat* color the greater the percentage of reflected light and therefore better adapted to tropical and sub-tropical conditions. (See also A. O. Rhoad, Proc. Am. Soc. Animal Production, p. 291, 1940.)

## V. BODY-TEMPERATURE REGULATION, AIR-CONDITIONING, AND RELATED PROBLEMS

This subject covers a huge territory but only a limited area can be considered.

1. *Physical vs physiological temperature*: While the dry-bulb thermometer indicates air temperature only, the animal body reacts with feelings of heat and cold to virtually all meteorological factors: air temperature; air humidity; air movement (breeze and draughts); atmospheric pressure; radiations from (or to) sun, sky, earth, walls, ceiling, floor, buildings, trees, other animals, and so on. This reaction of the body to the combination of all the meteorological factors constitutes the *physiologically-effective temperature* as contrasted to *physical temperature* measured by an ordinary thermometer. A given physiologically-effective temperature may be synthesized by combining the several meteorological components in different proportions; two environments may thus have the same physiologically-effective temperatures despite quite different air temperatures.

The air-conditioning engineer's *comfort zone* is the *physiologically-effective temperature* at which one feels most comfortable, and it may be estimated for man, under a given set of conditions, by asking him whether he *feels* cold, hot, or comfortable. How should one estimate it for cows that do not talk? The air-conditioning engineer's comfort zone is probably identical with the physiologist's *thermoneutrality* shown by point A or rather by segment B′-B in Fig. 15, at which heat production is lowest; at which the environmental temperature is perfectly adjusted to keep the body temperature normal without resorting to the body's chemical thermo-regulative devices. If so, the comfort zone in animals may be estimated from the curve relating heat production to environmental temperature, as indicated in Fig. 15 supplemented, if possible, by the temperature curves of other cardiorespiratory activities, including the rates of respiration, pulse, pulmonary ventilation, and body temperature.

The position of the comfort zone, in Fig. 15, and the qualitative manner of response of the animal to a change in environmental temperature varies with many factors, including age and body size, species and nature of protective coverings (Fig. 16 to 20), acclimatization (Fig. 21), capacity and opportunity for evaporative cooling (Figs. 22-25), but mainly on the activity level of the body. For instance, a resting, post-absorptive, man in the nude feels most comfortable at about 85° F; after a meal of beefsteak, perhaps 75° F; during a Marathon race, possibly below freezing. The critical temperatures B′-B in Fig. 15 are thus variables conditioned by many circumstances, and since their published values were obtained on fasting and resting animals, they are not applicable to normally-fed active and productive animals.

The comfort zone as defined by segment B′-B is probably not the best for highest productivity. It may be pleasant to live in a warm climate, but not particularly stimulating for high physiological productivity in farm animals or high intellectual activity in man. This is because productive processes involve a heat increment not

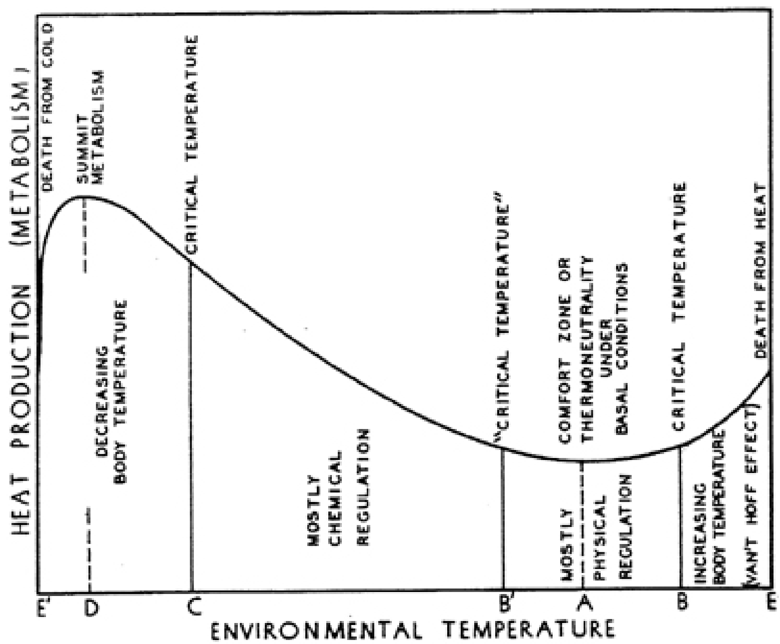


Fig. 15.—Generalized diagram of the influence of environmental temperature on heat production in warm-blooded animals. Note the broad accommodation range to low temperatures and restricted range to high temperatures. The increased heat production with increasing cold (from B′ to D) is a biological adaptation, protective to the animal; the increasing heat production with increasing heat (from B to E) is a consequence of a physico-chemical necessity expressed by the van't Hoff-Arrhenius generalization, and is destructive to the animal, ending in death (E). One purpose of our project is to obtain data for part of this diagram as related to dairy cattle of different size and productivity.

easily dissipated in a warm environment, and they also involve a high level of neuro-endocrine activity which is depressed by hot environment, as exemplified by the decline of thyroxine production with increasing environmental temperature. A cool environment, below temperature B′ in Fig. 15, is probably more stimulating to high activity and productivity than is the warmer temperature B or even A.

2. *Physiological mechanisms in animals and engineering devices by man for controlling "private climates"*: While there is no sharp dividing line between them, it is customary to divide animals into

three categories: *A.* cold-blooded or poikilotherms; *B.* partly warm-blooded or hibernators; *C.* warm-blooded or homeotherms.

A. *Cold-blooded species* are exemplified by ocean fish. They inhabit a virtually constant-temperature medium; therefore, they have no temperature-regulating problem and no temperature-regulating mechanisms.

B. *Partly homeothermic, hibernating* species are exemplified by the duckbill and Australian anteater that normally have relatively

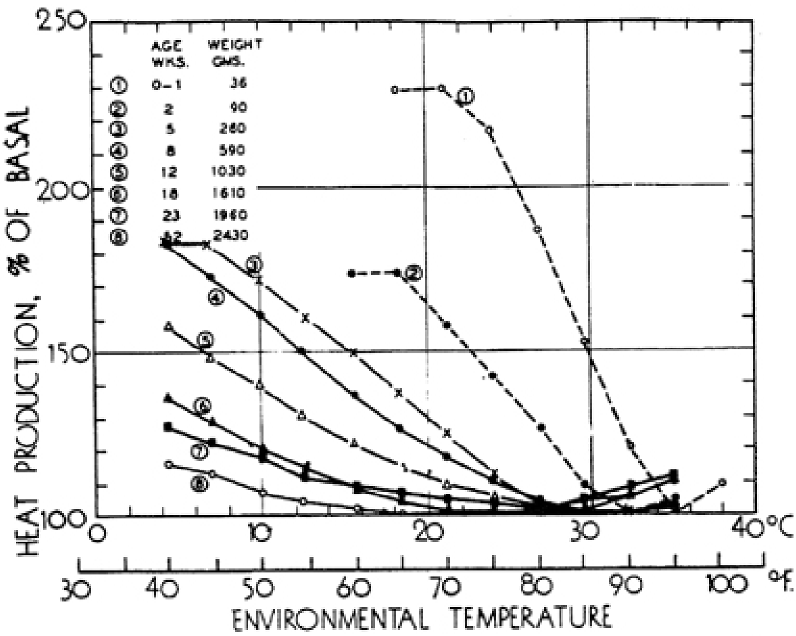


Fig. 16.—Heat production in chicks and chickens increases with declining environmental temperature so as to maintain constant the body temperature. The rate of heat production increases more rapidly in the smaller (younger) than in the larger birds. Contrast the relative adaptational range to decreasing and increasing temperature. Recomputed and plotted from data by Barrott and Pringle, J. Nutr., *31*, 35, 1946.

low body temperature (25°C or 77°F) and whose body temperatures decline by 10°F when the optimal environmental temperature declines by 30°C. In the same category are the bat, woodchuck, dormouse, ground squirrel, hedgehog, ground hog or marmoset, prairie dog and oppossum. These animals maintain a fairly constant body temperature during the summer but on approach to winter, when their temperature-regulating mechanisms begin to fail, they retire below the frost line into burrows or migrate into caves and enter their winter sleep, or hibernation, until the coming spring. The body temperature during hibernation falls to a few degrees above freezing and the metabolic rate and pulmonary ventilation may decline to but one per cent of the normal summer level. In the famine areas of Russia, man has been known to "hibernate" during most of the winter months. Unlike the marmoset, however, man's body temperature probably does not fall appreciably below normal during his "winter sleep". The "hibernation" of the bear is probably of the same category, not loss in ability to maintain normal body temperature but a way of saving energy by sleep. Hibernation is probably an evolutionary adaptation to prevent starvation during periods of food scarcity.

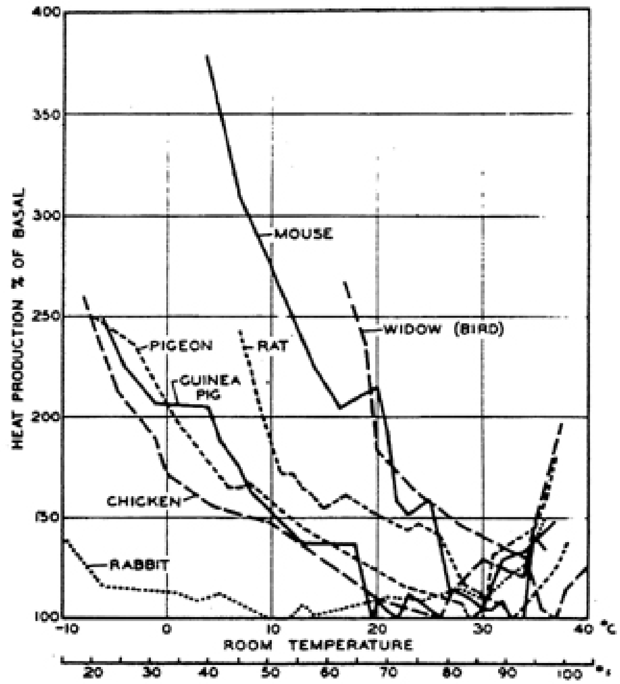


Fig. 17.—Further illustration of increasing heat production (chemical method of thermoregulation) with decreasing environmental temperature but in mature animals of different species. The smaller the animal the steeper the rise in heat production with declining temperature because of the larger heat dissipating surface areas per unit weight in the smaller animals. From data by E. F. Terroine.

*Poikilothermic estivating* species which sleep during the hot, dry, summer are exemplified by frogs, crocodiles, and alligators. Estivation is probably an evolutionary adaptation to periods of water scarcity. The hibernation and estivation of insects and soil inhabitants are of considerable agricultural interest.

Before a certain age chick embryos are cold-blooded, and even after hatching they have to be kept in incubators until after they perfect their homeothermic mechanisms. The same is true, in various degrees, of other warm-blooded species such as very young rats (Fig. 18b), and pigs which may die from chilling (Fig. 18a) or crushing in their attempt to keep warm by getting too close to their mother's body.

C. *Warm-blooded species or homeotherms* maintain their *internal* temperature constant in the face of widely changing *external* temperature. For instance, the annual atmospheric temperature range in Montana may be over 150° F (–40 to +100° F), yet the body temperatures of the horses, cattle and sheep wintering outdoors is constant to within 1° F. How does the horse, for example, maintain such delicate body-temperature regulation?

On the approach of *cold weather,* cold-weather homeothermic mechanisms develop: growth of highly insulating hair and subcutaneous fat; contraction of the superficial blood vessels, thus driving the blood out from the skin and making it non-conductive; increase in thyroid activity; consumption of great quantities of food which warm the animals by their "specific dynamic effect" or "heat increment of feeding" (Figs. 9-10); seek protective shelter and warming solar radiations; save community heat by such methods as huddling; increase in activity, voluntary and involuntary (such as shivering), to increase heat production, and so on.

On the approach of *hot weather* cooling mechanisms come into action, such as avoidance of the heating solar radiations; depression of thyroid activity; refraining from work, including agriculturally productive processes since they increase the production of heat, difficultly dissipated in hot weather.

As previously explained, moisture vaporization is the most important and above 95°F the only cooling mechanism in man in hot weather (Figs. 22-24). Profusely sweating species can, therefore, withstand very high environmental temperatures. Most non-sweating or slightly sweating species attempt to compensate their inability to sweat by panting, often protruding their tongues and blowing air rapidly over the moist surface, thereby accelerating vaporization rate.

Most species enjoy wading in water during hot weather, but to such non-sweating species as swine, access to mud wallows or similar facilities is a matter of life and death. Domestic swine quickly die when exposed to an atmosphere of 100° F in a dry sunny lot, whereas they can withstand this temperature indefinitely when given access to mud wallows (Fig. 24).

A long series of papers recently appeared on sprinkling as a method of cooling cows (C. F. Kelley and H. R. Ittner, Agr. Engr. *29*, 239, 1948; F. C. Minett, Journal Animal Science, *6*, 35 and 258, 1947; Seath, D. M. and Miller, G. D., Journal Dairy Science, *30*, 255, 1947-8 and Journal Animal Science, *7*, 251, 1948). While sprinkling increases the air humidity and thus depresses vaporization, wetting in a mud wallow allows the hog to retire to relatively dry shaded air and keep cool for a considerable period of time by evaporation of the

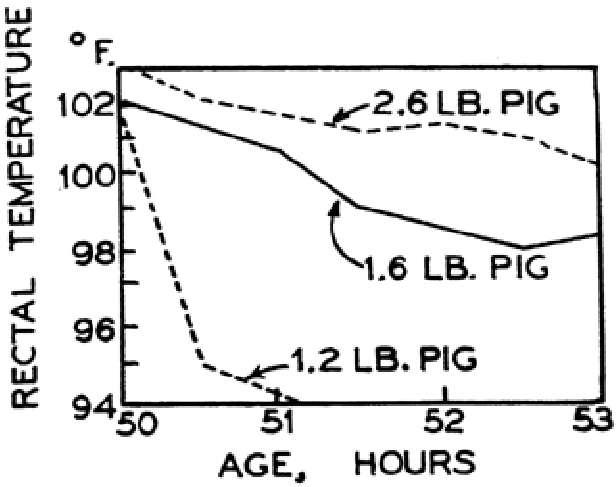


Fig. 18a.—Influence of size of pig (50 hours after birth) on his temperature when exposed to a cool environment (37° F). The smaller the pig the greater his temperature drop because of his larger heat-dissipating surface per unit weight. Courtesy D. P. Wallach, H. W. Newland, and W. N. McMillen, Mich. Agr. Exp. Sta. Quarterly Bull. *30*, 277, Feb. 1948.

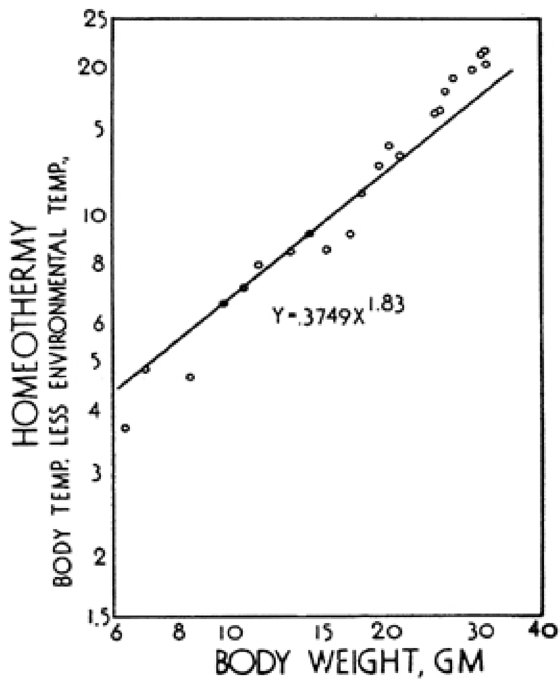


Fig. 18b.—As the animal (white rat in this case) grows older (and larger) the ability to maintain constant the rectal temperature ("homeothermy") increases. In this case the rate was placed in an environmental temperature of 14.5° C (58° F), and "homeothermy" is represented by the difference between 37.3° C (normal rat temperature) and 14.5° C (the environmental temperature). From unpublished data by E. B. Brody.

moisture from the colloidal clay, not unlike the evaporation of moisture from a profusely sweating animal.

A similar principle was used by the writer (Ref. 1, pp. 298-300) by placing over the animal a very porous rubber sponge blanket, with many holes in it to allow rapid vaporization, with a porous water sack built into the blanket. The cow's non-sweating skin was thus kept cool by steady vaporization, like a profusely sweating man's skin, and the blanket also furnished a mobile shade. As indicated below, shading is a very important factor in protecting animals from solar radiant heating.

From the standpoint of ability to withstand high temperatures, homeotherms are, therefore, divided into sweating species evolved in cool regions, including European cattle, swine, sheep, poultry; and also such laboratory animals as rabbits, rats, mice, which apparently neither sweat nor pant, but often instinctively wet themselves with saliva, urine, and in other ways. Elephants frequently pour water over themselves.

Temperature-regulating mechanisms are usually divided into *physical,* not involving extra heat production; and *chemical,* involving extra heat production by various methods, ranging from shivering to increase in thyroxine production.

As previously explained, temperature B′-B in Fig. 15 represents thermo-neutrality where chemical thermo-regulatory devices are not employed. As the temperature falls below B′, heat production increases to counteract the heat loss. The highest heat production, D, is two- to ten-fold the "basal" metabolism, depending on species, body size and conformation, amount of fur, feathers, and fat, and on the degree of acclimatization (Figs. 16, 17, 21). When the environmental temperature rises above E or falls below D, the temperature-regulating mechanisms break down, followed by death (Figs. 19 and 20).

While the rise in heat production with declining temperature, from B′ to D (Fig. 15), helps keep the body temperature constant in the face of falling environmental temperature, the rise in heat production with increasing environmental temperature, from B to E, which takes place as a physico-chemical necessity, in accordance with the van't Hoff rule, increases the body temperature above normal. Moreover, the higher the body temperature the greater the heat production and the greater the heat production the higher the metabolism (a vicious circle). This explains why segment AE′ (reaction to cold) is so much longer than segment A-E (reaction to heat); and the danger to life in passing temperature B. For instance, decreasing the environmental temperature for a sheep by 90° F, from 60° F (thermoneutrality) to -30° F, will not harm it, whereas increasing the environmental temperature by 90° F, from 60 to 150° F, will quickly kill it. The species, weight and age difference in the relative adjusting ability of the body to heat and to cold are illustrated in Figs. 16 to 20.

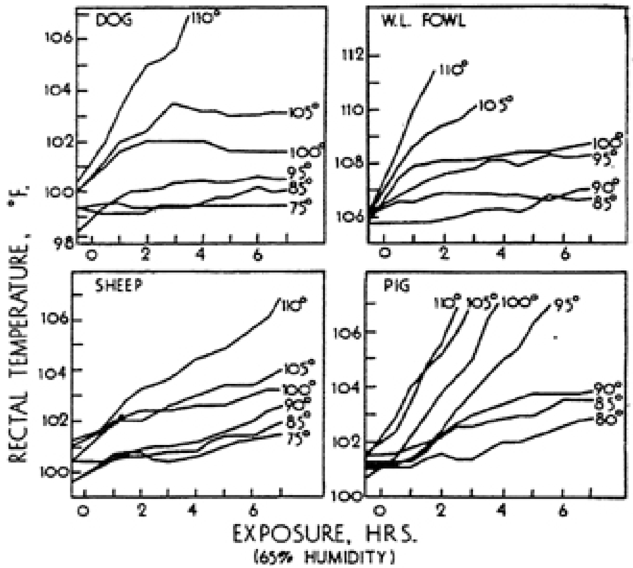


Fig. 19a.—Exposure of most farm animals to environmental temperatures above 70° F increases their body temperature. Plotted from data by Douglas H. K. Lee and associates, Proc. Royal Soc. Queensland, vol. *53*, numbers 7 to 12, 1941.

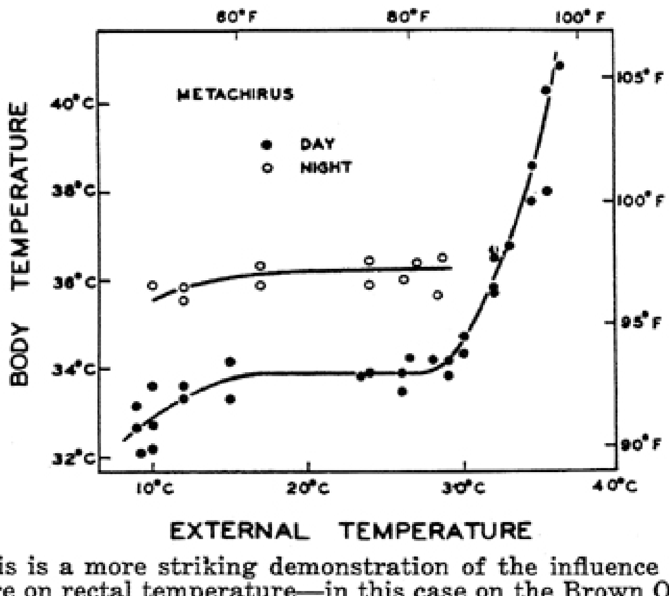


Fig. 19b.—This is a more striking demonstration of the influence of environmental temperature on rectal temperature—in this case on the Brown Opossum, an imperfect homeotherm. Courtesy P. R. Morrison, J. Cell. & Comp. Physiol., *27*, 1331, 1946.

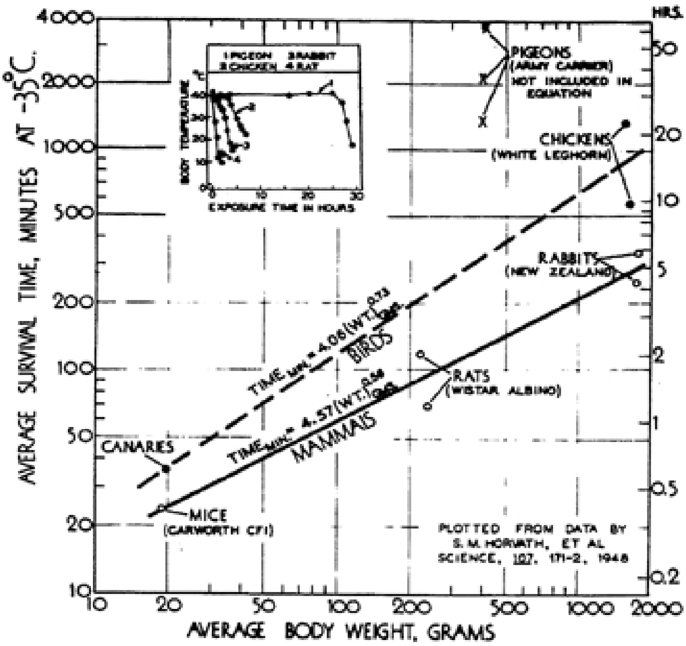


Fig. 20.—Time taken to die from exposure to cold (environmental temperature, -35° C or -31° F) as function of body weight and species; and rate of decline in rectal temperature as function of exposure time to this cold environment.

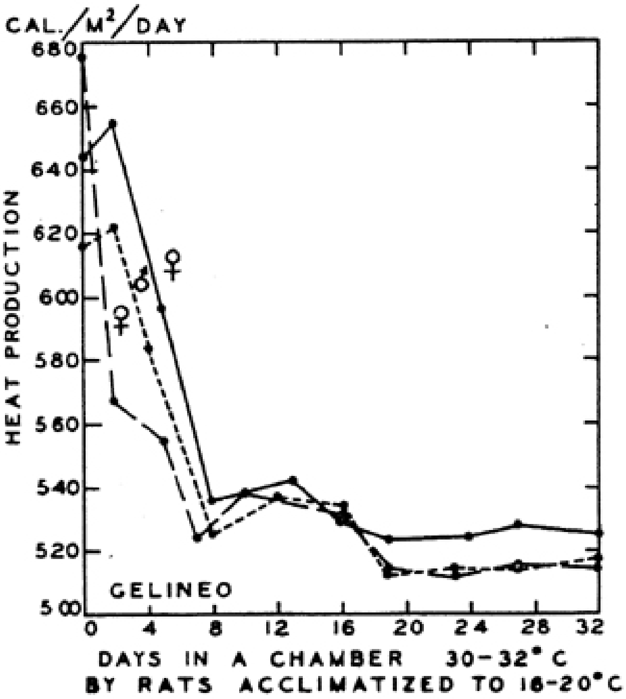


Fig. 21.—When a white rat is transferred from an environment of 18° C (64° F) to one of 31° C (88° F) the heat production is reduced from about 650 Cal/sq. m to about 510 Cal/sq. m. (about a 20 per cent reduction). But it takes from one to three weeks to reach the full acclimatization level for metabolism. How long does it take a farm animal, such as a cow, to reach such an acclimatization level? Data by Gelineo (see Ref. 1).

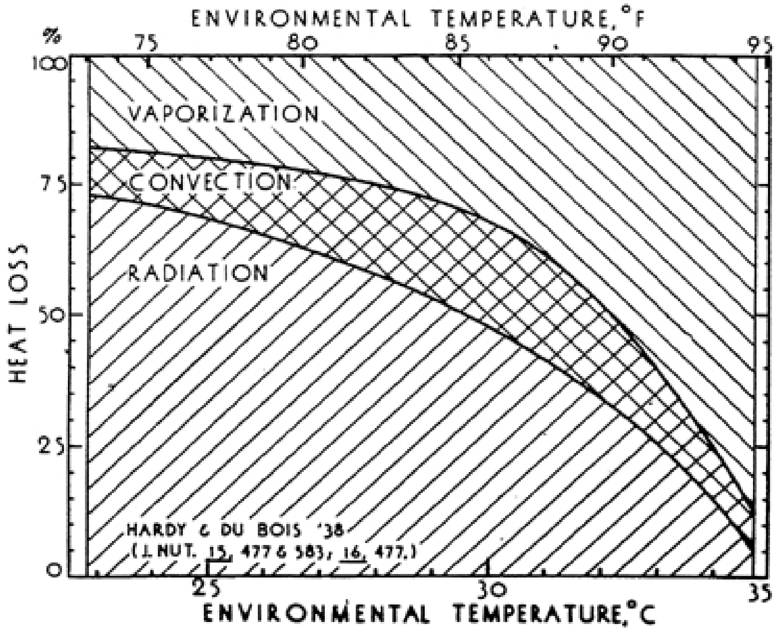


Fig. 22a.—The burden of heat dissipation is shifted from radiation and convection at the lower environmental temperatures to vaporization at the higher temperatures.

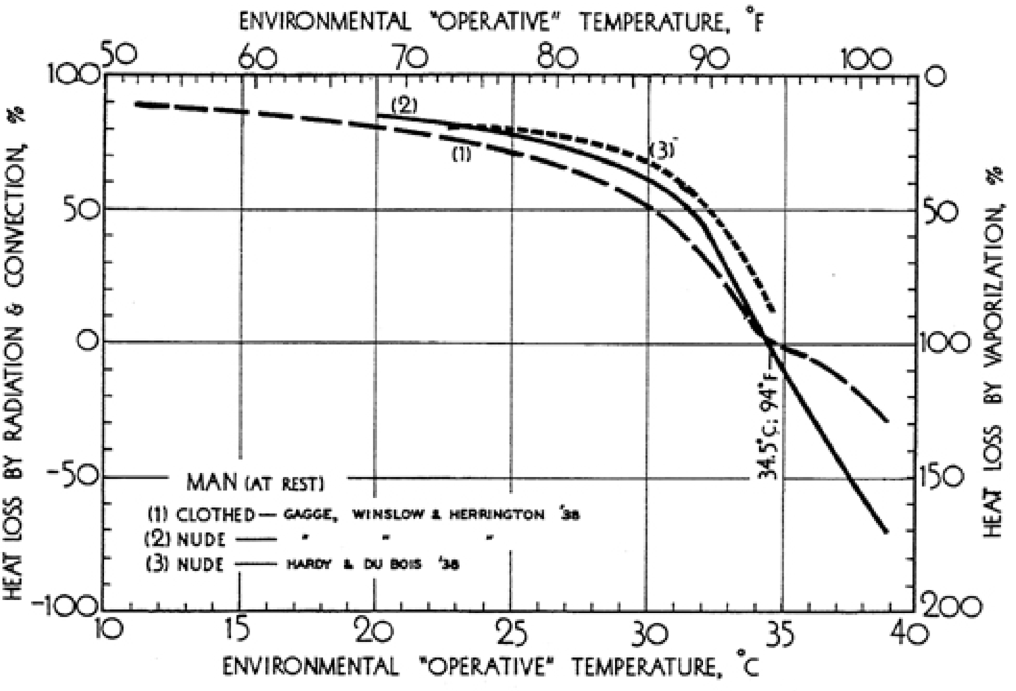


Fig. 22b.—The influence of environmental temperature on the relative heat losses by vaporization (right axis of ordinates), and by radiation and convection (left axis of ordinates). Note that precisely 100 per cent of the heat produced is lost by vaporization at 94° F or 34.5° C.

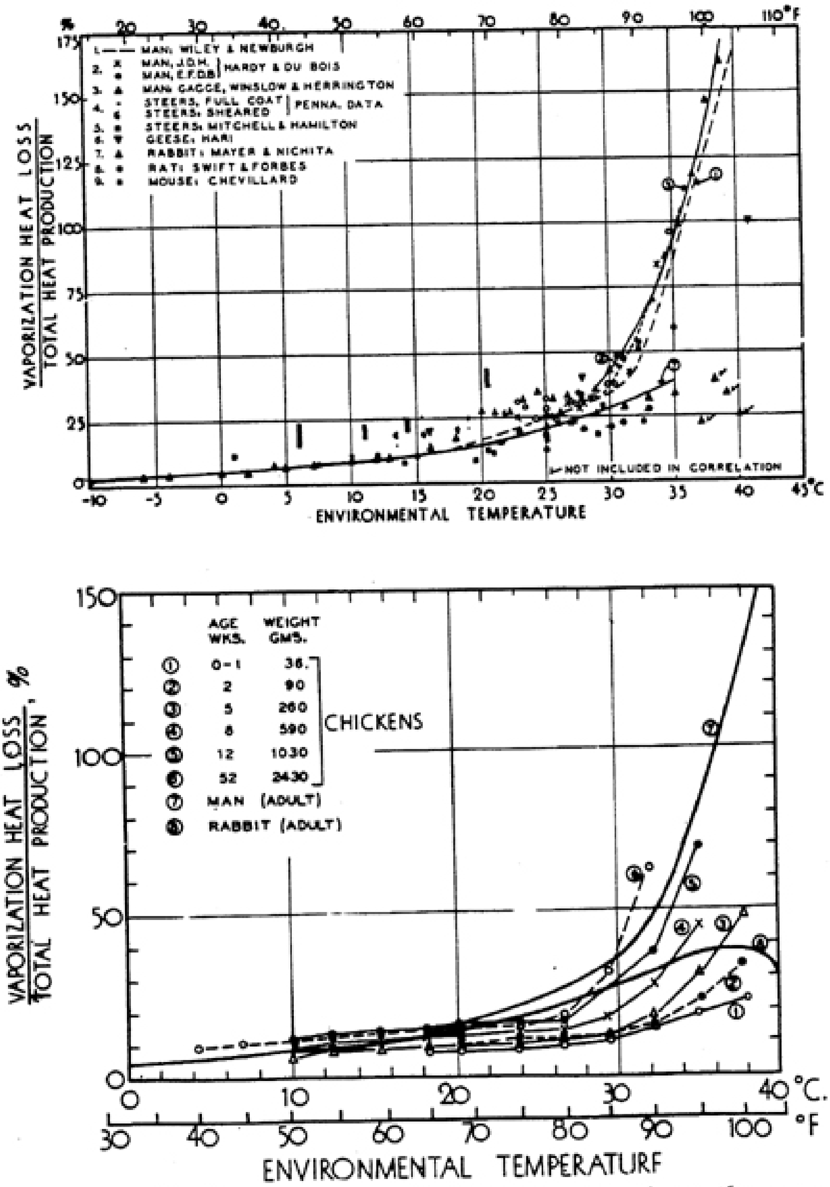


Fig. 23a & b.—As the environmental temperature rises, the percentage of the total heat dissipated by vaporization rises. Fig. 23b, which shows the influence of age of chickens on the percentage of heat dissipation by vaporization, was recomputed and plotted from data by Barrott and Pringle, l. c. in Fig. 16.

One is tempted, in conclusion, to call attention to the analogies between biologic and engineering temperature-regulating devices, The aim is the same in both, to free the organism from climatic limitations. For instance on approaching winter, farm and game animals grow winter coats of fur or wool; and man puts on his sheep skin, fur coat, or other winter clothing. To keep warm in cold weather, both, animals and man, utilize the radiant heat from the sun and from other animals, and seek protective shelter; and to keep cool in hot weather both use shade for protection from the sun's heat, and employ moisture and enlarged surface areas, such as the huge dewlaps, sheath, and naval flap in Indian cattle (Fig. 12b), to facilitate heat dissipation. Panting and fanning are functionally analogous. The basic air-conditioning devices seemed to have been standard

Fig. 24.—Swine (non-sweating species) keep cool by wallowing in mud.

Fig. 25.—Straw as shade and protection against summer heat and winter cold widely used, from time immemorial, among the East-European peasants. This photograph by Zeller at the U. S. D. A. Experiment Station at Miles City, Montana, was given the author by Dr. W. A. Craft, in charge of the U. S. D. A. Regional Swine Breeding Laboratory.

equipment in warm blooded animal bodies before the advent of man; and the modern housing engineer appears to be an evolutionary adaptation on a conscious level to free man and his animals from climatic limitations.

3. *Causes, mechanisms, and prevention of death from overheating with special reference to solar radiation.* A major cause of overheating fatalities of man and horse during the peak of the Middlewest summer heat, is exposure to direct solar radiation, especially during hard muscular work.

If the environmental temperature is appreciably below the skin temperature, the body is pleasantly warmed by the radiant energy from the sun and terrain. But if the environmental temperature is near to or above that of the skin, the radiant energy is absorbed by the body and overheats it unless the extra heat is promptly dissipated by moisture vaporization. According to Adolph and associates, exposure of man in an atmosphere of 90° F to sunlight approximately doubles his sweating rate over that in the shade, that is, it doubles his burden of heat dissipation. It is said (H. F. Blum, Physiol. Rev. *25*, 483, 1945) that the maximum solar heat load in man may be two to three times the resting heat production in shade. This demonstration of the great heating effect of solar radiations indicates the importance of shade in hot weather.

Tree shade is coolest because of the cooling effect of moisture evaporation from the trees without interfering with air circulation. According to Kelley and Ittner (l. c.) the temperature of the air above an alfalfa field is 5° F below that of a recently plowed field. While, however, trees make excellent shade for man, they are not as useful for farm animals since the animals congregate around the trees, deposit their manure, which is usually washed away; and, moreover, the animals ring the trees thus destroying the thing they love. C. M. Long has suggested the use of movable shade for cattle, and Kelley (l. c.) is apparently working on this problem. Fig. 25 shows an inexpensive, simple type of straw thatch shade widely used by East-European peasants. White clothing, not interfering with air circulation, and related coverings, such as feathers and hair, especially if white, are good protectors from solar radiation. (See p. 20 citing Bonsma on hair color in cattle as an adaptation to the tropics.)

Muscular work increases heat production and therefore increases the sweating rate in man. It has been reported (E. F. Adolph and D. B. Dill, *Am. J. Physiology, 123,* 369, 1938; Adolph, "Physiology of Man in the Desert", 1947) that under unshaded day desert conditions, a working man vaporizes 1.7 kg (3-¾ lb.) moisture per hour. Since the latent heat of vaporization of skin moisture is 580 Calories per kg, the vaporization rate of 1.7 kg per hour is equivalent to heat dissipation rate of about 1,000 Calories, 12 to 13 times the average normal resting heat production, a very impressive demonstration of the evaporative cooling ability of man. This rate of sweat production can, moreover, be doubled in a moisture-saturated atmosphere, which does not allow sweat vaporization, with consequent overheating the skin and overstimulating the sweat-producing mechanism. The sweating rate is, then, increased to 3.5 kg (7.1 lb) per hour, equivalent to a potential heat dissipation of over 2,000 Calories per hour—some 26 times the resting heat production at thermoneutrality. This is much greater than the heat production associated with the hardest kind of "steady" muscular work (that is, lasting over 5 or 10 minutes). Man thus has amazing abilities to withstand high temperature at low humidity.

Sweating (in man)* tends to reduce the body water, and reduction of the body water by 2 per cent of the body weight (about one quart in man) is followed by serious consequences: (1) There is reduction in blood plasma volume (with directly proportional increases in plasma solids, NPN, Cl, sugar, hematocrit). (2) The plasma volume deficit decreases the blood volume. (3) The effective blood volume for the heart is further decreased by the vasodilating increase in the vascular bed. (4) There is, therefore, not enough blood to fill the heart and the blood vessels, with consequent reduction in stroke volume and increase in pulse rate, which reduces the efficiency and increases the work load of the heart with consequent additional increase in heat production and in body temperature. (5) The increased solids and viscocity of the blood adds to the work load of the heart and, therefore, to heat production. (6) The rise in body temperature increases the heat production in accordance with the van't Hoff-Arrhenius rule. (7) As the heat production increases, the body temperature further increases, and so on in a vicious circle to a fatal issue. (8) Blood volume reduction tends to lead to cerebral anemia, ischemia of the nervous system that regulates cardiorespiratory activities, perhaps associated with compensatory hyperventilation, which in turn may lead to tetany, convulsive vomiting and defecation and paralysis.

Death usually follows when the rectal temperature exceeds the normal level by about 8°F (Fig. 20). Since 8°F above the normal

*At very high temperatures profusely-sweating man tends to be *dehydrated* due to greater moisture loss by sweating than gain by drinking, slightly sweating European cows tend to be *hydrated* due to greater water gain by drinking than loss by sweating. This paragraph, then, applies to dehydrated man, not to the hydrated cow.

body temperature in man or rat, for example, is normal for some other species (the normal rectal temperature is about 99° F in man and rat, 101°F in cattle, 103°F in sheep, swine, and rabbit, 104°F in goat, 107°F in chicken, 109°F in small birds), it would seem improbable that death occurs by protein denaturation or colloidal flocculation, although there may be some species differences in the colloidal properties of proteins, but rather on a higher organismic level, most probably by circularatory stress, as is generally believed for man and as outlined above.

One may, however, advance any number of hypotheses or conjectures for species differences in normal body temperature. For instance, the structural configuration (not necessarily chemical composition) of the bird's respiratory enzymes may be more stable than in mammals, with consequent necessity for a higher body temperature for metabolizing at the required level. This could be tested experimentally by a study of the enzymes from animals at low, normal, and high, lethal, body temperatures.

A similar experiment on a cellular level could be done for testing the hypothesis that high body temperature disorients the respiratory or other enzymes by affecting different enzymes to different degrees, and thus upsetting the normal sequence in the metabolic chain. For instance, two critical enzymes may have different $Q_{10}$ values (See ref. 1, p 267). A slight temperature rise would then speed up one reaction more than the other and lead to death by throwing the normal body sequences and mechanisms out-of-balance.

One could also subject to experimental test the hypothesis that the selective permeability of the cell and its ability to do osmotic work changes with subjection to high temperatures.

The lipids in animals that live in hot regions have a higher melting point than the lipids in animals that live in cold regions (V. Henriques and C. Hansen, *Skand. Arch. Physiol.*, *11*, 151, 1901). Therefore, when the body temperature suddenly rises, and no time is given for acclimatization of the melting points of the lipids, the cell lipids, many of which are in the form of a lipid-protein-calcium complex, may melt and in that way injure the selective permeability of the cell and upset other equilibria. The melting point of dietary and body fat affects resistance of animals to high temperatures (L. V. Heilbron, Am. J. Physiol. *69*, 190, 1924; & "Outline of General Physiology", 1937).

The effect of possible inadequacy of oxygen supply associated with high temperature on the central nervous system was already noted and may be emphasized here in connection with the effects on enzyme activity on the cellular level.

4. *Some regional adaptations of animals and possibility of developing heat (or cold) resistant strains.* Animals and plants are products of heredity and environment. A given hereditary pattern is, however, itself the product of environment because mutation rates and selective survival are conditioned by the environment. Different climatic regions, in this way, mould plants, animals, and peoples into patterns particularly adapted to given regions. This may be illustrated by the contrasts in hair growth in cattle that evolved in Tibet and in Southern India (Fig. 12a and b).

The animals evolved in cool regions are adapted to cold weather by their abundance of wool or hair and subcutaneous fat; the animals evolved in hot regions are adapted to hot weather by the sparcity of wool or hair and subcutaneous fat. The reserve fat in the hot-country animals is presumably stored in the humps of cattle (Fig. 12b) and in the fat tails of sheep. In this way the fat does not interfere with heat dissipation from the body. This may also be the significance of the excessively fat buttocks in the otherwise lean women in some tropical regions.

Ralph W. Phillips (Director Agricultural Division, Food and Agriculture Organization of the United Nations) does not think that the local fat deposition in tail and hump is correlated with environmental temperature. Dr. Phillips tells me that while the one-humped camel of India and Afghanistan stands heat well, the two-humped camel of Central Asia does not stand heat well and is found in the relatively cold regions of Northern China and Mongolia. Similarly, long fat-tailed sheep are found in hot regions (Northern Africa and Southwestern Asia) and in cold regions (Central Asia), and short lean-tailed sheep are found in both hot India and in the cold high Tibetan Plateau. But these apparent anomalies may be due to relatively recent migrations rather than to long-range evolutionary adaptations.

For instance, some members of the camel family (alpaca and llama—the "desert ships of the Andes") that inhabit the mountain regions of Western South America, look more like crosses between goats and ostriches than like camels. There are evidently many categories of evolutionary adaptations and superadaptations, ancient and recent, that complicate the thinking and generalizing about them.

Returning to regional adaptations of cattle, several features distinguish Indian from European cattle: (1) Indian cattle have excellent heat radiators—enormous dewlaps (loose, pendulous skin under the throat which extends back between the legs and along the belly) and sheath, or (in females) navel flap, and long ears (Fig. 12a). Their bodies tend to be small with consequent large surface area per unit weight, their skin has little hair. European cattle, on the other hand, have hairy, fat, tight hides, undeveloped dewlaps, and relatively small ears. (2) Indian cattle have evaporative coolers —they sweat—while European cattle apparently do not, or sweat but slightly, so that their evaporative cooling from the skin is mostly, if not entirely, of "osmotic moisture" or "diffusion moisture". (3) The hair color of Indian cattle tends to be lighter, and it may reflect more sunlight than that of European cattle. (4) Indian cattle are more immune to ticks, flies, mosquitoes, and other pests than are European cattle. These factors may account for the greater adaptability of Indian cattle to hot-weather regions, such as to the Mexican Gulf Coast, especially in Texas, Louisiana, and Florida where there are said to be over 70,000 registered Brahman cattle, mostly of the Guzer and Nellore strains, employed extensively for cross-breeding with European beef cattle (see below). (The Sahiwal or Montgomery breed is perhaps the best milk producer in India.)

A curious, apparently irrational, adaptation in man concerns his skin and hair color. There seems to be a pigmentation gradient ranging from the darkest races in tropical Africa, India, and the Pacific to the lightest in cool Northwestern Europe.

Since, as previously noted, the reflectance of light (0.4 to $0.7\mu$) is very much greater from light than from dark skins, it would seem to be advantageous, from the homeothermic viewpoint, to have light skin and hair in hot regions so as to reflect and avoid heating by the light energy, and to have dark skin and hair in cool regions so as to absorb and be warmed by the light energy. But the opposite seems to be true, the darkest skins are, as a rule, in the hottest regions and the lightest in the coolest regions. How should one explain this apparently anomalous type of adaptation?

According to Edwards and Duntley (see page 19) skin pigments include melanin, black to yellow, produced from tyrosine under the influence of tyrosinase, dopaoxidase, and copper; melanoid, a melanin derivative richer in yellow; carotene, a copper yellow lipochrome; oxyhemoglobin; and hemoglobin. White-skinned persons develop temporary melanin pigmentation, or at least freckling, when exposed to sunlight; but colored people have the melanin or melanoid pigments as genetic characteristic.

Ultra-violet light is known to be bactericidal, and toxic to skin and nerve. E. A. Hooton (in "Up From the Ape", 1946) believes that melanin protects nerve and skin, and perhaps the general blood chemistry, from the injurious ultra-violet radiations; and it protects the deeper layers from excessive warming by yellow-red rays, thus partially regulating body temperature. In this sense, pigmentation of tropical races has adaptive value.

It is also conceivable that the pigmentation may have an overall cooling effect on the skin in spite of the greater absorption of light energy. The accelerated sweating induced by the heating of the pigmented skin may more than offset, by sweat evaporative cooling, the greater heat absorption. Is it not said that drinking hot tea, while adding heat to the body, yet, by stimulating profuse sweating and evaporative cooling, exerts an overall cooling effect in hot weather? Sweating and (in non-sweating species) panting have heat increments, yet exert an overall cooling effect by increasing evaporative cooling. The more abundant sweat may, moreover, exert a protective action on the skin. It is unbelievable that, with the few exceptions perhaps due to relatively recent migrations, there should be such a conspicuous orderly skin-pigmentation gradient in man from the tropics to the cool temperate regions without evolutionary physiological significance. Some desert reptiles and birds have scaly coverings which are definitely reflectors of radiant energy.

If it were not for the protection against the toxic effects of ultra-violet radiations, animal and man would obviously be better off to be light-skinned in hot, sunny, regions and dark-skinned in cool regions, so as to reflect the radiant energy of the visible spectrum in hot weather and absorb it in cold weather. One is tempted to suggest to paint the animal's hair black in the winter to help it keep warm by absorbing radiant energy in the visible spectrum, and white in the summer to help it keep cool by reflecting radiant energy just as it is customary to wear lighter colored clothing in hot than in cold weather.

The significance of skin and hair color in relation to environmental temperature in farm animals deserves investigation on a scientific level (Bonsma, l. c.).

Selective and cross breeding may similarly be used for developing other desired characteristics most suitable for a given climate. The Santa Gertrudis breed of beef cattle particularly suited for our Gulf Coast region was developed, by R. J. Kleberg on the King Ranch in Southern Texas, by crossing Brahman bulls with Shorthorn cows. The Bureau of Animal Industry, United States Department of Agriculture, is similarly developing a suitable beef breed of cattle by crossing Brahman bulls with Angus cows at the Iberia Livestock Experiment Farm at Jeanette, Louisiana; and the Bureau of Dairy Industry, United States Department of Agriculture, is experimenting with crossing Brahman (Sindhi) dairy cattle with European dairy cattle. The Berkjala hog was developed in the Philippines by crossing Berkshire and native Jalajala hogs. Selective breeding is also employed for developing desirable dairy or beef quality within the tropical breeds of cattle and for desirable climatic adaptations within the European breeds. Extensive discussions and bibliographies on this subject are given by Phillips (Ref. 2).

5. *Fitness index of thermal stress.* Selective breeding for fitness to withstand thermal stress involves the use of measures of thermal stress wherewith one could follow quantitatively the inheritance of the fitness.

The most obvious index of thermal stress is body temperature response. Deviation from the normal rectal temperature indicates that the animal is under stress, that its homeothermic mechanisms are overtaxed.

Change in body temperature, however, induces other changes. For instance, as might be inferred from the van't Hoff-Arrhenius rule, increasing body temperature by 1° C may increase the heat production by 20 per cent and the pulse rate, perhaps, by 20 beats per minute. Therefore, rectal temperature, pulse rate, and heat production may be used as indices of reactions to thermal stress. In panting animals, as cattle, the respiration rate is an excellent index to thermal stress. Parenthetically, fitness indices for heat stress are in many cases (especially when involving circulation stress) the same as for muscular work stress.

A. O. Rhoad (*Tropical Agr.*, *21*, 162, 1944) suggested a thermal "Adaptability Coefficient" or "The Ibernia Heat Tolerance Test" for cattle based on the rectal temperature response to a given environmental temperature. For instance, if the rectal temperature is increased by 2.8° F above normal, the "adaptability coefficient" to the given temperature is (100-28), or 72. (It is 100 less 10 times the rectal temperature increase above the normal.)

Rhoad also used a "water economy" test based on urinary nitrogen and fecal moisture levels (Rhoad, *Empire J. Exp. Agric.*, *8*, #31, 1940: *Proc. Am. Soc. Animal Production*, 1938. Unlike Rhoad's, our preliminary observations indicate that the higher the environmental temperature, the more dilute the urine, presumably because more water is consumed for its cooling effect and, unlike in man, it is not lost to the same extent by sweating. In European cattle, the respiration rate is probably the most sensitive simple index of thermal stress, supplemented by rectal temperature; in man, a non-panting species, pulse rate is probably the most sensitive simple index of thermal stress, supplemented by rectal temperature. These methods have been used on man by physicians from time immemorial.

While thermal stress is reflected in the easily observable changes in pulse rate, respiration rate, and rectal temperature, the whole body, as previously explained (pp. 8-11), including nerves, endocrines, enzymes, metabolites and metabolic rates, react to the thermal stress by an elaborate series of chain reactions which need clarification by detailed investigation.

## VI. DATA WE ARE NOW COLLECTING

As previously explained (pp. 8-11), weather changes probably affect the animal body by a series of simultaneous consecutive reactions involving: (1) the nervous system; (2) the endocrine system; (3) the enzyme system; (4) the rates of metabolic reactions (including heat production); (5) levels of metabolites; and (6) the rates of the agriculturally important processes, including the rates of feed consumption, milk production, growth and so on. According to this organismic chain-reaction theory, a comprehensive investigation of the effects of changes in weather on animals should include a study of all changes in function and structure. Since it is not practical to undertake such an integrated attack on this problem, the immediate research objectives are necessarily more limited.

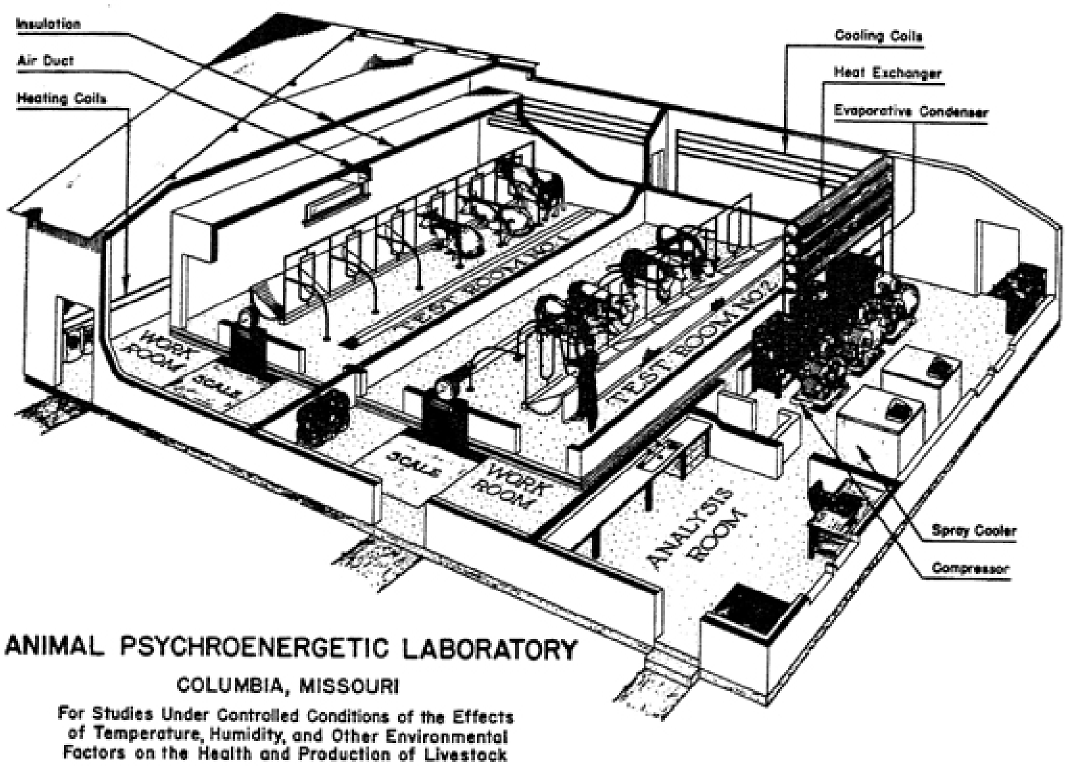


Fig. 26.—The Climatic Laboratory, Columbia, Missouri, where the temperature studies are now being conducted. See Ref. 3 for details.

By way of preliminary trials we are at the time of this writing investigating 12 cows, 6 of which are kept in a control chamber (see Fig. 26) maintained at approximately 50° F and at approximately 60 to 70 per cent humidity, and 6 are in the experimental chamber in which the temperature is increased by 5° to 10°F at two to three-week intervals with the humidity kept approximately constant, between 60 and 70 per cent. The following measurements are being taken.

1. Feed and water consumption; body weight; urine and feces output.
2. Milk production, volume, and composition (fat, solids not fat, total nitrogen, chlorides, lactose, vitamin A and carotene).
3. Blood volume and composition (total and plasma solids; total and non-

protein nitrogen; hematocrit, hemoglobin and differential blood count; lipids, including cholesterol and fatty acids; vitamins A, D, and C; calcium, magnesium, phosphorus, glucose; blood carbon dioxide and carbon dioxide capacity; phosphatase, catalase, protease, lipase, and cholinesterase; (it is hoped to determine thyroxine eventually).

4. Rectal, skin, and blood temperature.
5. Cardiorespiratory activities, including:
   - A. Pulse rate.
   - B. Respiration rate.
   - C. Tidal air.
   - D. Pulmonary ventilation rate.
   - E. Oxygen consumption.
   - F. Carbon dioxide and methane production.
   - G. Blood pressure.
   - H. Electrocardiograms.
6. Heat production from 5E above (employing open- and closed-circuit mask methods) for the practical purposes of developing the functional relations between heat production and environmental temperature and determining therefrom the "comfort zone", or the region of thermoneutrality, for animals of different size and productive levels; and the influence of the amount of hair or other covering on the rate of heat production and cardiorespiratory activities.
7. Heat dissipation by: radiation; convection; conduction; and vaporization (from exhaled air, skin, and total insensible loss).
8. Occasional observations are made on activity of the animals (frequency of getting up and lying down); frequency of drinking; frequency of urine and feces output; and so on.
9. In addition to the above data, primarily of physiological interest, data are being collected on temperature of walls, ceilings, floors; temperature, humidity, movement of air in various regions of the chambers, primarily of air-conditioning interest and useful for computing heat dissipation by vaporization, radiation, convection, and conduction, since heat dissipation by each method depends not only on the body temperature but also on the environment.

The animals are kept during the entire observation period in the chambers illustrated in Fig. 26, described by our BPISAE collaborating agricultural engineers (Ref. 3). The first observation period, beginning during the second and third months of lactation, will be about five months. There is no outdoor light; no exercise outside of walking down to the scales (see Fig. 26) for weighing and for determining the insensible loss. Cod liver oil is added to the usual dairy ration (alfalfa hay, grain, beet pulp) to make up for the lack of sunshine. Each animal in the "experimental chamber" (in which the temperature, or other factor, is changed at two to three week intervals) is "paired" with one in the "control chamber" in which the conditions remain constant. Each chamber contains five lactating and one non-lactating cow. At the present time half of the cows are Holstein and half Jerseys to indicate what effect body weight (and possibly breed) has on heat (or cold) resistance. At a later time we hope to include one or more sweating (Brahman) cows in each chamber.

Briefly, the "Psychroenergetic Laboratory" (Fig. 26) consists of two insulated test chambers each 26 x 18 x 9 ft. together housing 12 cows. The temperature (approximate range 0° to 110° F, but depending on the outdoor temperature), humidity, air movement, light, and ventilation rate of each chamber can be varied independently of the other.

These two chambers are within an insulated 40 ft. x 60 ft. steel frame structure covered with galvanized iron.

The chamber floors are 4-inch concrete over 4-inch hollow tile laid upon two-inch foam-glass insulation. The hollow tile in the chamber floors is arranged so that conditioned air may be forced under the floor for floor temperature studies.

The chamber ceilings and work rooms (space around chamber) are well insulated. The spaces between chamber and outside walls contain cooling and heating coils, ducts for circulating the conditioned air, and so on.

The equipment room houses air-conditioners, brine-conditioners, hot-water boilers, evaporative condensers, Freon compressors, etc. The analysis room contains the control and recording equipment for the air-conditioners as well as other temperature-measuring equipment.

The investigational techniques are fairly standard (Ref. 1) and will be outlined in detail when reporting the data.

## SUMMARY AND ABSTRACT

Climate is conceived to regulate productive processes by a series of simultaneous-consecutive, or chain, reactions.

One hypothesis conceives climate to affect successively, in chain-reaction fashion, soil fertility, plant productivity (including nutritional value of plants), nutritional conditions of animals and, consequently, human welfare.

Another hypothesis conceives climate, especially its seasonal rhythms, to affect successively the nervous, endocrine or hormone, and enzyme systems, metabolic levels, metabolic rates and, consequently, the rates and qualities of all productive processes, including, perhaps, the behavior of man.

The involved mechanisms of these and other processes including: evolutionary adaptations to given climatic regions, mechanism of death from overheating, measures of thermal stress, the relative importance of heat loss (or gain) by radiation, convection and vaporization, control of "private climate" by biological and engineering methods, are discussed in some detail. The "Psychroenergetic Laboratory" on the University of Missouri Agricultural Campus and the observations now being made are briefly outlined.

## REFERENCES

There is an enormous literature on the subject matter of this paper. To save the labor and space of listing the literature, several general references are cited in which detailed references may be found.

1. Brody, Samuel, "Bioenergetics and Growth", Reinhold Publishing Corp., 1945. Chapter 7 is concerned with the neuro-endocrine (hormone) factors in productive processes; Chapters 8 and 9 with seasonal and diurnal rhythms; Chapters 10 and 11 with the effects of temperature and related factors; Chapter 12 with methods of measuring heat production; 13 to 15 and 24 with heat production and related cardiorespiratory activities in relation to body size, age, and work.
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