Heat Tolerance in Cattle-its Concept, Measurement and Dependence on Modifying Factors

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INTRODUCTION

Heat tolerance may be defined as the ability of the body to endure the impact of a hot environment without suffering ill-effects.

In this general form the definition probably satisfies most of the people interested in heat tolerance. However, different people will give different interpretations to the term "ill-effects". To the animal husbandry man it may mean a poor performance with respect to grazing, thrift and milk yield, to the veterinary practitioner alow fertility and proneness to disease, and to the physiologist a displacement from the normal of body functions such as body temperature and respiratory activity. As a consequence, various people will judge heat tolerance by a number of different criteria; they speak, with regard to heat tolerance, "different languages", which makes any comparison difficult.

Yet, physiologically there are no completely isolated reactions to heat because of the relationships existing between the various body processes. Whether or not certain body functions, such as milk secretion, are economically exploited by man, does not make any difference. Heat tolerance is essentially an entity which is merely looked at and approached from different angles by people differing from each other with respect to interest, training and facilities.

It would appear therefore physiologically reasonable and, from the standpoint of general applicability, desirable to find a way of assessing an animal's innate overall capacity to cope successfully with a hot environment. Any attempt in this direction is faced with difficulties both fundamental and practical.

Three main factors have to be considered: the hot climate(the stress producing agent), the animal body (the target) and a suitable scale for expressing numerically the effect of the hot climate on the animal body.

The aim of this paper is to discuss various aspects of heat tolerance in cattle by attempting to answer the following questions:

- (1) Which of the many climatic factors have to be taken into consideration for sheat tolerance test?
- (2) At what intensity should they be applied?
- (3) What is the relation of some selected body structures to heat tolerance?
- $m{(4)}$ Which body functions are eligible for use as criteria in a heat tolerance test? $m{(5)}$ Which are at present the best ways of expressing the impact of a hot climate on the
- (6) Which factors influence heat tolerance in a given animal, and how strong are these influences?

CLIMATE

GENERAL

A heat tolerance test, in order to give reproducible and comparable results, must be carried out in a standard thermal environment. This is difficult to achieve in the field where one has to accept the atmospheric conditions prevailing at the moment.

It is true that animals tested simultaneously in the same geographical area may readily be ranked according to their heat tolerance which in turn allows selection of those animals (of one or of many different breeds) which stand up best to a given local climate. But, since the atmospheric conditions vary in a given area with time, and in agiven time with area, results so obtained represent only relative values, i.e., they are not comparable to results obtained elsewhere or at another time. Extrapolation to a standard climate by using correction factors, may be possible, but can hardly be considered satisfactory. The controlled atmosphere of a hot room is generally preferable, although this also has its limitations.

In choosing the atmospheric conditions for a heat tolerance test, it has to be decided what climatic factors should be considered and at what intensities they should be used.

QUALITATIVE ASPECTS

The principal component factors of a thermal environment are temperature, humidity, wind and solar radiation. Ideally they should all be included in a heat tolerance test either in combination or singly one after the other. Each climatic factor affects the body in a different way thereby making demands on specific structures and mechanisms of the body. A high environmental temperature, provided it does not exceed body temperature, interferes with the dissipation of body heat by convection and radiation, which emphasises the importance of factors such as the ratio of body surface to body mass, the circulation of the blood and the vascularization of the skin. A high air humidity interferes with dissipation of body heat by evaporation. It thus plays a role in evaluating an animal's capacity for evaporative cooling by sweating and panting. In a non-sweating non-panting animal, air humidity would be of minor importance as a climatic factor. Wind promotes distingation of body heat by convection, (provided air temperature does not exceed the body temperature); it also assists evaporation. Therefore, the larger the (relative) surface area of an animal and the higher its rate of skin evaporation, the more it would benefit from the cooling power of wind.

Solar radiation, in contrast to the other three climatic variables, imposes a heat load on the body by transferring energy to it from outside. The presence of solar radiation in a heat tolerance test allows a determination to be made of an animal's capacity for absorbing solar radiation, which is largely dependent on the characteristics of its skin and hair coat. The superiority in heat tolerance of an animal having a glossy, light coloured, i.e., a highly reflecting coat, over an animal having a dull, dark coat, can only be evaluated in the presence of solar radiation or a suitable artificially produced substitute.

Since all these climatic factors can affect the animal's thermal balance, it would appear desirable to express them jointly as a single figure, so that different climates, in spite of differences in their component factors, would be mutually comparable. Warious attempts have been made to combine two or more climatic factors into a single index. A well known index of this kind is the "cooling power" which is a measure of the amount of heat lost by a specified body under given conditions of temperature, wind velocity and radiation. Since such an inert body cannot make adaptatory adjustments, its response to climatic stress will, of course, not reflect quantitatively the response of a living body; it will, however, express in a single figure the thermal demands made by the combined action of several climatic factors on the temperature regulating mechanisms of the animal body. In this respect combined climatic indices may serve a useful purpose.

In heat tolerance studies, however, it may be important to know the isolated effect of single climatic factors. Indeed, heat tolerance may be limited by a "climatic master factor", such as solar radiation in the desert and air humidity (at an elevated level of air temperature) in the jungle, emphasising the importance of coat character in the one instance and of evaporative cooling in the other instance. Thus, for different types of "hot" climates selection of heat tolerant animals may have to concentrate on different and specific animal characters. For this reason one might conceive several different heat tolerance tests, each giving specific information on the effect of one dominating climatic factor. In this way one could think of a dry heat tolerance test, a humid heat tolerance test and a radiant heat tolerance test.

There is also the possibility of using non-climatic factors as stress producing agents in a heat tolerance test. Heat generated in the body by physical exercise and drug-induced fever are two such possibilities. In heat tolerance tests with man it is common practice for the subject to perform work in a warm atmosphere. Consequently these subjects are exposed to the combination of two stressors which are largely additive in their demands on the thermoregulatory capacity of the body. Such combined tests might be of use also in cattle, since a hot environment and the necessity to walk long distances (insearch of water and food) are often linked with each other in the tropics. A heat/exercise test for cattle, although of a special type, has been devised by Dowling (1956). Such tests, while giving most valuable information may be difficult in their interpretation. A good score in the test might be due to a high efficiency in eliminating heat from the body, or alternatively, to a high efficiency in producing physical work with a minimum caloric cost. Moreover, such tests usually require extra facilities and labour; they therefore should be made the subject of a special investigation rather than the basis of a standard procedure of a general heat tolerance test.

Even stronger reservations must be made regarding the use of drugs for raising body temperature in a heat tolerance test, because in fever, in contrast to hyperthermia, the setting of the central "thermostat" of the body is changed to a higher level so that thermoregulatory reactions work in relation to this new setting.

QUANTITATIVE ASPECTS

The effect of a hot environment on the body depends not only on the nature of the climatic factors involved, but also on their intensity. If the temperature of the environment equals that of the animal and, at the same time, the air is completely saturated with water vapour, the animal cannot lose any heat to the environment. Changes in body temperature, measured under such conditions, reflect the accumulation of body heat which cannot be dissipated.

In order to obtain information on the efficiency of the various channels of heat loss, gradients in temperature and humidity between an animal and its surroundings must be established by lowering the environmental temperature, the air humidity or both. If the air humidity is lowered, heat loss becomes possible, but only through evaporation. A dry atmosphere at body temperature has the advantage that the number of possible explanations for any physiological changes observed in the animal is reduced. It is obvious that a heat tolerance test, intended to give information on the efficiency of sweating, has to be conducted in a relatively dry atmosphere, in order to allow the sweat secreted to have a cooling effect.

Considering the overall intensity of a climate, not in terms of physical units, but in terms of animal response, 4 degrees of severity, namely, mild heat, moderate heat, severe heat and excessive heat may be arbitrarily differentiated and described as follows:

- (1) MILD HEAT: The thermoregulatory mechanisms of the body can cope completely with the heat load, so that body temperature remains normal.
- (2) MODERATE HEAT: The thermoregulatory mechanisms work at a highter intensity; body temperature can be stabilised but at an elevated level.

- (3) SEVERE HEAT: The functional reserves of the thermoregulatory mechanisms are becoming exhausted; body temperature rises continually.
- (4) EXCESSIVE HEAT: The thermoregulatory mechanisms are grossly overtaxed; the animal succumbs within a short time. A differentiation between severe heat and excessive heat may be difficult in some instances.

On which of these degrees of thermal intensity should a heat tolerance test be based? The use of mild heat might be advocated, because mild heat activates the heat loss mechanisms without causing a displacement of body temperature. To measure these early and subtle changes in the temperature regulating mechanisms might appear more satisfactory than to measure their activity at a level where they are already accompanied by signs of heat distress. Yet, under field conditions, significant changes in body temperature do occur, if only of a transient nature. An extrapolation from the effects of mild heat to those of moderate or severe heat may not be permissible. Indeed, such an extrapolation would appear as equally problematic as selecting a team of prospective Mount Everest climbers on the basis of tests carried out on lowland hills.

Moderate heat would best simulate conditions prevailing in sub-tropical and tropical regions at least over certain periods. It would also leave the animal in a state of thermal equilibrium which facilitates the measurement of various body functions.

With regard to severe heat, it is true, of course, as has been pointed out by Ladell (1957), that any climate in which thermal equilibrium cannot be attained or established, is, strictly speaking, intolerable. But, severe heat will always be tolerated for a limited period. This happens for instance during the diurnal cycle of a tropical day, when the heat load becomes maximal for a few hours around mid-day. It would not therefore be unrealistic to test an animal's heat tolerance under the impact of severe heat. Heat tolerance may then be expressed in terms of tolerance time, by measuring the time for which a standard hot environment can be endured before the body reaches an arbitrarily chosen level of temperature.

Excessive heat has been used in several species of laboratory animals in order to determine lethal temperatures. The knowledge of the highest body temperature and the maximal environmental heat load just compatible with life would be of interest because it would furnish a ceiling value of heat tolerance. If the lethal body temperature of cattle were to be found to be a consistent figure, it could be made the upper limit of a heat tolerance scale. In judging an animal's heat tolerance, one might then state for instance: the animal's body temperature has approached its lethal value by x degrees, rather than state that its body temperature has risen y degrees above normal. It might well be possible that the lethal body temperature is less variable than what is accepted as normal body temperature so that it would be a more reliable base of reference. It also seems logical to express a physiological response as a fraction of its maximal response, thus getting an indication of the margin still in hand. Whatever useful information might be drawn for a heat tolerance test from the knowledge of an animal's lethal body temperature, this value could be established only in a limited number of animals. Excessive heat, therefore, cannot be applied in routine heat tolerance tests.

From these considerations it would appear that the choice for a suitable thermal environment for a heat tolerance test would be between moderate heat and severe heat. Both conditions are realistic, in that they may occur naturally.

Since, with rising intensity of the external heat load, the duration of a heat exposure may (in some cases must) be shortened, heat tolerance tests carried out in severe heat are of short duration, which is convenient in routine testing of large numbers of animals. In these conditions individual differences in heat tolerance will also show up best which will facilitate the subsequent selection of animals.

It is appreciated, of course, that what is mild heat to one animal may be moderate heat to another animal. These categories simply relate to the response of the average animal with extreme animals varying upwards or downwards. The interest with regard to animal selection lies with the heat tolerant individuals, i.e. with those whose response to heat is below average.

BODY STRUCTURES

Various structural features of the animal body, such as the surface/mass ratio and the texture and colour of the hair coat, must, from a consideration of physical laws, be expected to have a bearing on the body's thermal balance. A large relative body surface, in particular large body appendages (dewlap, navel fold, ears, tail), a short glossy coat and a well pigmented, movable skin are generally considered as characters associated with a high heat tolerance.

To what extent this represents a direct causal relationship is not yet sufficiently known. McDowell, Lee & Fohrman (1953) did not find significant differences in the surface/mass ratio between European and Zebu cattle, which otherwise differed in heat tolerance. McDowell (1958) found that surgical removal of hump and dewlap in Red Sindhi bulls did not depress their heat tolerance, as judged by rectal temperature and respiratory rate, although it would appear that the test atmosphere employed (40.5°C) would not exclude the possibility that such appendices at lower air temperatures could be useful devices for losing heat by radiation and convection.

A clear relationship has been established between coat texture and heat tolerance (Bonsma, 1949). Animals with a sleek coat withstand heat better than animals with a woolly coat Similarly, a high proportion of medullated hair fibres in the coat favours heat tolerance (Dowling, 1959a). Recently Turner & Schleger (1960) have described a subjective method for scoring of cattle coats which seems to afford a good prediction of cattle performance in a hot climate.

The establishment of such correlations may be of great practical value for several reasons. Many of these body structures can be determined very easily, some of them even without instrumental measurements (see: felting test, p. 15). They also tend to have a high degree of heritability which facilitates their genetic fixation by breeding. Structural features which have clearly been shown to be correlated to physiological responses indicative of an animal's heat tolerance, possess prognostic value. The knowledge of these features may enable a breeder to predict the future heat tolerance of a young animal. Moreover, this can be done, without subjecting the animal to heat, i.e., in a temperate climate.

It should be realised, however, that any such structure is not eligible as a criterion in a heat tolerance test proper, because it does not change measurably during exposure to an acute standard heat stress.

BODY FUNCTIONS

A hot environment affects the entire animal. This means that a great number of physiological activities undergo specific changes. The information derived from a heat tolerance test should thus be expected to become more complete the larger the number of activities observed.

However, the use of a large number of criteria in a heat tolerance test, has the disadvantage of complicating the performance of a test. Also in view of using the result of a heat tolerance test for animal selection, a large number of criteria may be undesirable since selection becomes progressively more difficult and less effective, the larger the number of animal characters that are taken into account.

It is necessary, therefore, to make an optimal choice among the various body functions. Although there are interrelationships between the various physiological activities of the body, suggesting that the behaviour of any one of them might be representative of all the others, some of these activities will be better suited than others, to serve as criteria in a heat tolerance test. There are also some special points which have to be borne in mind, as may become clear from the following considerations:

- (1) Many body functions are related to and therefore indicative of either heat production or heat loss of the body. Yet, heat tolerance is the resultant of both these processes. Although a heat tolerance test is not a procedure meant to measure an animal's thermal balance this is the object of calorimetry it is not entirely satisfactory to judge heat tolerance only in terms of either a heat loss mechanism or in terms of a character pertaining to heat production.
- (2) The interpretation of isolated heat responses of the animal may be made difficult by two or more of them behaving in a compensatory fashion with each other. Man cools by sweating, but normally not by panting; the dog, in contrast, cools by panting but not by sweating. Cattle make use of both these avenues of cooling in variable proportions. Some cattle, notably European breeds, are poor sweaters. This inadequacy is to some extent compensated for by increased respiratory activity. Other cattle, notably tropical breeds, are better sweaters, which enables them to have less recourse to respiratory cooling, at least as long as the heat stress is moderate. If it becomes severe, even the good sweater will increase its respiratory activity and eventually bring it to the same level as that of the poor sweater. The good sweater, however, has the advantage of possessing a functional reserve of respiratory cooling which may be gradually mobilised as the environment becomes hotter. This point, incidentally, again stresses the importance of carefully choosing the degree of severity of heat used in a heat tolerance test. Compensatory changes between various avenues of thermal flow during acclimatization of man to dry heat have been described by Eichna, Park, Nelson, Horvath & Palmes (1950).
- (3) With rising environmental heat load, the action of the various heat loss mechanisms seems to take place in a sequential manner emphasising several "lines of defence". In a temperate environment body cooling occurs principally by radiation and convection. As the environment becomes warmer, skin evaporation is intensified, which in turn becomes supplemented in a progressive way by respiratory evaporation. This sequence, incidentally suggests a sequence of rising caloric expenditure per unit of cooling achieved. Losing calories by radiation and convection is an inexpensive way of cooling; losing them by the activity of sweat glands is probably more expensive; and losing them by forced convection from the respiratory tract is a most expensive way because it involves muscular activity. Cooling by a high respiratory activity not only has the disadvantage of being a heat producing process itself, but also one which may affect the acid-base status of the body by the elimination of an excessive amount of carbon dioxide (Dale & Brody, 1952; Bianca, 1955).
- (4) A further complicating factor arises from the fact that the process of losing heat by radiation or convection has a thermal reversal point. In an environment below skin temperature there is a thermal flow from the animal to the environment. Once the environment becomes warmer than the skin, the thermal flow becomes reversed. Consequently, radiation and convection, at first avenues of heat loss, become avenues of heat gain.
- (5) Finally, it is known that respiratory frequency, with increasing heat stress, acts in a discontinuous way. It rises rapidly to a maximum; if the demand for cooling continues to be high, it then declines (Findlay, 1957; Bianca, 1958). As the minute volume of respiration rises continuously throughout, this means that a given respiratory rate, say 150 respirations per minute, has a different significance as regards ventilation, in the rising phase from what it has in the declining phase.

These considerations show that it may be difficult to assess correctly what the action of a given isolated heat response means to the animal in terms of actual heat strain.

Bearing in mind difficulties of this kind, it may be postulated that a body function, eligible as a criterion for a heat tolerance test, should fulfil the following requirements:

- (1) It should be meaningful, i.e., directly related to the body's thermoregulation and consequently truly representative of the strain the animal may experience in a hot environment.
- (2) It should respond to envrionmental heat in a ready and reproducible way, i.e., show a clear dose/response relationship.

(3) Its measurement should be accurate, quick, simple, and inexpensive.
(4) It should have a normal base line, i.e., show relatively little variation in a temperate climate, both within and between animals, thus affording a proper base for any changes that might occur due to heat.

(5) It should be applicable also in the young animal, thus allowing an early prediction of an adult animal's heat tolerance.

When considering various animal functions, it is evident that body temperature meets these requirements best. In particular, body temperature is an expression of the body's thermal balance, since all heat gain and heat loss processes of the body are ultimately reflected in its temperature. Indeed, body temperature indicates in a single figure to what extent the thermoregulatory mechanisms have been successful in maintaining homeothermy. With regard to its measurement deep body temperature is adequately represented by the temperature of the rectum (Bligh, 1957).

There are three objections which might be raised against using body temperature as a criterion of heat tolerance.

- (1) In heat stressed man breakdown may occur without the body temperature being much elevated (Bean & Eichna, 1943). Here, body temperature obviously would be a poor incicator of heat tolerance. This behaviour, however, is probably more typical of man than of cattle. In man, who has an erect body posture and who sweats profusely, circulatory failure may develop before hyperthermia. In the bovine animal which has a non-erect posture and which sweats only moderately, this is not known to happen. Whenever cattle are distressed by heat, as evidenced by various signs such as profuse salivation, high respiratory activity and anorexia, body temperature is invariably above normal.
- (2) It might be questioned whether a rise in body temperature in a heat exposed animal would necessarily be a sign of heat intolerance. Might not a labile body temperature, at least within certain limits, be a means of losing heat, by establishing a larger gradient of heat flow between the body and its environment? Schmidt-Nielsen, Schmidt-Nielsen, Jarnum & Houpt (1957) express the view that a high body temperature in heat exposed cattle may be indicative of a high heat tolerance, and that in consequence, it may be unwise to select cattle for hot climates on the basis of a non-elevated body temperature. Schmidt-Nielsen et al. (1957) have shown that the camel's body temperature may have a daily variation in excess of 6°C. This variation does not indicate a failure of temperature regulation but is part of a well-regulated physiological mechanism for the conservation of water. While the camel seems to be adapted by evolution to tolerate an elevated body temperature without distress, or even without anincreased respiratory activity, the same cannot be said of cattle. In cattle a body temperature significantly above normal is always accompanied by anumber of obvious signs of heat distress. It may be noted that the variation in the camel's "normal" body temperature covers the range 34° to 41°C, i.e., it extends to very low temperatures. Thus, starting the day following a cool night with a body temperature of say, $34^{
 m o}$ C, would give the camel the advantage of a low "starting point" for the subsequent heating up period during the day. The possibility of a similar thing happening in cattle, although on a much reduced scale, has been discussed by Bianca (1959).

(3) Rapid changes of the thermal environment are not immediately reflected in the body temperature measured per rectum. Changes occur with a lag, and this lag increases with increasing size of the animal. This difficulty, however, may be largely overcome by a well-defined tecanique for measuring heat tolerance and by not comparing "incomparable" quantities. It is commonsense, for instance, to avoid a direct comparison between a small calf and a big bull, with respect to their tolerance time in an acute exposure to severe heat.

It would thus appear that body temperature, when properly used, is the best single physiological criterion of heat tolerance.

ECONOMIC TRAITS

The production of milk and of beef are physiological activities which are related to heat tolerance in two ways:

- (1) They involve the generation of extra heat, which reduces the capacity for heat tolerance.
- (2) They become depressed when the environment is very hot, which favours heat tolerance.

Should then, in view of this relationship, these economic traits be used as indicators of heat tolerance? Or indeed, should one go directly for the production of milk and meat, which after all are what cattle are bred and kept for, and dismiss heat tolerance altogether? Cartwright (1955) has found weight-gain in summer a more useful indicator of heat tolerance than rectal temperature, respiratory rate and heart rate, and Vernon, Damon, Harvey, Warwick & Kincaid (1959) in Louisiana have postulated that the selection of beef cattle on the basis of production automatically also includes sufficient selection for heat tolerance. Although this approach has much to recommend it, it also has its limitations, especially with respect to milk yield.

The most obvious limitation, of course, is that milk yield cannot be tested in young animals. This excludes the prediction of an animal's future performance from a calfhood index. Furthermore, milk yield is affected by a hot environment in an indirect way: a decline in milk yield is preceded by a decline in voluntary food intake. There seems to be no immediate effect of hot weather on milk production as long as food consumption is not affected (Johnston, 1958). At what magnitude of environmental heat load animals will begin to reduce their voluntary food intake, depends on their heat tolerance. European breeds have a lower threshold value than tropical breeds (Worstell & Brody, 1953), and there seem to be differences also between animals of the same breed. Thus, of two cows which have the same genetic capacity for milk yield, the one with the higher capacity for heat tolerance will be the better producer in a hot environment. It is possible that the reduction in voluntary food intake applies in the first place to food with a high fibre content, the digestion of which produces much waste heat. In this case a ration containing a high proportion of concentrates should be expected to interfere less with appetite and thus with milk production. There also seem to be individual cows whose "physiological wisdom" does not induce them to subordinate milk secretion to temperature regulation. They seem to do this, however, at the expense of a high body temperature. Payne & Hancock (1957) have reported such a case. It could be that this is the type of animal one should select for.On the other hand milk produced from cows in a febrile state may not be qualitatively satisfactory and the animal itself, under the double burden of producing large quantities of milk and combating heat at the same time may have a lowered resistance to disease and other stresses.

It may be said in conclusion that productive performance seems to be useful as an indicator to heat tolerance or indeed, as a quantity in its own right with beef cattle, but that it appears to be less useful in these respects with dairy cattle.

METHODS FOR GRADING HEAT TOLERANCE

GENERAL

There are two ways of expressing an animal's heat tolerance. (1) One may ask: How much does a certain body function change when the animal is exposed to a standard hot environment? This is the commonly used way, or (2) one may ask: Which heat load must be imposed on an animal in order to evoke a standard change in body function? This way is less common with respect to climate, but it is often used for testing tolerances to other stress producing agents. The tolerance to alkali, for instance, is measured by the amount of alkali that must be given in order to cause an alkaline urine. Both ways have merits and limitations, as may be seen from the following comparison.

The first way, which expresses heat tolerance in terms of animal response, has the advantage of being relatively easy to perform and of giving a precise numerical answer. It is, however, limited in its interpretation.

The second way, which expresses heat tolerance in terms of athermal environment, is less easy to perform and normally less precise in its result, because it requires each animal to be exposed in succession to a series of different environments possibly with interpolation to be made between the two nearest environments. On the other hand, it is more meaningful in its interpretation. It may result, for instance, in the statement that the animal under investigation is capable of tolerating an environmental temperature of X degrees before showing a certain standard response. This knowledge in turn may be of use in predicting this animal's reaction to the thermal conditions prevailing in a certain geographical region. Which of these two ways of expressing heat tolerance will be adopted depends largely on the special problems and the facilities available.

The following pages are devoted to a brief description of various tests which have been used or advocated for use in assessing and grading heat tolerance in cattle.

WATER EXPENDITURE TEST

Rhoad (1940) under field conditions measured parameters indicative of an animal's water loss through various channels, namely:

- (1) respiratory rate, as an index of moisture loss from the respiratory tract;
- (2) loss of moisture from selected skin areas;
- (3) nitrogen concentration of the urine, as an index to water expenditure through the kidneys;
- (4) moisture content of the faeces, as an index to water expenditure through the excreta.

The test periods ranged from 1 to 10 hours with an average of 3 hours. Water at atmospheric temperature was available at all times.

This is a most useful approach to an important side of the heat tolerance problem and Rhoad has been able to demonstrate with his method clear breed differences. It seems, however, that the method, even in the simplified field version used, is too complicated to be adopted as a heat tolerance test proper. On the other hand it does not measure an animal's water loss accurately enough. Rhoad probably did not intend to use the results of these measurements as components of a heat tolerance index, since he did not condense the data into any formula. For judging the "efficiency of heat disposal" Rhoad relied on the behaviour of rectal temperature, which, at a later stage, he extended to the Iberia heat tolerance test.

IBERIA HEAT TOLERANCE TEST

In this test, developed by Rhoad (1944) one determines how much the rectal temperature of an animal exceeds $101.0^{\circ}F$ (38.3°C) when the animal is exposed in the open field to the thermal conditions of a calm clear day with a shade temperature between 85° and $95^{\circ}F(29^{\circ}$ and $35^{\circ}C)$. The rectal temperature measurements are taken at 10.00 and 15.00 hours on three consecutive days and the results averaged. By using the formula

the result is expressed as a percentage of maximal efficiency in maintaining rectal temperature at $101.0^{\circ}F$, the average rectal temperature of cattle. Respiratory rate, which is counted at the same time, may be used as an additional criterion to differentiate between two animals showing the same rise in rectal temperature. The animal with the least rise in rectal temperature (and the lowest respiratory rate) is considered the most heat tolerant.

This test is based on a sound principle and is easily performed. It has been used extensively for differentiating between the heat tolerance of various breeds of cattle.

While it is thus a most useful test for field conditions, it has certain limitations which must be borne in mind when it is used for work demanding a higher degree of accuracy. The two main limitations are: (1) that the environmental conditions are not sufficiently standardized and (2) that 101.0°F, being an average figure for rectal temperature of cattle, does not make allowance for normal variation of this parameter due to age, breed, level of feeding, level of production, etc. The first point becomes apparent, for instance, in a comment by Phillips (1948) on an interbreed comparison: "These results cannot be considered conclusive evidence of superior heat tolerance in breed X, since the environmental temperature at which tests were made were somewhat lower than in the breed Y, and these differences may have been sufficient to distort the results". With regard to the second point it is particularly important to make allowance for the fact that, other factors remaining equal, young animals tend to have a higher normal body temperature animals. So, if a young animal has a normal body temperature of, say 102°F, rising to 104°F under the influence of a hot environment, its heat tolerance figure is 70 if calculated on the basis of 101°F, but 80 if calculated on the basis of 102°F. In other words, the test tends to give falsely low figures for young animals due to their higher initial level of body temperature. Conversely, the test tends to give falsely high figures for animals whose normal body temperature is below 101.0°F. This dependency of the result of the Iberia heat tolerance test on the animal's normal body temperature may be further exemplified by a report of an investigation of the heat tolerance of agroup of young animals (0-1 years) and that of a group of older animals (1-4 years). The test yielded 77 for the young group and 89 for the older group. If the heat tolerance of the two groups are computed on the basis of the body temperatures actually measured in these animals in a temperate environment, figures of 79 and 86 are obtained. This means that the difference in heat tolerance between the two age groups shrinks from 12 to 7 units,i.e. it becomes almost halved. It has to be realised, of course, that it may be very difficult or even impossible under field conditions to obtain a "normal" body temperature, in which case recourse must be had to a fixed standard figure.

R-VALUE HEAT TOLERANCE TEST OF LEE

Lee (Phillips & Lee, 1948) developed what he termed a laboratory analogue to the Iberia heat tolerance test. Essentially, it consists of a 7 hr exposure of the animal to a series of atmospheres at different known temperatures and humidities. The rectal temperature is measured periodically and an expression of its mean behaviour, called R-value is calculated.

The R-value represents the area between the abscissa and the curve in a time-rectal temperature diagram. From the R-value for the different combinations of temperature and humidity the value of the constants a, b and c in the equation log R = at + bh + c, where t is temperature and h is vapour pressure, may be calculated. The values of a, obtained upon two different animals indicate the relative fashion in which the rectal temperature rises in response to atmospheric temperature for a given humidity, and those of b in response to a rise in atmospheric humidity, for a given temperature, over the range of conditions used in the series of experiments. Similar procedures can be adopted with respect to respiratory rate, pulse rate, etc.

This test has the merit of a controlled environment and an integrated response of the animal. On the other hand whether an animal was in a steady or in arising phase with regard to the parameter investigated cannot be derived from an isolated R-value. Furthermore, if, as a result of a too rapidly rising body temperature, an animal has to be removed from the test atmosphere before the 7 hours of exposure have elapsed, an extrapolation technique has to be used (Robinson & Klemm, 1953).

BENEZRA'S COEFFICIENT OF ADAPTABILITY

Benezra (1954) postulates a summation of the body temperature response and the respiratory rate response by using the formula body temperature (in 0 C)/38.33 + respirations per min/23 = 2. A value of 2 would represent the norm or a state of maximal adaptability, a value above 2 a state of a lower adaptability. While it seems a reasonable idea to take into consideration also an animals respiratory response, it is not correct to give it equal weight with the body temperature response. A 10% increase in body temperature i.e. to 42.2°C, would eventually cause death, while a 10% increase in respiratory rate i.e. to 25 respirations per min is physiologically meaningless and probably even lies within the counting error.

LINES OF EQUAL EFFECT

Barrada (1957) constructed empirically lines of equal effect by charting separately the reactions of rectal temperature, respiratory rate and respiratory volume of cattle to different combinations of wet and dry bulb temperature in a temperature-vapour pressure diagram. He found that these lines change their slope as one passes from cooler conditions to hot conditions in much the same way as those obtained for humans. This is a very useful concept for the description of the combined effect of temperature and humidity on physiological reactions. The procedure may, however, be too elaborate to be used as a test of heat tolerance.

VARIOUS TESTS OF ADAPTABILITY OF CATTLE TO LIFE IN HOT COUNTRIES

Bonsma (1949) has described a number of procedures which are not heat tolerance tests in the strict sense of the word, but tests which give valuable information on an animal's general capacity to live in a hot country under ordinary field conditions.

In the "felting test" a sample of hair is taken from the animal, damped with water and rubbed between the hands. If the hair forms a firm mass, i.e. felts, this indicates a smooth coat, if the hair rubs away, this indicates a woolly coat. Confirmatory evidence of this behaviour of the two types of coat was obtained by subjecting the hair samples to a felting process in a wool factory and testing the resistance of the compressed hair mass to a pulling force. According to Bonsma a woolly coat is associated with a low heat tolerance and a smooth coat with a high heat tolerance. Thus, examination of a hair sample would afford a simple means for judging indirectly an animal's heat tolerance. Apart from its simplicity such a method has the merit of being applicable to very young animals and not requiring exposure to a hot environment.

The work of Bonsma can hardly leave any doubt that there is a definite association between coat character and heat tolerance; also the work of Yeates (1955), Dowling (1959b) and that of Turner & Schleger (1960) leads to the same conclusion. It would be desirable, however, if the coat characters could be expressed in a more quantitative and objective way and if the nature of this association could be further elucidated. It is for instance not entirely clear to what extent it is a dense coat per se that depresses heat tolerance by interfering with heat loss from the skin, and to what extent a dense coat is only the outward sign of an inner function, probably of endocrine nature, more directly related to heat tolerance. Thyroid activity, for instance, is known to affect hair growth as well as heat production which in turn influences heat tolerance. It could be speculated that a thin coat could be a "byproduct" of the chain of events, connecting atmospheric heat, over depressed thyroid activity, reduced metabolic rate and lowered heat production with increased heat tolerance. There is also the possibility that in contrast to the more obvious case that the coat affects the heat tolerance, the heat tolerance could affect the coat. This could be the case, for instance, when an animal with a low heat tolerance would reduce its food intake which would then cause a state of malnutrition and of lowered resistance to disease, leading to changes in coat character.

In "walking tests" and in "water deprivation tests" Bonsma (1949) demonstrated the superiority of African cattle over European type cattle in covering long distances and in going without water over certain periods of time, in a semiarid region.

"COOLING EFFICIENCY" TEST OF DOWLING

Dowling (1956) considers the Iberia heat tolerance test as unsuitable in the hot dry inland climate of Australia, because the excessive solar radiation may cause loss of control of body temperature regulation in the animals, in which state, in Dowling's opinion, body temperature would not be a meaningful criterion of adaptability to heat. Hetherefore proposes a heat tolerance test which should be based solely on an animal's capacity for dissipating excess body heat, without the complication of a simultaneous heat load from solar radiation. His procedure is as follows: The animal is exercised on a warm day for about half an hour until the rectal temperature reaches about 40°C (104°F), after which it is allowed to stand in the shade to cool down. The rate of cooling is followed by periodic measurements of rectal temperature. The animal which shows the highest rate of decrease of body temperature is considered to have the highest "cooling efficiency".

The concept of cooling efficiency is, no doubt, an interesting one. It would appear, however, that the higher the intensity of solar radiation the more important it would become for an animal not only to have a high capacity for dissipating heat but also to have structural features, especially of the coat, which oppose the absorption of radiant energy from the sun. When devising a heat tolerance test for animals living in a region where solar radiation is excessive, thus constituting the limiting climatic factor for heat tolerance, it would seem to be more realistic to include this very factor in the test than to exclude it. In order to avoid the development in the animal of serious hyperthermia, the duration of each test would, of course, have to be restricted in time. Although in a test based on a short exposure to an extreme heat load, as Dowling has realized, the animal is in a state of acute thermal imbalance, the result of such a test may still be of value because it includes the effect of the principal stress producing climatic element, which, in this case, is solar radiation.

PREDICTED HEAT TOLERANCE FROM CALF TOTAL MOISTURE VAPORISATION RATES

Yeck & Kibler (1958) reported that the ratio total evaporation (skin plus respiratory) in an environment of 270C/total evaporation in an environment of 10°C, correlated very well with the relative heat tolerance of calves of 6 different breeds. The highest ratio (2.75) and the highest heat tolerance were found in the Brahman; the lowest ratio (1.35) and the lowest heat tolerance in the Shorthorn, with the other breeds in between in the following order of falling heat tolerance: Santa Gertrudis, Brown Swiss, Jersey, Holstein. These ratios changed very little for each breed with advancing age.

This is an impressive demonstration of the role played by evaporative cooling in the thermoregulation of cattle. As the accurate measurement of total evaporation is a fairly elaborate procedure it may be simpler to assess heat tolerance by amore easily measurable character such as body temperature.

HUMAN HEAT STRESS INDICES

The literature contains a number of indices devised to assess the severity of hot climates or the physiological strains resulting from them in man. The best known of these indices are:

- (1) Effective temperature, Houghten & Yaglou (1923).
- (2) Standard operative temperature, Gagge (1940).
- (3) Index of physiological effect, Robinson, Turrell & Gerking (1945).
- (4) Corrected effective temperature, Bedford (1946).

- (5) Predicted four hour sweat rate, McArdle, Dunham, Holling, Ladell, Scott, Thomson & Weiner (1947).
- (6) Heat stress index, Belding & Hatch (1955), and
- (7) Singapore index, Webb (1959).

These indices are mostly highly specific for humans. They make use of constants derived from humans; some depend on the sensation of warmth rather than objective measurements of physiological reactions of the test subjects; the predicted four hour sweat rate, which at present is considered the best index, is based on sweating, a heat response which in cattle does not play an equally dominating role as it does in man; and there is also the complication arising from the consideration of modifying factors such as clothing and physical activity.

These human heat stress indices, therefore, are not readily applicable to cattle. A possible exception may be the index of physiological effect, which may be modified to suit cattle.

From this description of various methods for grading heat tolerance it would appear that many of them provide useful information but that none of them is entirely satisfactory. Rhoad's "classical" Iberia test probably is still one of the best. In view of the necessity to select cattle for hot climates there is a definite need for an improved method for assessing heat tolerance.

FACTORS WHICH MODIFY HEAT TOLERANCE

GENERAL

Every animal character is a function of heredity and environment. Heat tolerance as an aid to selection for subsequent breeding is of interest only as far as it is genetically determined. The genetic potentialities for heat tolerance can only find their full expression in the presence of appropriate conditions of nutrition, management and disease control. Furthermore, heat tolerance depends on factors which will or may vary during the life of the individual, such as age, state of activity, level of production, and acclimatization. In some cases these factors have to be accepted, as they are; indeed, they may be pertinent to the problem under investigation. It is important, therefore, to know which factors influence heat tolerance and to what extent they do so. Once this is known one can either standardize these factors, or, if this is not possible, eliminate their effects by making suitable adjustments. Although it is realised that many of these factors are inter-related it is convenient to discuss each of them separately.

AGE

A few preliminary remarks of general character may be appropriate. Tolerance is the reciprocal function of sensitivity (Loewe, 1959). The young animal tends to be more sensitive in that it reacts more violently than the adult animal to an environmental stimulus of a given strength; it shows, in other words, a greater response. If one accepts this as being true also with regard to atmospheric heat as a stimulus, the young animal, by definition, would be less heat tolerant than the adult animal.

This statement, however, depends on two assumptions: First, that the young and the adult animal have the same range, i.e., functional capacity of response, and second, that a given deviation from the norm (of a given response) means the same to the young as to the adult animal with respect to discomfort and damage. There is some evidence against these assumptions. As regards the first point, it is known that young animals, when exposed to severe heat, have a higher maximum level of respiratory rate than adult animals. Thus a

respiratory rate of, say 180, might represent 70% of the young animal's, but 100% of the adult's full capacity. Similar conditions probably exist for heart rate.

The second point actually ties up with the first point. The discomfort experienced or the damage caused by a given level of response, probably depends on the maximal level of this response, meaning that the young animal working at, say 70% of its capacity is less stressed than the adult animal working at say 100%.

The obvious answer to this problem would be to express a heat response as a fraction of its maximal value. The assessment of the maximum value of a heat response does not present much difficulty with respiratory rate; it would also be possible with skin evaporation; it could, however, be dangerous for heart rate and certainly would be lethal for body temperature.

To what extent these points have to be taken into consideration in assessing heat tolerance in cattle of various ages cannot be decided at present. More work on the dose/response relationship of animals of different age groups is needed. In the meanwhile, the same conventional concept of heat tolerance will be used for judging the heat performance of cattle of different age groups.

Heat tolerance has been shown by various workers to increase with age.Klemm & Robinson (1955) found falling R-values for rectal temperature in Australian Illawara Shorthorns and in Zebu-Hereford crosses from 2 to 12 months of age. Walker(1957), using the heat tolerance test of Rhoad (1944), noticed a general rise of heat tolerance in Africander, Angoni, Barotse and Tonga cattle between the ages of 1 and 4 years, the largest rise occurring between 1 and 2 years. In Jersey cows ranging in age from 2 to 6 years and over, Galaas (1947) found the lowest heat tolerance in the 2 to 3 year class, the highest in the 3 to 4 year class. Bonsma (1949) concluded from his extensive investigations carried out in South Africa on cattle of various breeds and types: "The work indicates beyond all doubt, that an animal's heat tolerance coefficient increases considerably, especially after the second year".

The increase in heat tolerance with age does not occur in a linear way. The increase appears to be largest between calfhood and adulthood. In the adult animal heat tolerance, if not complicated by other factors such as level of production, seems to remain fairly stable. Whether heat tolerance decreases in the old animal, as one might expect it to do, is not known. When comparing the age-heat tolerance relationship of various breeds of cattle it is important to bear in mind that the chronologic age of an animal need not be identical with its physiological age. Tropical breeds tend to be later maturing than temperate breeds.

The problem of the influence of age on heat tolerance needs further investigation; not only because the problem is of immediate practical importance, but also because the know-ledge of the age-heat tolerance relationship may help the nature of heat tolerance to be better understood. If we find that heat tolerance shows a significant increase from say half a year to 2 years, this must be accompanied by corresponding structural or functional changes in the animal, taking place over the same period. Characters which during this period do not change or even change in the wrong direction obviously cannot be made responsible for the observed changes in heat tolerance. This consideration would apply to sweat gland density, i.e. the number of sweat glands per unit of skin surface, which has been shown to decrease with age (Findlay & Yang, 1950; Carter & Dowling, 1954; Walker, 1957). It would also apply to the surface mass ratio of the animal, to the capacity for maximum respiratory rate, and to the amount of subcutaneous fat, all of which with advancing age tend to change in the direction of a lowered capacity for heat tolerance.

On the other hand there are body functions which tend to change with age in the direction of an elevated heat tolerance. Skin evaporation, in spite of a decrease in sweat gland density and probably due to an increase in the size and the efficiency of the individual sweat gland, increases with age (Klemm & Robinson, 1955; Kibler & Yeck, 1959). Heat production per unit body weight declines with age (Kibler, 1957) and this seems to be paralleled in part by a decrease in thyroid activity (Blincoe, 1958; Lennon, 1958). Closer in-

vestigation of these functions may lead to a better understanding of the factors that control heat tolerance in cattle.

NUTRITION

Nutrition can affect heat tolerance in several ways.

- (1) A high plane of nutrition is associated with a high resting metabolic rate, which in turn depresses heat tolerance. Robinson & Lee (1947) have reported that sheep, pigs and hens on a high plane of nutrition had a reduced heat tolerance as indicated by elevated levels of body temperature, heart rate and weight loss during the test. Similarly, Yeates (1956) found well fed cattle to be less heat tolerant than poorly fed cattle, the respective heat tolerance coefficients (Rhoad, 1944) being 43 and 55. The work of Sorensen, Hansel, Hough, Armstrong, McEntee & Bratton(1959) suggests that an increased thyroid activity is involved in this elevated resting metabolic rate of cattle on a high plane of nutrition.
 - A high level of nutrition may reduce heat tolerance not only by raising resting metabolic rate, but also by causing interference with heat loss through the deposition of fat under the skin. In this context it is of interest to note that Zebu type cattle, seem to lay down body fat preferentially in the interior of the body, while European type cattle do so under the skin (Ledger, 1959).
- (2) The processes of prehension, mastication, digestion, absorption and metabolism of food generate heat, which again depresses heat tolerance. While these processes are going on, especially in the early phases, body temperature, heart rate and respiratory rate of calves are elevated, even in a temperate climate (Bianca, unpublished data). Conversely, starvation is accompanied by a fall in heat production and heart rate (Blaxter & Wood, 1951). Furthermore, it has been shown by Yeates (1956) that the important factor in the feeding/heat tolerance relationship is the current rate of feeding. In other words, it is relevant how much the animal, whether lean or fat, has eaten shortly before the performance of a heat tolerance test. An adequate period of starvation before a heat tolerance test is therefore essential for obtaining reproducible results. On the other hand, since animals, in order to live and produce, have to eat, it is, with respect to heat tolerance, important that the various processes associated with the intake, digestion and absorption of food, produce a minimum of waste heat. Obviously the animal which does so, i.e., which utilises food efficiently, must be more heat tolerant than an otherwise similar animal which utilises food less efficiently. This applies in particular to roughage since this contributes the bulk of the food and requires much energy for its breakdown.
- (3) The composition of the food mry affect heat tolerance. Cows and buffaloes fed on hay had significantly lower respiratory rates than animals fed on straw (Badr,1957). Similarly, a ration with a low fibre content, as compared to one with a high fibre content, had a beneficial effect on the performance of cows in Arizona when air temperatures exceeded about 27°C (81°F): respiratory rate was lower by 14 beats/min and body temperature by 0.5°F (0.3°C). The production of fat corrected milk was higher by 1.2 lb per cow and day (Stott & Moody, 1960). According to Page, Erwin & Nelms (1959) cattle which were deprived of vitamin-A reserves were unable to withstand high summer temperatures. It was also shown that the hot climate itself was the predisposing factor for a low vitamin A level; calves maintained at a high ambient temperature lost three times as much vitamin A from their livers than their co-twins at a normal temperature. Similarly, rabbits deficient in vitamin A had a reduced time of survival when exposed to heat (Kurokawa, 1941). Mineral deficiencies in the food may likewise affect body structures and functions which play a role in thermoregulation.

The depressing effect of a high food intake on heat tolerance does not continue without counter-action. With rising environmental temperature food intake is reduced and eventually completely suppressed. This means, that food intake acts as a temperature regulating

mechanism, i.e., that the amount of food eaten is determined, at least partly, by the organism's ability to dissipate the heat of food metabolism, as has been suggested by Brobeck (1948). This regulating action of appetite should be expected to set in earlier, i.e., at a lower environmental temperature, in heat intolerant animals than in heat tolerant animals. There is some evidence that heat anorexia occurs earlier in European type cattle than in tropical cattle (Johnson, Ragsdale & Yeck, 1958).

While heat tolerance is affected unfavourably by a high food intake, it is affected favourably by a high water intake, because water is the indispensable raw material for evaporation, which plays a vital part in heat tolerance. A high water intake in itself does not necessarily guarantee a high heat tolerance. Consuming cool water, warming it to body temperature and excreting it through the kidneys will, of course, have a cooling effect. Indeed, the "famous" Jersey cow 212 (Thompson, Worstell & Brody, 1949) when exposed to an environment of 38°C (100°F), by drinking the unusual amount of 195 litres of water per day, in this fashion rid herself of over 4,800 kcal per day. Yet, evaporating the water instead of circulating it through the body, is a much more efficient way of utilizing the cooling potentialities of water. If all the 195 litres of water could have been evaporated, the cooling effect would have been about 23 times greater. Kibler and Yeck(1959) expressing vaporized water as a percentage of consumed water, found higher percentages in Santa Gertrudis and Brahman cattle than in Shorthorn cattle, indicating that the former two breeds were more efficient in utilizing consumed water for evaporative cooling. It thus appears, that consuming more water than the organism can readily evaporate is of relatively little value to the body, with respect to heat tolerance.

The effect of a deficiency of water on heat tolerance is not sufficiently known. If cattle, exposed to heat and at the same time deprived of water would behave the same way as man is known to behave under similar circumstances, they would keep up a high rate of evaporation and consequently dehydrate their body. In such a case, heat tolerance would not be lowered at least not until dehydration would affect other body functions which play a part in thermoregulation.

ACTIVITY

Physical exercise produces extra heat which has to be eliminated from the body; it is thus inversely related to heat tolerance. It is obvious, therefore, that heat tolerance tests should be carried out only in well rested animals. In a hot environment animals tend to reduce their activity; but in search of food and water they have to do a certain amount of walking, especially when the grazing is scarce and the number of water places restricted, as is frequently the case in hot countries.

The degree to which exercise depresses an animal's heat tolerance depends largely on its body build and its state of training. A slim, long legged "respiratory-type" animal will experience less thermal discomfort than a bulky, short legged, "digestive type" animal when covering the same distance, and both types will perform their task progressively in a more efficient way as their bodies get used to the exercise. Striking differences in walking capacity between Shorthorn and Hereford cattle on the one hand, and Afrikaner cattle on the other, have been demonstrated by Bonsma (1949). The superior performance of the Afrikaners - they could walk farther and showed less elevation in their body temperature - seems to have been due partly also to the smoothness of their coat, which allowed a better heat dissipation from the skin.

REPRODUCTION

It is known that the body temperature of cows fluctuates with the oestrus cycle (Wrenn, Bitman & Sykes, 1958; Fallon, 1959). The temperature is lowest just before heat, high on the day of heat, low again at the time of ovulation, and high during the luteal phase of the cyle. The difference between the lowest and the highest rectal temperature during

oestrus cycle can amount to half a degree F.This temperature pattern has been attributed to the thermogenetic influence of endogenous progesterone.

Body temperature is also affected by pregnancy; it is at a higher level and a few days before calving there is a precipitous decline of about 1.0° to 1.6° F $(0.6^{\circ}$ to 0.9° C)(references under Wrenn et al., 1959).

Thus, under these conditions "normal" body temperature will differ considerably from what might be expected in a "normal" animal. This would introduce an element of uncertainty into any heat tolerance test that contained normal body temperature as a base of reference. Furthermore, the specific physiological changes of the body associated with contained pregnancy are likely to affect an animal's capacity for tolerating ahot environment.

LEVEL OF PRODUCTION

An animal with a high level of production has a high heat production and consequently a low heat tolerance. Each 1b of fat corrected milk produced by the animal increases metabolic heat production by approximately 10 kcal per hour. A 1,000 1b cow with a resting heat production of 500 kcal per hour, producing 50 1b of fat corrected milk per day would have a total metabolic heat load of 1,000 Calories per hour, or double the resting heat load (Johnston, 1958). The level of production, of course, is closely related to the level of feeding. As the food intake becomes voluntarily reduced in a hot environment the production goes down. These two changes, however, may be somewhat out of phase with each other. The results obtained by Worstell & Brody (1953) suggest that the fall in food intake precedes the fall in production which then leads to a loss in body weight.

As a consequence of this dependence of heat tolerance on milk yield the same animal will give different results of heat tolerance according to whether it is dry or lactating and while it is lactating the result will vary with the amount of milk produced. Similarly, high producing and low producing animals (of the same breed or of different breeds) will vary among each other in heat tolerance. This, of course, makes the interpretation of any heat tolerance test difficult and calls either for comparisons to be made only at the same level of production, or for correction factors to be used.

While the level of production, plays an important role in heat tolerance it is by no means the only factor involved. The superior heat tolerance of tropical cattle is not entirely the result of their lower level of production. As shown by Johnston, Hamblin and Schrader (1958), for the same level of milk yield, Red Sindhi crossbreds were more heat tolerant than European type cattle. If Zebu cattle produce milk at the same caloric cost as European cattle, which seems a reasonable assumption to make, their superiority in heat tolerance would be the result of a lower resting metabolic rate, of a higher loss or of both.

ACCLIMATIZATION

When an organism is repeatedly or continuously exposed to an environment hotter than that normally experienced, it may develop functional and structural changes which result in an increase in its ability to live without distress in a hot environment. A heat acclimatized organism is thus an organism which has reached its maximal heat tolerance.

There is ample evidence of heat acclimatization in man, but little in cattle. Calves, in response to repeated short exposures to a hot dry and to a hot humid environment show progressive reductions in rectal temperature, skin temperature and heart rate, as well as changes in respiratory activity (Bianca, 1959a, b).

A special case of acclimatization is that due to season. In regions where there are pronounced seasonal climatic changes the animals go through cyclic phases of acclimatization and de-acclimatization. As these seasonal climatic changes occur very gradually, the animal has ample time to undergo adaptive changes. The most evident among these changes is that

of the hair coat. A heavy winter coat interferes with heat dissipation and therefore depresses heat tolerance; a light summer coat interferes less with heat dissipation and therefore conveys a higher degree of heat tolerance to the animal. Dowling (1959b) has shown that the heat tolerance of the same animal at different seasons can be attributed to changes in the hair coat. Yeates (1955) has observed that the principal climatic factor responsible for these seasonal changes is the duration of daylight, and has shown (1957) that the equatorial photoperiod eliminates the natural coat cycle of European cattle, tending to maintain them in a heat retaining type of coat. Seasonal acclimatization probably also involves changes in thyroid activity and in metabolic rate, so that the effect on heat tolerance may be one of heat loss as well as of heat production.

In view of this dependence of heat tolerance on the state of acclimatization it is imperative that animals which are compared for heat tolerance are in a comparable state of acclimatization. This may be achieved either by artificial acclimatization or by testing all animals in the same season. The importance of the latter procedure is well exemplified by the work of McDowell, Matthews, Lee & Fohrman (1953). These authors, when conducting a series of heat tolerance tests found that the repeatability coefficients for rectal temperature responses in Jersey heifers remained fairly low until the data had been sorted into seasonal groups. Under the climatic conditions prevailing in Louisiana the maximum response of rectal temperature occurred in February, the minimum response in May-June. The observation that the response of rectal temperature to an acute heat stress was also elevated in August, points to a partial loss of heat tolerance at the end of a long continued period of summer heat. The same tendency has been observed in calves at the end of a series of short daily exposures to severe heat (Bianca, 1959a). Thus, a state of "over-acclimatization" may develop whenever the forces of adaptation become exhausted. This emphasises the importance of employing the correct "dose" of heat when acclimatizing animals.

MANAGEMENT

Most managerial devices such as sun shades, fanning, etc., are means for reducing environmental heat load on the animal by providing a suitable microclimate. Proceeding in this direction would ultimately lead to air conditioned byres, in which case heat stress would be completely eliminated and heat tolerance no longer a character looked for in animals. Thus, these devices do not affect the heat tolerance of the animal.

There are,however,managerial procedures which do affect an animal's heat tolerance, if only temporarily. Cooling of the drinking water which has already been mentioned in the section on nutrition and the use of showers are examples of this type of procedure. Alonger lasting effect on an animal's heat tolerance is achieved by clipping its coat. The magnitude of this effect seems to depend on various circumstantial factors. Clipping a heavy (winter) coat was found to be more effective than clipping a light (summer) coat (Bianca, 1959c). Similarly, clipping a coat of non-medullated hair improved heat tolerance more than clipping a coat of medullated hair (Dowling, 1959b). Clipping the coat resulted in a significant increase in skin evaporation of crossbred cows in Israel (Berman, 1957), but it affected only slightly the thermoregulatory reactions of heat acclimatized dairy heifers kept in a hot room at 32°C (89°F) (Berman & Kibler, 1959). The effects of clipping are qualitatively comparable to those of seasonally induced coat shedding. They are, however, more pronounced because the change is more complete and it occurs more abruptly. It is self-evident that clipping affects heat tolerance in a favourable way only in the absence of intensive solar radiation. In its presence the bare skin absorbes more radiant heat than the hair covered skin which results in a lowered heat tolerance.

STATE OF HEALTH

In man impairment of physical fitness tends to reduce performance in a hot environment (Bean & Eichna, 1943). Fitness in this context probably extends primarily to the circulatory system which, certainly in profusely sweating man, bears the main burden of heat dis-

sipation. Herrington (1952) has even suggested that heat tolerance might be predicted from exhaustion times in work under cool conditions.

In cattle the state of physical fitness is not easily assessed and it is not certain whether circulation plays an equally important role for heat dissipation in cattle as it does in man.

Riek, Hardy, Lee & Carter (1950) found that heat tolerance in sheep kept on various levels of nutrition was not highest at the lowest level of nutrition, as might have been expected, but at the medium level of nutrition. They thought this to be due to the inefficiency of all body functions including the thermolytic processes of respiration, cutaneous circulation and sweating in the nearly starved animals. Thus, heat tolerance figures from under-nourished animals may be falsely low.

A particular disorder interfering with the power of temperature regulation is that of chronic panting which has been observed in India as a sequel to foot and mouth disease (Minett, 1948). The state of the animal is characterized by a high respiratory activity and a long, rough hair coat. It was concluded that there was a more or less permanent failure of temperature regulation due to defective functioning of the endocrine glands. It hardly needs stressing that the performance of such animals in a heat tolerance test will give a grossly distorted picture. Less obvious cases of disease, such as the early phase of an infection, however, may escape attention thus leading to wrong heat tolerance results.

EMOTIONAL EXCITEMENT

Testing for heat tolerance involves a certain amount of handling of the animals. If not used to it, animals may work themselves into a state of excitement, as evidenced by an increased cardio-respiratory activity and in more severe cases even by a rise in body temperature, resulting in a reduction in heat tolerance. Moreover, such changes are unpredictable in their intensity and therefore adjustment for them is not easy. Excitement may be overcome with tranquilizing drugs, but these have side effects on physiological functions involved in thermoregulation which makes them unsuitable for use in heat tolerance tests. It is therefore important to reduce excitement to a minimum by allowing the animal to get used to the environment in which the test takes place, to the person who is conducting the test and to the procedure itself. Otherwise the innately excitable, brisk animal, as compared to the tranquil, docile animal, will be underrated in its capacity for tolerating heat.

SUMMARY AND CONCLUSIONS

Heat tolerance is a complex phenomenon, since it involves the impact of one complex system - the thermal environment - on another complex system - the animal's body. The numerical evaluation of an animal's heat tolerance in form of a test cannot take into consideration all climatic elements and all animal characters. A selection of the most important and most suitable factors has to be made.

Many climatic environments are adequately characterised by temperature and humidity. Some, however, require the inclusion of solar radiation. The heat load imposed on an animal in a heat tolerance test should be large enough to evoke a pronounced response but not so large as to cause damage.

Various morphological features such as texture and colour of the hair coat are directly or indirectly related to heat tolerance. Although they cannot be used as criteria in a heat tolerance test proper, they have prognostic value, in that they allow a breeder to make a certain prediction of ayoung animal's future heat tolerance, which is of great practical importance.

Among the various body functions, body temperature is the best single criterion of an animal's heat tolerance. Representing the resultant of all heat gain and heat loss processes of the body it is physiologically meaningful; furthermore, it is relatively stable in a temperate environment, it responds readily and in a repeatable way to heat stress and it is easily and accurately measured. Estimating heat tolerance from respiratory activity or cutaneous evaporation alone is less satisfactory for reasons discussed.

Live weight gain in hot conditions may be a useful indicator of an animal's heat tolerance, while milk production seems to be less suitable in this respect. The question whether or not the concept of heat tolerance based on various thermoregulatory reactions of an animal should be abandoned altogether and replaced by production records, is touched upon.

From a description of various methods for assessing heat tolerance, it is concluded that none of them is entirely satisfactory and that in view of the necessity to increase animal production in hot countries there is a definite need for an improved method.

An animal's inherent heat tolerance - the determination of which is the aim of a heat tolerance test - is modified by a number of conditions and factors which will or may vary during an animal's individual life. The most important of these are age, nutrition, activity, reproduction, level of production, acclimatization, management, state of health and emotional balance. It is important to know how and to what extent these factors influence heat tolerance; they then may be eliminated, standardized or adjusted for.

Considering the problem of heat tolerance of cattle in its widest context, a general four-step procedure may be envisaged:

- (1) Young animals are selected for heat tolerance on the basis of structural characters, for which correlations with suitable thermoregulatory responses has previously been established. Various properties of the hair coat are, at present, the most promising characters to be used in this way.
- (2) At an age not less than about half a year the animals so selected are subjected to a suitable heat treatment in order to allow their temperature regulating mechanisms to attain maximal efficiency, i.e. to become fully acclimatized.
- (3) These preselected and pretreated animals are then subjected to one or several suitable heat tolerance tests which include, as stress producing climatic factors, environmental temperature, air humidity and radiation in suitable intensities, and in which body temperature occupies a central position among the physiological variables measured.
- (4) Once the animals selected in this way have reached their productive stage and are living in or have been transferred to a warm environment, they are finally selected on the basis of their productive level.

For the adoption of such a procedure which would consider, in successive steps, several different animal characters, it would be valuable to have more specific information on the role played by selected body structures in thermoregulation and there is clearly a need for a well defined and accurate test for assessing an animal's inherent capacity for tolerating a hot environment.

ABSTRACT

Heat tolerance is a complex phenomenon. Its study involves three factors: the thermal environment, the animal body and a suitable scale for expressing numerically the effect of the thermal environment on the animal body.

Since each of the principal component elements of a thermal environment, temperature, humidity, solar radiation and wind, makes specific demands on thermoregulation, it is desirable in a heat tolerance test to consider all of them. The total heat load imposed on an animal should be large enough to evoke a pronounced response, but not so large as to cause damage.

Various morphological characters such as the texture and the colour of the hair coat may have prognostic value, in that they allow a certain prediction to be made of a young animal's future heat tolerance. This is of practical importance for the breeder. Among the many physiological variables body temperature is considered the best single criterion of heat tolerance. Productive performance as an indicator to heat tolerance seems to be more useful in beef cattle than in dairy cattle.

From a description of the various methods which have been used for assessing heat tolerance, it is concluded that none of them is entirely satisfactory and that there is a need for an improved method.

An animal's capacity for tolerating heat is influenced by a number of modifying factors the most important of which are age, nutrition, physical activity, reproduction, level of production, acclimatization, management, state of health and emotional balance. Unless these factors are taken into consideration, heat tolerance tests will give misleading results.

ABSTRAKT

Hitzetoleranz ist eine komplexe Grösse. Für ihr Studium müssen drei Faktoren berücksichtigt werden: die thermische Umwelt, der tierische Organismus und ein geeigneter Masstab, der die Einwirkung der thermischen Umwelt auf den tierischen Organismus zahlenmässig zum Ausdruck bringt.

Da jedes der vier Hauptelemente einer thermischen Umwelt, nämlich Temperatur, Feuchtigkeit, Sonnenstrahlung und Wind spezifische Anforderungen an die Temperaturregelung des Körpers stellt, ist es wünschenswert, dass alle diese Elemente in einem Hitzetoleranz Test Berücksichtigung finden. Die gesamte Wärmebelastung, der ein Tier in einem Hitzetoleranz Test ausgesetzt wird, soll grosz genug sein um deutliche Reaktionen hervorzurufen, aber nicht so grosz, dass das Tier Schaden nimmt.

Verschiedene morphologische Merkmale wie z.B. die Beschaffenheit des Haarkleides können prognostische Bedeutung besitzen; d.h.sie können eine gewisse Voraussage der zukünftigen Hitzetoleranz eines jungen Tieres gestatten. Dies ist für den Tierzüchter von praktischer Bedeutung. Unter den zahlreichen physiologischen Grössen, die zur Beurteilung der Hitzetoleranz herangezogen werden können, ist die Körpertemperatur das beste Einzelkriterium. Unter den Nutzleistungen scheint das Körperwachstum geeigneter zu sein als die Milchproduktion.

Aus einer Beschreibung der verschiedenen Methoden, die als Bewertungsmasstäbe für die Hitzetoleranz verwendet werden, wird gefolgert,dass keine dieser Methoden vollständig befriedigt. Eine geeignetere Methode muss entwickelt werden.

Die Fähigket eines Tieres Hitze zu ertragen wird durch eine Anzahl modifizierender Faktoren beeinflusst. Die wichtigsten sind: Alter, Ernährung, Körperbewegung, Geschlechtsfunktionen, Nutzleistung, Akklimatisation, Haltung, Gesundheitszustand und emotionelles Gleichgewicht. Werden diese Factoren in einem Hitzetoleranz Test nich berücksichtigt, so entstehen irreführende Resultate.

RÉSUMÉ

La tolérance à la chaleur est une notion complexe. Trois facteurs doivent être considérés dans son étude: le milieu thermique, l'organisme animal et une unité de mesure capable d'exprimer quantitativement l'influence du milieu thermique sur l'organisme animal.

Un test de tolérance à la chaleur devrait tenir compte des quatre facteurs principaux du milieu thermique: la température, l'humidité, le rayonnement solaire et le vent, car chacun d'eux influence spécifiquement les mécanismes de régulation thermique du corps. La quantité totale de chaleur fournie à un animal au cours d'un test doit être suffisante pour déclencher des réactions nettes sans causer de troubles pathologiques.

Divers caractères morphologiques, comme par exemple l'état du système pileux, peuvent fournir une indication sur la résistance future à la chaleur d'un jeune animal; ceci présente une utilité pratique pour l'éleveur. Parmi les nombreuses mesures physiologiques qui peuvent servir à l'appréciation d'un test de tolérance à la chaleur, la température corporelle est le meilleur critère. Parmi les fonctions physiologiques, l'augmentation du poids du corps semble un critère plus utile que la production de lait.

L'examen des différentes méthodes utilisées pour évaluer la tolérance à la chaleur montre qu'aucunes d'elles n'est tout à fait satisfaisante. Une méthode plus appropriée doit être créée.

La résistance à la chaleur d'un jeune animal est influencée par une quantité de facteurs. Les plus importants sont l'âge, la nutrition, les mouvements, les fonctions sexuelles, le travail utile, l'acclimatation, la posture, l'état de santé et l'équilibre affectif. Les résultats d'un test de résistance à la chaleur qui ne tiendrait pas compte de ces facteurs sont douteux.

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