
Lecture Note

303711 Environmental Physiology of Farm Animals

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303 711 Environmental Physiology of Farm Animals

- I. Fundamental of Environment (4.5 hr)**
 - A. Setting the stage**
 - B. The definitions and related concepts (adaptation, acclimation, acclimatization, stress, strain, etc.)**

- II. The Animal-Environment Relations (6hr)**
 - A. Physiological adjustments**
 - Homeostasis
 - Neural and endocrine control
 - Stress and principle of stress physiology
 - B. Behavioral management**

- III. Light and Biological Rhythms (9hr)**
 - A. Terminology: Endogenous and exogenous rhythms time givers**
 - B. Direct and indirect effects of light**
 - C. Light and reproduction**
 - D. Light and growth**

- IV. The Animal and Its Thermal Environment (9hr)**
 - A. Thermoregulation**
 - B. Animal reproduction and thermal environment**
 - C. Animal energetics and thermal environment**

- V. Osmoregulation and Excretion (7.5hr)**

Examination:

- Midterm (I and II) 30%**
- Final (III, IV, and V) 55%**
- Term paper 15%**

THE INTRODUCTORY COMMENTS

Of all the known forces which have directed the evolution of man and his ever-changing civilization, none have had more effect over a long period of time than the factors which constitute the climatic environment. Day-to-day changes in the weather, which includes temperature, light, moisture, air movement, a variety of radiation from the sun and outer space, and the long range weather patterns which characterize the climate, have a profound effect on plants, animals and man.

The climatic environment influences nearly every economic aspect of animal agriculture, crop yields and composition, animal growth, reproduction, milk production, egg production and the efficiency of conversion of feed stuffs to economic units.

Primitive man learned to use fire as a source of heat and light, but it is only in the last century that man has utilized central heating, the electric light, mechanical refrigeration, large scale cooling and dehumidification. During the nineteenth and early twentieth centuries, man subscribed to the philosophy that the control of his own private climate was possible but animals should be selected for specific climatic conditions. As a result, there are hundreds of breeds of cattle, swine, sheep and poultry scattered over the globe. Most of these have been selected for survival under very local environmental conditions. Unfortunately, the great majority of these livestock breeds are of extremely low productivity and are not known outside their local areas.

It is now clear that there is an optimum climatic environment for every body function and it seems equally clear that advances in the biological and engineering sciences will make it possible to alter the animal environment to meet the requirements for maximum animal productivity and efficiency.

As animal production becomes more intensive in space and time, environmental aspects of animal management become more important (animal producers generally attack animal production problems in the order of their economic importance). The prevailing trend in production of farm animals for quite some time has been toward more and more confinement of the animals. A large increase in the overall economic efficiency of animal production accompanies confinement as the need for labor, which is relatively scarce and expensive, is less in confinement than in more extensive systems of animal management. Reduced need for high cost land and facilitation of waste management are other advantages of confinement. Further, environmental modifications that form an integral part of most confinement systems, such as more-or-less enclosed animal houses, make year-round operations possible in enterprises that once were restricted to certain seasons. Seasonal cycles in egg production, milk, and meat production are not as marked as they were before the advent of confinement and environmental modification. When seasonal differences in production level are minimized, the overall economic efficiency of an animal production operation is usually increased.

On the other hand, some effects of confinement are detrimental to animal function and performance, although they may temporarily increase the production per unit of labor

input or space. Many confinement-induced problems occur inadvertently simple because the animals' needs are not understood.

Confinement simplifies the animal's environment and consequently reduces the animal's opportunity to *choose, alter, and use its environment to its advantage*. The restrictions are not necessarily beneficial; producers and designers have not always been able to improve upon nature. For instance, consider sows that farrow and lactate in closed houses equipped with slotted, concrete floors. First the sows are deprived of the chance to build a nest, as they do in nature, to protect their cold-susceptible piglets. Second, the piglets in such an artificial environment are prone to develop iron-deficiency anemia because they have no opportunity to obtain iron by rooting about in soil as they would outdoors. These deficiencies give producers serious management problems. Piglets can perform well in such a house only if the producer modifies the farrowing stall so it furnishes the young animals a comfortable thermal environment, and only if he gives them supplementary iron.

Confinement also complicates the animals' environment in ways that may intensify environmental impingements. For instance, the frequency of certain diseases is generally higher under confinement than under more extensive animal management systems unless special preventative steps are taken. This is because confined animals are usually held at high density, which may lead to both an increase in the challenges by disease agents and a reduction in the animal's defenses against these challenges.

In short, confinement brings advantages and disadvantages, but the trend to confinement will continue as plus factors outweigh the drawbacks. The prospect is that the advantages will mostly continue to prevail, although there have been cases where the problems caused producers to reduce the degree of confinement and so-called "environmental control" employed. For instance, completely enclosed, "controlled-environment" houses were at one time used extensively in the broiler chicken industry in the southern region of the United States. Performance in such units often waned, presumably because the animals' needs were not being met economically in such units, or both. Broiler producers therefore have reverted to using more flexible houses to improve the animal's environment so as to increase profitability of the operations.

Animal producers generally want to use the highest degree of confinement feasible, but they also want to increase the overall efficiency of their operations. Having already gained most of the advantages of confinement itself, they will now have to concentrate on the problems of confinement. Most of these problems involve relations between the animal and its environment. Therefore, environmental aspects of animal management are becoming more important as animal production becomes more intensive.

The advances of intensive management systems not only increased the significance of environmental forces in animal production, it also changes the relative importance of the various *environmental factors* and the *nature* of the strategies that can be used to remedy animal environmental problems.

In the more natural environments of extensive animal production, thermal factors and light are most important. Little attempt is made to alter the animal environment, but rather production schedules are formulated with the seasonal changes in mind. In short, there is the tendency to fit the management systems and the animals themselves to the natural environment.

In intensive animal production, on the other hand, thermal and light factors are important, but so are social and other behavioral elements and disease factors. Further, in addition to some attempts to fit management and animals to the environment, there must be intensive animal production attempts to alter the environment to meet the animal's needs. There even can be attempts to stimulate animal performance by environmental modification.

Intensive confinement limits the animal's chances to seek more favorable surroundings. Hence, in confinement production units, the animal producer is responsible for providing the animal at all times an environment that neither harms the animal nor impairs the animal's performance or, better yet, one that actually stimulates it. In order to do this, the producer must understand animal-environmental relations.

THE DEFINITIONS AND RELATED CONCEPTS

The Environment

In its broadest sense, the environment includes all the combinations of conditions under which the animal lives, except for those imposed by heredity. These may be external (physical environment and social environment) such as solar radiation, oxygen pressure, air temperature, humidity, light, or interaction between herd mates; or they may be internal (biological environment), as in the case of disease organisms or parasites. The animal's environment is therefore exceedingly complex. To learn specific details of farm animal ecology it is necessary to understand concepts and terms common to all animal-environmental relations.

Adaptation

The concept of animal adaptation refers to the genetic, biological and physical changes taking place in an animal in response to internal and external stimuli. Genetic adaptation concerns selection by nature and man, whereas physiological adaptation concerns changes occurring within an individual, over shorter or longer periods. The concept of physiological adaptation may imply the capacity and process of adjustment of the animal to itself, to other living material, and to its external physical environment. The greater the extent of adaptation, the more the animal will tend to survive or to reproduce itself so that its biological characteristics may persist. It is in the light of this concept that the survival of living species becomes understandable. A considerable variation occurs between different species, and even between different individuals within a species in their capacity to adjust to environmental stress.

Adaptation is such a complex phenomenon that it cannot be reduced to a single type of measurement or basic definition without gross oversimplification. Adaptability may be evaluated by the animal's ability to adjust to average environmental conditions as well as to climatic extremes. Well adapted animals are characterized by: (a) minimum loss in body weight during exposure to stress such as nutritional deficiency, high milk yield or transport; (b) high reproductive rate, (c) high resistance to disease, and (d) longevity and low mortality rate.

Nutritional Adaptation

Genetic and physiological adaptations are associated with nutritional adjustments. Nutritional adaptations may occur as a result of limitations of climatic and ecological origin. The tropical climate for instance, imposes limitations upon nutrition. The soil and water of the tropics are notoriously low in calcium as it is leached out by the monsoon rains, the pastures are correspondingly low in this mineral. The low calcium intake is reflected by low serum calcium concentrations, but tropical animals appear to be tolerant of this and suffer no ill effects. Low protein intake does not apparently have marked adverse effects in all species. As a result of chronic protein deficiencies, certain animals may develop an ability to store protein.

Longevity and Mortality Rate

Longevity is an indicator of an animal's ability to withstand the cumulative effect of all environmental stressors. The mortality rate of native animals is much less than in exotic animals, particularly if the latter are transferred from one environmental extreme to another. The mortality rate and age at death of crossbreeds are intermediate between those of the two parental breeds.

Genetic Resistance to Disease

Disease may be defined as a condition of the body or of some part or organ in which its functions are disturbed or deranged. There are three major classes of disorder: (1) congenital in which malfunction results during prenatal development, (2) pathogenic when the body is invaded by pathogens, (3) environmental such as nutritional deficiencies, ingestion of toxic material, or exposure to climatic extremes or to soil stress. A common "climatic disease" in lambs is photosensitization of the skin resulting in eczema over the face and ears. In the afflicted lambs, the liver fails to excrete phyloerythrin, which is a product of the digestion of chlorophyll. The syndrome appears at the age of 5 to 7 weeks when the lambs graze outdoors. The severity of the injury depends on the intensity of solar radiation. Death ensues within 2-3 weeks after the appearance of the first symptoms. If the lambs are kept indoors during the day, and allowed to graze at night, they survive despite their abnormal metabolism.

Acclimatization

Acclimatization is a long-term physiological adjustment which results in an increased tolerance to continuous or repeated exposure to complex climatic stress (normally produced under field conditions). With increasing altitudes, for example, atmospheric pressure decreases at the rate of about 40 mm Hg per 100 m increase in altitude. The decline in oxygen pressure is about 1/5 of this. Typically lowland animals such as cattle and sheep, have much less tolerance to high altitudes than the indigenous animals such as the llama. The llama is used as a pack animal in regions up to 6,000 m. Animals native to sea level, if transferred to high altitude (4,000 m), experience distress and severe fatigue. If they are however, transferred to a moderate altitude (2,000 m) and kept there for several weeks, they normally become "acclimatized" and can then be transferred to higher altitude with less discomfort.

The process of acclimatization to altitude involves several physiological mechanisms: an increased affinity of hemoglobin for oxygen, an increased oxygen-carrying capacity of the blood resulting from an increased concentration of red blood cells, increased myoglobin and an increased ability of tissues to utilize oxygen at low pressures. Thus, high altitude acclimatization consists of alterations in the circulatory and the respiratory systems and in cell metabolism. Similarly, an animal heat tolerance is modified in the course of acclimatization by alterations in its heat loss and heat gain mechanisms.

Acclimation

Acclimation refers to relatively long-term adjustments in response to a single environmental factor under laboratory conditions. This concept is applied when animals are maintained for days or weeks in climatically controlled chambers.

Habituation

Repetition of stimuli (as experienced during acclimatization) may be accompanied by gradual quantitative changes in responses to these stimuli, a process described as "habituation" Habituation is perhaps the simplest kind of adaptive learning. Upon repeated exposure to a stimulus the animal decreases its natural responses until it may disappear entirely. For example, an animal will orient toward a moderate sound, but with each successive exposure, it orients less and less until it no longer orients. That is, change is not merely fatigue or sensory adaptation is evident, for the decrement in response grows with repeated exposure to the stimulus and will last over prolonged periods of time without stimulation (ex., a pig raised near an airport).

PHYSIOLOGICAL ADJUSTMENTS

The meteorological elements—air temperature, air humidity, wind and solar radiation impinge on the surface of the animal. These factors operate in two ways; first by direct interaction with the skin and hair and second, by affecting the receptors present in the skin or the retina of the eye. Information received by receptors in the skin is transmitted to the brain which sets into action compensatory mechanisms. Of special significance are the concepts and processes of homeostasis, hibernation, biological rhythms and stress syndromes.

Homeostasis

In 1878, Claude Bernard stressed the physiological significance of the *milieu interieur* (internal environment). Cannon (1932) drew attention to the ability of the body to maintain a constant condition or status of the entire body (body weight, blood pressure, body temperature, etc.) in the face of diverse, disruptive, external factors. The concept of homeostasis includes: heat balance and thermoregulation, chemical balance of water and circulatory balance of cardiovascular activities (ex., the chemical composition of the blood, lymph and other body fluids, for example, varies within narrow limits). Generally, deviation from the normal condition is prevented or corrected by several homeostatic mechanisms.

Animals living in hot or cold climates must undergo some functional adjustments to maintain their thermal balance; these may involve the rate of metabolism, respiration and blood circulation.

Although animals, for short periods, can tolerate some depletion of their body water, they must in the long run maintain their water balance. This means that all water loss (evaporation, urine, feces) must be offset by an equal intake (drinking, in food). Domestic animals, including birds, ruminants, monogastric mammals, and both large-sized and small-sized species. This diversity in size and structure is reflected in some variations in the homeostatic mechanisms. For example, the critical air temperature is 28°C in man, 7°C in cattle and -40°C in some arctic species. The critical temperature is the lowest ambient temperature at which a mammal or bird can maintain its body temperature at the basal metabolic rate. Critical temperatures: man, 28°C; dog, 25°C, rabbit, 17°C sheep, pig, 0°C, mountain goat, -30°C; some arctic species, -40°C.

Neural and Endocrine Control

The central nervous system and the endocrine system are ultimately responsible for the maintenance of the constancy of the internal environment. The nervous system consists of the nerve cells, their branches and the supportive tissue. The brain and the spinal cord form the central nervous system (CNS) and the various afferent and efferent nerve trunks conduct the sensory and motor impulses, respectively to and from the periphery, muscles and organs. The somatic or cerebrospinal part of the CNS controls voluntary muscles and the autonomic (involuntary) system.

Within the CNS, the hypothalamus is an important integrative organ for homeostatic mechanisms. The hypothalamus, a portion of the diencephalon, is the control center for thermoregulation, feed and water intake, osmoregulation, and cardiovascular activities.

The hypothalamus also serves as an important link between the nervous and endocrine systems through the release of or inhibiting of peptides (neurohormones).

There is also evidence that chemoregulatory systems to adjust feed intake to the needs for carbohydrate and fat may be located in the hypothalamus. The fundamental hypothalamic systems are affected not only by local events and peripheral afferent systems, but also by higher systems, particularly in the limbic or visceral brain, with which the hypothalamus has many associated pathways. Stimulation along several of these pathways has been found to influence several behavioral and physiological patterns of the animal.

The endocrine glands may be activated directly or indirectly in homeostasis. For example, there is an inverse relationship between environmental temperature and basal metabolic rate, which is regulated by the nervous and endocrine systems.

STRESS AND PRINCIPLE OF STRESS PHYSIOLOGY

Terminology

Stress

Overstress

Distress

Cumulative Stress

Strain

The Adrenal Gland and Stress

The adrenal consists of two glands that lie near the kidneys. This gland is a compound structure consisting of an outer cortex and an inner medulla. The hormones of the cortex are steroids, whereas those of the medulla are amines. It is only in mammals that distinct cortices and medulla are present. The two types of tissue are intermingled in the avian adrenal glands.

Animals with adrenal insufficiency are characterized by weakness and easy fatiguability, by hypotension, by gastrointestinal disturbances including vomiting, abdominal pain and emotional difficulties including anxiety and depression. Exposure of an animal with adrenal insufficiency to a sudden and unexpected event such as injury or infection lead to a kind of collapse called adrenal crisis.

The Adrenal Cortex

The adrenal cortex is involved in two main physiological functions: one associated with the metabolism of carbohydrate and protein, and with the capacity to withstand stresses of many types; the other, with water and electrolyte metabolism and the ability to reabsorb sodium from the glomerular filtrate, and to conserve this ion when it is available only in limited amounts.

Aldosterone is the main salt retaining hormone of the adrenal cortex, while cortisol (in man and pigs) and corticosterone (in birds and rats) are the principal glucocorticoids of the adrenal cortex.

When there is a lack of aldosterone, the most prominent feature of the defect is inability to reabsorb sodium and chloride from urine sufficiently rapid to prevent net sodium loss from the body under conditions of normal or reduced sodium intake. This is accompanied by K^+ retention and an increase in K^+ in the blood and loss of K^+ from the cells. Associated with this gastrointestinal disturbances. Deoxycorticosterone, a powerful salt-retaining hormone, can promote the reabsorption of sodium by the renal tubule but also diminish the sodium concentration of sweat, saliva, and intestinal secretions. The effect on sweat adds a new dimension to the adrenal cortex survival value, for heat exposure is a powerful stimulus to aldosterone secretion, and that the additional aldosterone secreted functions to diminish the sodium concentration of sweat. Thus the salt retaining activity of the adrenal hormones is of adaptive value not only when there is less salt available in the environment for ingestion but also when a hot environment leads to increased salt loss through sweating. The adrenal is essential to life because their salt retaining function is a vital one.

The glucocorticoid hormone deficiency leads to a decline in blood glucose and tissue glycogen levels upon fasting.

Adrenal glucocorticoids also play a permissive role in metabolism. This means that many cells which respond to a variety of other hormones or nervous effects only perform well when they are exposed to a certain baseline concentration of adrenal corticoids.

The cells of the adrenal cortex is controlled by a hormone called (ACTH) or adrenocorticotrophin hormone from the pituitary which stimulates them to produce more steroids such as cortisol or corticosterone. The cortisol produced then feeds back on the trophic tissues and instruct them to decrease ACTH release.

Increase in Cortisol Secretion

Injection of large doses of cortisol cause a very marked deposition of glycogen in the liver sometimes to a point 15%. The blood glucose may be elevated above normal levels. Associated with these changes in glycogen and blood sugar a marked effect on protein metabolism; i.e., a breakdown of muscle protein. Skeletal muscle mass decreases in size and muscular weakness. This effect is secondary to influences on carbohydrate utilization. Since cortisol has been found to enhance gluconeogenesis from amino acid.

Increase in cortisol secretion cause a decrease in white blood cells and antibodies production.

Cortisol and the Stress Concept

One of the dominant themes in adrenal cortical physiology has been the theory that the pituitary-adrenal axis participates prominently in the “non-specific systemic reactions of the body which result upon exposure to stress”. In 1936, Selye called attention to the fact that noxious stimuli produced a rather stereotyped response in rats. At the time, the main features of this response were adrenal enlargement and reduction in the white blood cell numbers. Subsequently, it was found that following heavy muscular exercise, cold exposure, infection and psychological trauma and increase in output of adrenal glucocorticoids.

Inborn Errors of Metabolism of Adrenal Cells

Several types of patients have been found who exhibit virilism and adrenal hyperplasia. This can manifest itself as masculinization in the female. The biochemical locus of the metabolic defect is known; it can be identified by chemical analysis of the urine. The block is in the 21-hydroxylation reaction from 17-OH progesterone to 17OH deoxycorticosterone. The urine contain a large amount of 17-ketosteroids. In these kind of patients there is a deficiency in cortisol production caused by genetic enzyme defect. This in turn, is interpreted by ACTH-producing department as a need for more ACTH, which is secreted in large amounts. The net effect of the increased outpouring of ACTH is to increase the production of substances behind the block and in turn increase androgen production.

Porcine Stress Syndrome (PSS)

This is a condition observed with increasing frequency among lean strain of hogs. This condition is apparently under genetic control. Stress-susceptible pigs are prone to sudden death when exposed to excitement in a warm environment. Pigs suffering from

this condition show anxiety, extreme muscularity, tail tremors, leg weakness, high blood ACTH or low cortisol-ACTH ratio.

The muscle of these animals show the typical PSE (pale, soft, exudative) pork. Apparently this is due to the rapid depletion of muscle glycogen.

The Adrenal Medulla

The adrenal medulla is a functional part of the nervous system. It is specialized sympathetic ganglion which is innervated by preganglionic neuron. Upon activation of the neuron, the medulla discharge stored epinephrine and norepinephrine directly into the blood. Thus, a nerve-born message is converted into a blood-born one. The discharge of the adrenal medulla constitute the first and timed series of responses to meet an emergency. Unlike the adrenal cortex, the adrenal medulla is not essential for life.

Synthesis

Physiological Effects

Epinephrine and norepinephrine have an effect on all organ systems of the body.

Central Nervous System

It causes excitation of the nervous system. This may be characterized generally by being more alert and a facilitation of the passage of information into and out of the brain. This is done by measuring reaction time to a stimulus.

Effect on Blood Vessels

They constrict cutaneous blood vessels and dilate skeletal muscle vessels. Norepinephrine is far more potent general vasoconstrictor than epinephrine.

Cardiac Effects

The effects of the two catecholamines on the heart are quite different. Most of the cardiac effects are produced by epinephrine. It causes (1) an increase in the rate of cardiac contraction, (2) an increased force of contraction, and (3) these are the basis for increased cardiac output.

Respiration

Both hormones accelerate the rate and increase the depth of respiration. This appears to be due to the CNS excitation induced by these compounds.

Skeletal Muscle

Contraction of the skeletal muscle is prolonged by epinephrine, and to increase the force of contraction in fatigued muscle. One of the most prominent metabolic effects of epinephrine is seen in skeletal muscle—namely a rapid glycogenolysis with the accumulation of sufficient lactic acid to raise the level of lactate which is carried to the liver where it is resynthesized to glycogen and recirculated as glucose. It also travels to the heart which uses lactate very efficiency as an energy source.

The Liver

One of the most striking effects of epinephrine is the production of hyperglycemia. This hyperglycemia is mainly due to hepatic glycogenolysis. Norepinephrine has only 1/5 the effect of epinephrine.

Calorigenic Action

Mobilization of carbohydrate from the liver is only a small part of the mobilization of caloric reserves that occurs when epinephrine is given. The catecholamine hormones act on the cells of adipose tissue to produce a release of free fatty acids. (FFA).

There is one detectable theme in many of these effects. The over-all response to the effect of catecholamines, increase in cardiac output, increase in pulse rate, rise in blood pressure, similar to those seen at the beginning of exercise. Also there is an increase in respiration. A dilation of the skeletal muscle vessels increase blood flow to the muscle, which anticipates muscle work. The central nervous system arousal effect of the catecholamine results in alertness and quick responsiveness. Hepatic glycogenolysis and the mobilization from fat deposits of a large supply of free fatty acids, all collaborate to provide a quick charge of readily available energy to muscles that may be called upon. Chemical changes in the muscle themselves increase their capacity for work and possibly diminish the generation of a fatigue signal by the muscle.

The fact is that the over-all effect of catecholamine release is to mobilize the animal to meet an emergency. Cannon's came with the fight-flight theory.

Hibernation

Factor that induce hibernation and which wake the animal in the spring are not completely clear, change in environmental temperature are important, but changes within the animal body as also involved. Hibernation is an interesting physiological-behavioral response whereby the homeothermic animals escape the rigors of environmental extremes. Hibernation refers to a cessation of coordinated locomotor activity and a reduction in body temperature, total metabolism, heart rate and respiration during winter. However, the capacity to return spontaneously to normal homeothermic levels without external heating is retained. Hibernation is not exhibited by any of the farm animals.

Stress Syndromes

The animal may be exposed to different types of unfavorable environments : (a) climatic stress such as extreme cold or heat or intense solar radiation, (b) nutritional stress due to feed or water deprivation, (c) social stress due to holding a low rank in a peck order, or (d) internal stress caused by pathogens or toxin. The exposure of the animal to stress may be chronic (gradual and prolonged) or acute (sudden).

When the animal is subjected to stress, three types of regulatory processes function:

I. The acute type of stress causes rapid physiological and behavioral changes referred to as Cannon's Emergency Syndrome or Cannon's Fight-or-Flight response.

An American physiologist, Walter Cannon, was responsible for identifying a hormone secreted by the adrenal glands in response to physiological stimuli which prepares and supports the body in fight-or-flight situations. He found that cats, placed in a holder and frightened by a barking dog, secreted “adrenaline” or epinephrine. Cannon later found that other emotional situations, such as taking difficult examinations or being involved in exciting football games, even as a coach or a player sitting on the bench, often were associated with epinephrine increases. Others soon determined that it was the inner or medullary part of the adrenal gland which produced adrenaline. Another hormone “noradrenaline” was also found to be secreted by the adrenal medulla upon exposure to stressful stimuli. This is also called norepinephrine.

These hormones are produced following nervous stimulation arising in the hypothalamus (pathway for epinephrine and norepinephrine).

II. Physiological Stress

The second regulatory process is specific for the conditions imposed and for which the body takes specific action; this has been dealt with under “homeostasis”

III. Regulatory mechanism is non-specific in nature, in which regardless of the type of stress imposed by the environment, the body reacts in a similar manner. Such a non-specific response has been termed by Hans Selye the **General Adaptation Syndrome (GAS)**. It is said to place the body in a general state of physiological stress.

When stressors continue to act over a prolonged period and are not so extreme as to be fatal in the short run, then Selye described a general adaptation syndrome as occurring. This syndrome was visualized as having three distinct phases:

(1) **Alarm reaction**: Selye found during this phase in laboratory animal (1) enlargement of the adrenal cortex, (2) lymphatic tissue atrophy, (3) bleeding ulcers in the stomach and duodenum appears and “resistance” to more extreme stress of the same kind or to other kinds of stress is reduced.

(2) **Stage of resistance**: The animal adapts for a period of time and appears to have overcome the stress. During this interval, it may be subjected to an increase of stress of the same kind with fewer ill effects than would occur in a previously unstressed animal.

(3) **Stage of exhaustion** : Under continuing action of the stressor, the animal’s resistance drops and it becomes obviously sick and may die. When the adrenal cortex responds, it is because the anterior pituitary gland has increased its output of adrenocorticotrophic hormone (ACTH) and the adrenal increased its secretion of glucocorticoids, cortisol, is the main corticoid in pigs, cattle, man, and corticosterone in the main corticoids, in rats and birds (pathway for glucocorticoids).

Hormonal Indicators

When a stressor acts on an animal, messages are received by the hypothalamic area of the brain. Thus alerted, the hypothalamus responds in two basic ways, as shown in the figure. Fast traveling nerve impulses pass along the sympathetic nervous system to the adrenal medulla, which then increases secretion and synthesis of adrenaline and noradrenaline. The other hypothalamic response involves hormonal pathways which usually requires minutes or hours before measurable responses are apparent, in contrast to the nearly instantaneous fight-or-flight responses. A “releasing factor” passes from

the hypothalamus into the anterior pituitary, thereby increasing ACTH secretion. In response to ACTH stimulation, the adrenal cortex secretes steroid hormones or "corticoids" (cortisol and corticosterone) which have a variety of physiological effects. (1) The metabolic rate increases, protein and fatty tissues break down and blood cell count decreases; (2) antibody production decreases, (3) reproductive capacity decreases, and (4) ulceration of the stomach and intestinal tract may occur (in mammals, but not in birds). The psychological influences, as well as physical stressors, could produce the stress syndrome.

Quantitative measures of adrenal hormones in the circulating blood or in the urine would appear to be useful indicators of stress. However, elaborate precautions are necessary; the acts of forcefully restraining animals and drawing blood samples from them, could in themselves, cause a significant rise in hormone levels.

Adrenal weight and ulcer production may be useful in animals that are to be slaughtered as an indicator of stress. Various supposedly stressful conditions (low social status, crowding, social disruption, etc.) increased adrenal weights. Ulceration of the digestive tract does not occur in poultry, but has been used as a criterion of stress in swine.

Examples on Stress and Performance in Farm Animals

Although symptoms of stress are generally regarded as indication that all is not well, studies with laboratory rats suggests that relatively brief period of exposure to stressors during the infantile period elicit adrenal response and may be beneficial in preparing the animals for challenges encountered later in life.

Behaviors not seen or occurring at low frequencies in relatively natural environments but which become evident under high-density management systems are often regarded as indicating distress and reflect environmental deficiencies. However, "abnormal" behaviors exhibited under conditions of close confinement may be poor indicators of stress, as indicated by either direct physiological measures (as for adrenal corticoids) or by indirect measures of well-being, such as body weight or reproductive functioning. Nevertheless, some abnormal behaviors, such as "cannibalism" in chickens, tail biting in pigs, "wool picking" in sheep, and excessive riding of certain steers (the "buller" syndrome) in feedlots are clearly harmful and victims are stressed.

Anomalous Behaviors

Not all animal behaviors are conducive to productivity. Domestic animals often behave eccentrically as they adjust to artificial environments. Thus, aberrant behaviors in essence reflect environmental deficiencies. Some are ordinarily innocuous, but also among them are noxious acts by which an animal damages itself or a groupmate.

Bizarre activities occur more frequently and intensely in domestic animals than in their wild progenitors. Any of them may affect health, reproduction, and productive processes. Noxious behaviors can even cause trauma and death. An understanding of these things begin with an understanding of frustration.

Frustration and Its Consequences

Any behavioral pattern is homeostatic and must be instigated by some external or internal stimulus. Most activities are comprised of a series of preliminary (appetitive) behaviors aimed at putting an animal in a position to make the final (consummatory) act

in the behavioral pattern. If an animal is unable for any reason to make one or more of the necessary preliminary acts, of course, the final act is impaired as well. This constitutes the clearest class of frustrating situations.

Consider a hungry calf in a feedlot. In order to eat feed, it must make its way to the bunk, extend its neck, lower its head, open its mouth, scoop-up a quantity of feed with its tongue, suck it into the mouth, chew it and mix it with saliva, and finally swallow it. If anything--fence, groupmate, broken leg, sore tongue--prevents the calf from completing any of these appetitive acts, it is frustrated in its attempt to eat.

Frustration of a strong drive also may set the stage for a conflict between the tendencies to express the drive and to avoid the frustration, and such a conflict itself may have unfavorable consequences.

Causes of Frustration

Blocking one of its strong drives--such as eating or nesting--is the most obvious way to frustrate an animal. Frustration of this type occurs frequently in commercial animal production. There are several other conditions an animal may encounter that may also be frustrating.

Movement restraint. Animals prevented in any way from moving or traveling when they try to do so are thwarted in these drives. Most domestic animals now possess high frustration thresholds in these respects, due to many generations of natural and artificial selection. But there are still many signs of frustration in domestic animals restricted in their mobility by cages, walls, fences, and so on. Pawing by sows in farrowing crates is one example. A newly weaned calf pacing stereotypically back and forth along the fence-line separating it from its mother is another.

Environmental stimulation. If the surroundings are either too dull or too exciting, it seems, animals are likely to react by behaving in unusual fashion. Those in monotonous environments often develop tics, for example. On the other hand, moving an aggregation of animals from familiar surrounding to strange ones may incite a round of fights within the group. In these ways, perhaps, the animal is simply injecting acceptable, albeit purposeless, behaviors into unacceptable existences.

Key stimulus. When a key stimulus to a rewarding activity is missing from the environment, animals sometimes accommodate the frustration due to its absence by substituting another object for it or by engaging in another activity altogether. An example of the former is the intersucking prevalent in some groups of calves and lambs being fed without artificial teats. In this case, the key stimulus--the dam's teat--is absent, and the frustrated animal substitutes a groupmate's navel or scrotum for it. As for the other possibility, it has been suggested that absence of nesting material is partly responsible for the sow's excessive prepartal activity in modern management systems.

In practical situations, it is common for more than one frustrating factor to be present. Unfortunately, present knowledge does not permit their quantification, let alone estimation of combined effects.

Alternatives When Frustrated

The behaviors that result from frustration tend to be unusual. The particular one expressed depends on many things, including the animal's previous experiences, the

strength of the frustrated drive, and the animal's perception of its environment at the time of the frustration.

Principal alternatives. An animal thwarted from completing a goal-oriented behavior pattern has four principal alternatives of action. It may repeatedly make the same preliminary acts leading to the same goal--being frustrated time and again--and eventually develop stereotyped behavior (tic). A second alternative is to adopt different appetitive acts in trial-and-error fashion, but without changing the final goal. Thirdly, it may continue the same preliminaries, but redirect the consummatory act at a different target. And lastly, the frustrated animal may change both appetitive and consummatory behaviors by commencing an irrelevant (displacement) activity.

The first two alternatives (stereotyped movements and trial-and-error seeking) cause the animal to waste energy. Redirected and displacement activities may be aggressive or self-directed and damaging in nature.

Stereotyped behaviors. When an animal repeats a set movement or series of movements regularly, its behavior is said to have become stereotyped. Severely frustrated animals sometimes react in such a fixed manner regardless of the external stimulus. For example, wild animals confined in zoos are commonly obsessed by tics.

A few stereotypes are recognized in domestic animals, too. Hens kept in individual cages in one study had twice as many head tics (rapid head movement from center to one side and back) as those kept in groups on litter. Head tic may have been substituted for some shaking, stretching, extending, agonistic and environmental pecking, and 180°-turning, all of which behaviors occurred much more frequently in hens kept on the floor. In another experiment, hungry hens were frustrated in their attempts to eat by placing a piece of clear glass or plastic over the feed. An early reaction to this was a large number of escape movements; the hen would walk quickly back and forth in front of the door. These actions soon became modified and stereotyped, and resulted in the expenditure of considerable energy.

Bar-biting by a tethered sow and foot-stamping by a cornered ewe are other examples of stereotyped movements.

A special kind of fixed action pattern involves regression--adopting behaviors typical of an earlier age. Intersucking by young or adult cattle and sheep is regressive, for example.

Trial and error. Animals sometimes attempt to overcome obstacles by going around them. A familiar example is the newly weaned calf or lamb searching for and trying holes in the fence separating it from its mother.

Redirection. Sometimes a frustrated or frightened animal will continue expressing a complete behavioral pattern, but redirect the final act. An example of this is the pig challenged by a dominant penmate at the feeder, that directs its rebuttal not at the challenger, but at a hapless subordinate animal nearby. Another form of redirection occurs as a frustrated chicken suddenly redirects its pecks from the feed to the feeder.

Displacement. When an animal is frustrated in a goal-oriented act, it sometimes commences a behavior out of context with those immediately preceding and following it. Frustrated chickens sometimes engage in frantic grooming of the feathers (displacement preening). Displacement grazing may occur in frustrated ruminants. An nursing lambs and calves often wiggle their tails vigorously when the flow of milk wanes. Certain aggressive acts comprise still another form of displacement activity.

According to one theory, displacement activities are normally inhibited, but may be released upon repression of their respective inhibitors. For example, assume eating inhibits preening in chickens. Then when eating is repressed, the drive to preen would be released. So when a hen's drive to eat is in conflict with a tendency to avoid feed (due to approach blockage by a dominant flockmate), the drive to preen would be able to express itself.

Other alternatives. In addition to the principal ways an animal may react to frustration, there are several other possible adaptive responses. D.G.M. Wood-Gush and others identified them as follows: inhibition of all but one response--as when a lamb's hunger drive is overwhelmed by the drive to flee an approaching coyote; intention movements--as when a hen's drive to nest is incompletely inhibited and she makes repeated approaches to the nest without ever nesting; ambivalent behaviors--as when two reactions are triggered weakly and simultaneously and the resulting acts comprise a mixture of appetitive acts of both patterns; compromise behaviors--similar to the ambivalent case, except that a single behavioral pattern (expressing both tendencies) is shown, as when a cock both approaches and flees an antagonist via a waltz display; vacuum activities occur in an environment providing insufficient stimulation, as the animal performs movements associated with phantom tasks, such as nest-building; alternation--in conflict situations, such as tendencies to both approach and avoid an object, the animal may alternate the two patterns; and immobility responses--frustrated or frightened animals sometimes assume a frozen posture.

Frustration and Aggression

Noxious behaviors are extreme forms of aggression in which one animal attacks another of the same species and actually inflicts injury. Intraspecific conflict is wide-spread in the animal kingdom, as individuals compete for food, mates, and territory. But violence as it occurs in farm flocks and herds is atypical of animal life in general. Of course, in the wild, an attacked animal usually flees its aggressor, while in domestic situations it is severely limited in its opportunity to get away from a combative groupmate.

Agonistic behaviors--running the gamut from threatening displays through deadly attacks--are triggered by external stimuli, although combative tendencies lie closer to the surface in some animals than others. Aggressive and escape behaviors lack preliminary phases; animals normally do not seek conflict in response to any internal trigger nor do they retreat unless threatened. Likewise, once the stimulus disappears, such behaviors cease. For example, induce to attack a groupmate, an animal usually continues the assault until the stimulus (the other animal) is eliminated by being driven away, subdued, injured, or killed.

Primary triggers. The major primary stimuli for animal aggression are pain, invasion of individual space, territorial trespass, and competition for feed of a mate. Novel animals, surroundings, and objects also incite attacks. Animals sometimes learn secondary aggressive stimuli, too.

Secondary factors. The sex hormones are predisposing factors in aggression. One reason for castrating male animals is to eliminate androgen production and thus reduce aggressiveness. Female temperament, especially around the time of parturition, is related to circulating concentrations of sex steroids, too.

Frustration is another indirect precursor of agonistic activities, and a common one in animal production. The frustrated state excites the animal, heightening its sensitivity to

primary and secondary releasers of aggression. Some of the experimental evidence comes from studies of hens may react in any of several ways depending on her experiences, the strength of her hunger, and the environment she perceives when frustrated.

The social environment plays an especially crucial role. A frustrated hen isolated from others may show displacement preening, displacement sleeping, or redirected pecking. Of course, she has no opportunity to attack another hen. But when two hens familiar with each other are frustrated at the same time, the dominant one shows a large amount of agonistic activity. And when three hens that form a stable dominance order are frustrated two at a time, a hen shows increased aggressiveness only if she is the dominant one of the pair : frustration makes the middle-ranking hen feistier when she is in the presence of the lowest-ranking one, but not when her partner is the highest-ranking hen.

Some consequences of various aggressive acts in production herds and flocks are discussed in a later section.

Other effects of frustration. The aberrant antics an animal sometimes displays in response to a frustrating situation are in one sense quite natural and useful. They apparently provide the animal a variety of behavioral outlets so it can try to keep its distress at a harmless level. Nonetheless, such behaviors indicate the animal is undergoing stress and suggest the possibility of subtle, deleterious consequences of the frustration itself or of the conflict situations it often leads to.

Stress hormones. There is every reason to believe that frustration increases the release of corticosteroids and catecholamines from the adrenal glands, but direct evidence has been difficult to obtain due to technical problems.

When young pigs' eating drives were experimentally frustrated, their plasma concentrations of adrenocorticotropin and the glucocorticoids all rose greatly. As for the catecholamines, rhesus monkeys kept continuously in primate-restraining chairs excreted about four times the normal amount of epinephrine in the urine during the first three days of chair restraint, but not thereafter. Similar studies on domestic animals have not been reported.

Effects of glucocorticoids on productive processes are discussed elsewhere in this book. The catecholamines may adversely affect several productive and reproductive processes. For instance, they antagonize oxytocin's actions in both milk ejection and uterine motility in ungulates. Also, there is indirect evidence in the hen that frustration increases catecholamine secretion rate and that this effects oviposition : both frustration and an epinephrine injection delay the time of egg laying.

Energy wastage. An animal engaged in agonistic, stereotyped, or trial-and-error behavior spends energy, and this reduces the efficiency of feed use for productive processes. Of course, this may be acceptable in view of the benefits the animal derives from certain ones of these activities.

Distraction from eating. The frustrated animal not only spends energy in its behavioral diversions, but most such acts interfere with feed intake. Time spent pacing cannot be devoted to eating, for example. Whether the animal can compensate for the lost opportunity depends on the distraction's duration and the nature of future opportunities to eat.

Anomalous Behaviors

Because of adverse effects of various anomalous activities, animal managers need to be able to recognize those seen frequently in practical settings so as to be able to remedy the causative environmental problem if feasible. Following are brief discussions of several such patterns of behavior.

Noxious behaviors Noxious behaviors have more serious consequences in intensive systems of management. This is because the attacked animal has such limited opportunity to escape from its attacker in such situations.

Pulling and swallowing hair, wool, and feathers. A mild form of aggression in cattle, sheep, and poultry involves pulling cover elements from their follicles in the victim's skin. This not only damages the attacked animal, but the aggressor can hurt itself by swallowing what it has pulled.

In chickens, turkeys, and ducks, feather-pulling alone usually impairs the performance of the individual bird. Also, the value of a carcass from which feathers have been pulled is frequently reduced. But often even more important is the fact that feather-pulling may serve as a prelude to more vicious attacks. Effects of swallowing feathers on the aggressor are minor.

Wool-pulling episodes occur in some sheep flocks, especially in confined sheep limited diets composed of small particles. Several sheep--as in vicious attacks by poultry--may join together in attacking one animal, often the same individual year after year. Wool-pulling rarely leads to more extreme forms of aggression, but can cause sores on denuded areas of the skin and leave these areas prone to sunburn. Of course, it decreases the current fleece's value, and can even have permanent effects because coarse, black fibers come in to replace the wool fibers pulled. Further, wool balls are often formed in the rumen of the puller, and they can block the gastrointestinal tract.

Self-and social-licking by cattle--while not aggressive acts--nevertheless may be noxious. Licking involves some hair-pulling and often results in the formation of hair balls. These also can occlude the gastrointestinal tract and cause death.

Cannibalism" in poultry Vicious behavioral patterns have been recognized in domestic birds for over a century. They can lead to serious problems in poultry operations. In chickens, it appears that feather-pulling and more violent acts of aggression are both triggered by similar environmental inadequacies, but otherwise they represent separate behaviors. Further, two kinds of "cannibalism" have been identified. Vent pecking, which often leads to evisceration and death, is independent of feather-pulling, but pecking the toes, wings, and other parts of the body is triggered by skin wounds that result from feather-pulling.

Outbreaks of these noxious activities in poultry are unpredictable. Heredity plays an important predisposing role, as do high light intensity, crowding and caging. Yet there seems to be no single causative factor in any case. The problem is complex and involves relations between the individual birds and the environments they perceive.

Various methods of controlling viciousness in chickens have proved beneficial, but once it breaks out it may be difficult to stop. Probable the most effective control measure is debeaking, in which about half the beak is removed. Of course, this procedure merely removes the bird's major tool of aggression; it does nothing to reduce the impact of stressful factors. It is conceivable that debeaked chickens--having less ability to vent their frustrations--are actually more frustrated than if they were intact. Further, debeaking itself slows the birds' growth.

Keeping light intensity as low as possible without impairing performance is also helpful. Use of red lights in lightproof houses reduces vicious tendencies, too, because under red light, blood—a prime trigger of severe aggression—appears black. Various appliances, such as “peck guards” and “specs” (blindings), have also been used with some success.

Vicious acts in swine Pigs, too, are relatively aggressive by nature, and reports of vicious behavior among domestic swine predate this century. The problem has become serious in confinement production systems. At the least, an outbreak of violence necessitates the extra work of removing the victim from its group and caring for it separately. In addition, it causes restlessness and energy wastage, reduces growth rate, and leaves wounds that may become infected and lead to decreased carcass value or even death.

Tails and ears are the easiest targets of aggression. Tail-biting usually breaks out first, as ear-chewing is an outrageous sign of aggression and invites immediate retaliation. An episode often starts as an exploratory nip on the tail tip that draws blood. As the victim shakes its bleeding tail, further biting is stimulated, and this may continue quickly until only the tail stump remains. Death due to loss of blood may come within minutes at this point. Sometimes the victim’s ears are attacked next, and the pinnas are frequently devoured completely.

The exact cause or causes of tail-biting and ear-chewing remains obscure. Large groups and crowding have been documented as predisposing factors. Physical discomfort is recognized as a contributing factor, emphasizing the need for a comfortable physical environment. Frustration of various kinds also have been implicated, as have high light intensity and introduction of a strange pig into the group. Because outbreaks are sporadic, it has been speculated that they are related to weather changes. However, there is still not scientific support for this view.

Prevention. Docking most of the tail soon after birth is the most effective means of preventing tail-biting in swine. Odor-masking sprays are regrouped or moved to a different pen. A variety of objects, such as automobile tires and bowling balls, have been placed in pens in attempts to alleviate the pigs’ “boredom” and reduce agonistic activity. These have often been of some initial benefit, but the pigs seem to become habituated to their novelty quickly.

Savage sow syndrome The sow ordinarily forms social bonds with her piglets during the first few days after farrowing. After this, she protects her own young against all approaching animals, including piglets not her own, by attacking them. However, some sows turn savage during or soon after parturition—before forming bonds with their newborn young—and injure, kill, or eat some or all of their piglets. This anomalous behavioral pattern is unpredictable, but seem to follow maladjustment to the farrowing quarters.

Moving sows to the farrowing facility several days before parturition is expected gives them an opportunity to adjust to the environmental change before the piglets come. Removing piglets from the sow as they are born, keeping them away until the sow has settled down (usually shortly after parturition is completed), and then returning them as a group to the sow has also proved a successful way of controlling this syndrome. Tranquilization of the sow by drugs has been of some value, also.

Other Bizarre Behaviors

Intersucking. Non-nutritive sucking is a redirected behavior that may arise in cattle, sheep, or swine. It occurs frequently in young animals being reared artificially. When the habit persists into adulthood, it comprises regressive activity as well.

The target of intersucking in young pigs is usually the ears only, and thus such behavior is ordinarily of little consequence. Newly weaned pigs do sometimes nuzzle their penmates'; abdomens, mimicking early stages of nursing, and this may be so frequent as to interfere with eating and other activities. In lambs and calves, on the Other hand, such attempts to satisfy the suckling drive are aimed in addition at scrotal, navel, and preputial structures, and this often has serious effects on both perpetrator and victim. Sucking animals often take in large quantities of urine, which may reduce feed intake. Umbilical hernias sometimes develop on sucked individuals. All animals involved have impaired have impaired growth.

An apparent substitute for sucking in some individuals is licking. The young animal may lick itself or a penmate, and, in either case, it may swallow so much wool or hair while licking that balls form in the rumen. One means of trying to prevent intersucking is to wait until the animals are at least a month old before grouping them. Individual offenders may be continuously isolated for even longer, or they may be separated from the group for a while after each feeding. In any case, remedies must be applied quickly because the habit spreads readily.

Persistence of this vice into adulthood is especially prevalent and troublesome in dairy herds. In some cases, a large number of coes practice intersucking, and the economic drain can be significant. One herd of about fifty cows finally had to be dispersed because the problem had become huge and apparently insoluble. Muzzles of various sorts are sometimes used on individual heifers or cows in attempts to arrest the habit early.

Social isolation and restraint. All food animals are social by nature and become distressed when isolated from their groupmates. Visual contact is a partial ameliorant when physical isolation is required. All species tend to defecate, urinate, and vocalize in special ways, frequently during temporary social isolation. Other reactions tend to reflect fear : avoidance, immobility, and shivering.

Varying degrees of short- and long-term restraint are stressful, too. Common reactions include struggling, immobility, and, in pigs, tantrum behavior. Physiological manifestations undoubtedly accompany the frustration due to movement restraint, but they have been difficult to document.

Some bizarre behaviors in layers. Once a laying hen chooses and enters a nest, she normally settles down and makes clucking sounds until she lays the egg. However, hens held in cages often pace stereotypically for a period of up to more than an hour before oviposition. This activity presumably represents adjustment to frustration of some sort, but it wastes energy, too.

Another problem in some layer flocks is avian hysteria, which usually occurs in the second half of the production year. The hens become increasingly nervous over a period of months until, one day, an episode of hysteria breaks out. It ordinarily lasts about a minute. Hens may be injured and even killed during the pandemonium. Although it may start with one bird, it very quickly involves all the hens in her group a cageful or a roomful. High population density in colony cages is an important predisposing agent, but hysteria appears to be triggered by pain. During periods of frequent episodes, egg

yield is severely decreased. Certain strains of layers have a genetic propensity to hysterical behavior. The most effective remedy is a reduction in social pressure.

In some chicken-breeding operations, floor-laying of eggs by pullets reared in floor pens interferes with the estimation of individual egg production, usually accomplished through trap-nesting. The tendency to lay on the floor instead of in an artificial nest is heritable. It is also encouraged by confinement, as opposed to range-rearing, and high light intensity in the vicinity of the nests.

Some of the confined sow's idiosyncracies. Sows tethered or confined to stalls engage in bar-biting as an apparent vacuum activity throughout the day. They also may grate their snouts on the floor or front of the stall and rub their backs against the sides repeatedly. Furthermore, they may stand motionless for long periods. These behavioral outlets signal that some sort of frustration is present, and occur more frequently around feeding time and immediately before defecation or urination.

The confined sow is extremely restless during the day before she farrows, as she presumably substitutes various other activities for the nest-building she is driven to engage in. The typical waves of high activity at this time do not seem to be affected by the presence or absence of nesting material. Whether or not this intense behavior interferes indirectly with parturition, the initiation of lactation, or maternal behavior is not known.

Cattle and sheep. Calves and lambs fed low-fiber diets often gnaw wooden pens, perhaps in trying to increase fiber intake. Once started, this habit may be continued into adulthood. Ruminants also rub their necks and sides against the enclosure when closely confined, and it has further been suggested that the rate of eye-blinking is directly related with anxiety in these animals.

LIGHT AND BIOLOGICAL RHYTHM

Biological Rhythms

The environment of continuous light and continuous darkness would be extreme and would demand physiological adjustments no matter whether a mammal experiences them naturally or in an environmental chamber. We must also realize that the light cycle of day and night results in two sets of environmental extremes. The sensitivity of the mammalian retina to light need hardly be stressed (the light of a match can be detected for a long distance—supposedly at 1 mile). Yet the eye in day light must frequently tolerate or protect itself from as much as 10,000 foot-candles in direct sunlight. Some mammals alleviate this situation by being nocturnal or by staying under trees in the forest where F.C. 100 in summer and 3000 in winter. Regardless of the habitat there has been a powerful daily cycle of light and darkness which has continued to influence the animal group. This influence is unlike those of partially localized environment; i.e., temperature, water or mountain, in that all mammals at same time have had to experience the light-darkness extremes. This is one factor of evolutionary pressure which almost all mammals have in common, along with other forms of life such as plants. The result has been that in some way a phenomenon common to plants and animals has been coupled with the light-darkness cycle. The phenomenon, we call “the 24-hour”, solar, or circadian biological rhythm, can be detected in the physiology or behavior of most animals and green plants.

Since the daily biological events does not usually begin exactly every 24-hours, today its timing is called circadian, meaning (about 24 hours). It is not only coupled with the light-dark cycle but was probably caused by it. Although, the light-darkness cycle is coupled with the circadian rhythm, this cycle is reinforced by lesser factors such as temperature.

Typical Example

Typical circadian rhythms are found in records of locomotor activity of rats or hamsters. Soon after sunset nocturnal rodents will begin to exercise on running wheel. This can

continue without stopping for rest or food. The pattern of day active animals may be the same but reversed to day light. The time of starting activity is very regular.

When other functions are recorded, the resting temperature or “core temperature” is higher than the resting daytime, and the resting heart rate is 5% higher than resting daytime heart rate. Similar figures have been obtained for oxygen consumption, total activity, kidney activity and many other functions and mechanisms.

The concept has been advanced that there are actually two animals. The day animal and the night animal.

Terminology

The typical rhythms are synchronized with the powerful solar light-darkness cycles. The first stage in the study of any rhythm is invariably to test for the dependence of the rhythm upon the light cycle, by placing the animal under constant conditions of darkness or light, temperature and sound. Using rodents the results of this test shows that the amplitude and period (length) of the activity rhythm does not depend upon a light-darkness cycle. For many months in continuous darkness nocturnal rodents make activity records which can hardly be distinguished from records made with a light cycle. Such activity rhythm is referred to as free running. The duration of the rhythm is usually about 23 or 25 hr rather than 24 hr; under these circumstances the designation “circadian” is especially appropriate. It is certainly preferable to the term “diurnal”.

In certain cases, the rhythm does not persist under continuous conditions (free running), then the rhythm is called exogenous rhythm; if still present it is called endogenous rhythm. It is conceivable that an animal may show both exogenous and endogenous rhythm.

Time Givers and Clues

Today, realization of the importance of time givers replaces the earlier belief that the whole day light period was of the major importance in determining biological rhythm. Before I described how animals show with regulatory sequence of approximately 12 hr activity followed by 12 hr of rest. This was an over simplification. The important concept is not the length of the two units, but there is a sequence which adds up to 24

hrs. The components of the series of events follow each other in a chain pattern (sleep-feeding-running-defecation-feeding...etc.). Changing the light cycle by 12 hrs will cause the entire sequence as a unit to “rotate like a dial” to match the new light cycle. The natural “chain of functions” is not exactly 24 hrs, but frequently 23 or 25 hrs. Certain events which occur once in 24 hr set the rhythm; these events might be:

- (a) the start of the light cycle
- (b) the end of the light cycle
- (c) regular artificial feeding time
- (d) regular noise of other animals in cages

A flash of light at the end or the beginning of a photoperiod will be sufficient.

Such physical events were given different names: Zeitgeber (time giver), synchronizers: or clues (dawn or dusk are time givers); persistent rhythm is detected by removing a known “time giver”.

Biological Clocks

The usefulness of time givers to maintain a rhythm close to 24-hrs, rather than other potential rhythm, such as 23 or 25 hrs, may suggest that mammals do not need an internal system for time measurement.

“Many animals can measure time accurately; a clock is an internal part of animal physiology.”

There are advantages for these clocks for animals in free-environment.

- (1) In the free environment time givers are not regulars. Sunrise may be completely hidden for a number of days, at the same time the barometer may be unusually high and the environmental temperature may show a large change. When such a disturbance occur the internal clock of the animal maintains its program.
- (2) To assist in orientation; ex., birds travel by maintaining an appropriate angle to the sun or to polarized light (when the sun is not visible). They must change this angle according to the time of the day. Thus, they must know or measure time accurately in order to make appropriate corrections.

Suppose you maintained blind folded for two days then you were taken in a boat, away from land and then were told to go to shore. You know the shore is the west, but if you do not know the time of day (by good physiological time piece) then you can not tell the difference between different positions of the sun as at 10:00 a.m. or 2:00 p.m. and you would not know which direction to go. The birds know the time, even when kept in darkness for several days.

Schools of Rhythm Causation

Three theories as to the origin of 24-hr rhythm:

- (1) a conditioning theory
 - (2) an inherited 24-hour-clock theory
 - (3) a cosmic receiving station theory
- (1) A conditioning theory assumes that as animals develop, they are arrhythmic, they then learn what is approximately 24-hr rhythm from environmental conditioning or from the behavior of the parents. This condition is reinforced and made accurate by the environment as the animal develops.
- (2) An inherited clock theory. The second theory assumes the presence of an *inherited circadian clock (the rhythm is born, not made)*. Direct evidence exist using birds as experimental material. Chicks were hatched and raised in a constant dim light and without any known periodic environmental factors. They developed a rhythm of slightly less than 24 hr. If an environmental factor was an influence, they would have acted as time givers and set up a more exact 24 hour rhythm in these birds. In summary, the *inherited 24-hr clock theory* assumes a genetically endowed fundamental pure rhythm with a free running period of 23 to 25 hr. In the free environment, time givers set this inherent rhythm at 24 hrs, permitting it to be the clock in animal navigation. Most of the direct evidence supports this theory of inheritance.
- (3) The cosmic receiving-station theory. The third theory assumes that animals respond to periodic cosmic changes other than daylight; that is they can act as “cosmic receiving stations”. Some of the periodic cosmic changes or periodic variables include cosmic ray, showers, air ionization, pressure and humidity.

Anatomical Location of the Timer

A number of investigators over the years have done experiments which were designed to locate a hypothetical biological clock.

- (1) Removal of stomachs
- (2) Removal of the adrenal
- (3) Removal of thyroid
- (4) Removal of cortex

Then it was suggested that the nervous system is all important.

However, it was stated that the concept of the localized center for the circadian rhythm is an over-simplification.

A new concept is proposed, according to which there is a basic 24-rhythm present in the cells of all animals and that this rhythm is inherited, the cells may not be all in phase with one another, and any cell or group of cells may constitute a "physiological clock" regulating certain activity, although always running to a 24-hr cycle, so that any animal may have a number of clocks all operating at once, either in phase or at variance with one another.

Adrenal cortical cells has 23.4 hr (in vitro)

Individual neurons can measure time

Biological clocks are probably not definite structures within organs.

In Humans

It was found that, sleep, heart rate, water excretion, temperature and potassium excretion.

Human has low metabolism at 4:00 a.m.

- (1) Maximum body temperature, heart rate and rate of excretion of potassium occur between 5-9 p.m.
- (2) But the rate of urinary flow occur later.
- (3) Peak steroids secretion cortisol between 7:00 a.m. and 12:00 noon.
- (4) The minimum count of white cells in blood near 9:00 a.m. with gradual rise to maximum after midnight.

- (5) A minimum mitotic activity in the epidermis in the morning with a maximum in the evening. These are responses occurring from the anterior pituitary under hypothalamic response.

The effect on the industrial worker of a change from day shift to night shift represent a practical problem.

- (1) How quickly can they change their normal rhythm by 12 hrs?
- (2) How complete is the physiological change when the subject appears to have made a normal adjustment?

In humans, it is very hard to know because social events keep them from having a 12hr shift. In animals (rodents) speed reversal has been determined to be 4 days with ordinary laboratory lighting. The feeding pattern changes also. It is normally harder to turn the clock backward than forward. In a lot of cases, man may not reverse his night physiology by day-physiology, 6 week kidney function.

Studies on switchboard operators even after being on the night shift for a considerable time, they do not completely adapt. The delay in answering morning calls by the operators (2-4 a.m.) is over two times as long as during the day time.

Jet-lag Sickness

There are a number of disturbing effects due to flying over a long distances today; some of the effects are immediate and due to inconvenience but the other influences may last over many days and should be called "time zone effect".

The overall discomfort which most individuals experience can be summed up as "jet-lag sickness". Ex., a typical west to east flight leaves N.Y. at 7:00 p.m. and arrives (by personal clock time) in Amsterdam at 1:00 a.m. The individual is ready for a good night's sleep. However the local time is 7:00 a.m. The individual takes a taxi to hotel, the room is not available until 1:00 p.m. This is a poor start to a trip.

The real time zone effects take place over the next few days. After each late night the person goes to bed tired but awakens alert and wide awake at 3:00 a.m., because by personal physiology time it is 9:00 a.m.

Studies showed that adaptation on westward is more easier than eastward. How long an individual takes to adapt to a new local time. It is essential that an individual allow

enough time for rephasing of the critical circadian rhythms as is necessary before that individual must accomplish some assigned tasks with complete efficiency.

Light

Light is the radiant energy that acts upon the retina of the eye, making sight possible. A form of radiant energy but not acting on the normal retina as ultraviolet and infrared radiation.

The length of electromagnetic waves visible to the animal's eye range from 0.37-0.77 micrometer. The color of visible radiation varies with its wavelength. Ultraviolet radiation ranges from 0.004-0.39 μm in wavelength. The human eye is most sensitive at 0.55 μm .

Characteristics of Natural Lighting

Animals evolved in an environment characterized by a special kind of photic energy, i.e., the light of the sun, filtered through the atmosphere and its surrounding layer of ozone.

Spectra Composition

The spectrum of the solar energies reaching the earth is highly characteristic. Essentially no wavelengths shorter than 290 nm (i.e., short-ultraviolet and some mid-ultraviolet) penetrate the atmospheric shield. The radiant energy at a longer wavelength increases sharply in the near-ultraviolet (320-380 nm) and visible (380-770 nm) portions of the spectrum, reaching a peak in the blue-green range between about 400 and 500 nm; it then decreases gradually into the infrared portion of the spectrum.

In incandescent light sources emit about 90% of their radiation in the infrared region which provide heat rather than light. Within the visible portions of incandescent spectra, the relative fluxes at different wavelengths are, as expected, maximum in red and minimum in the blue.

Fluorescent bulbs generate visible light by a different physical mechanism from that of the sun or incandescent bulbs. Their light output comes not as a consequence of heating but from activation of chemical phosphors by ultraviolet emissions generated in a low-

pressure mercury are discharge. The spectra emitted by fluorescent sources can be thus modified at will. This freedom in programming spectra has been utilized to design bulbs that, for a given total output, is as bright as possible.

Brightness is a subjective phenomenon and depends upon the extent to which photoreceptors in the retina are stimulated. Since photoreceptors are most sensitive to visible light in the yellow-green range (555 nm), most fluorescent light sources have been designed to emit a considerably larger fraction of their total light output in this region of the visible spectrum than the fraction present in sunlight.

Florescent light are usually designed to minimize the emissions in the ultraviolet and infrared ranges. *Animals in confinement* spent their hours under light spectra that differ considerably from those characterizing natural sunlight and that were chosen by the lighting industry in accordance with the view that the only significant effect of visible light on an animal is on his retinas, i.e., to enable it to perceive objects by their relative brightness.

There is evidence that lighting in the visible and near-ultraviolet ranges does considerably more to an animal than simply to provide substrate for vision.

Intensity

The light intensity provided in most artificially lighted barns is on the order of 0.5-10 F.C.

Animal Responses to Photic Stimuli

Direct and Indirect Effect of Light:

Each of the various effects of light on animal tissues can be classified as direct or indirect, depending on whether its immediate cause is a photochemical reaction occurring within that tissue or neuroendocrine signal generated by a photoreceptor.

Direct Effects: The direct effects of light can be defined as the chemical changes in the composition of a tissue that result from the absorption of light energy within that tissue. Natural sunlight acts directly on the cells of the skin and subcutaneous tissues to produce pathologic and protective responses.

Pathologic Responses

- (1) Sunburn: Mid-ultraviolet radiation (290-320) cause sunburn to appear within several hours of exposure. This reaction lasts for several days results from the release of vasoactive compounds from damaged epidermal cells. This compounds diffuse into the dermis, where they damage the capillaries, causing reddening, heat, swelling and pain. A variety of compounds have been proposed as the offending toxin (5-HT and histamine or polypeptide bradykinin).

Exposure to sun for many hours each day for many decades can cause permanent changes in skin structure. In susceptible individuals, it can cause cell carcinoma in the epidermis. Dermal changes include disintegration of collagen and elastic fibers. Cell carcinomas tend to develop on areas of the skin normally exposed to the greatest amount of sunlight (the nose). This is most curable surgically.

Protective Responses: Immediately after exposure to sunlight the amount of pigment in the skin increases and they remain hyperpigmented for few hours. This effect results from the photo-oxidation of colorless melanin precursor. This can be caused by both ultraviolet radiation and visible radiation present in sunlight. After a day or two, when the initial exposure to sunlight has subsided, melanocyte in the epidermis begin to divide and increase their synthesis of melanin granules; the granules then extruded, after they are taken up into the keratinocytes. This secondary hyperpigmentation can persist for several weeks following exposure to sunlight and provide protection against further tissue damage by sunlight. It is lost as the keratinocytes slough off, explaining the disappearance of a suntan a week or two after vacation's end.

Bilirubin and Light

Vitamin D and Sunlight: Vitamin D₃, or cholecalciferol, is formed in the skin and subcutaneous tissue when ultraviolet light is absorbed by its provitamin 7-dehydrotachysterol, it can be obtained by eating fish. It is caused by mid-ultraviolet

(0.29-0.32) and long-ultraviolet (320-400) irradiation. A related biologically-active compound vitamin D₂, can be obtained by consuming milk and other foods fortified with irradiated ergosterol.

Indirect Effect of Light: The indirect response of a tissue to light result not from the absorption of light within that tissue but from the actions of chemical signals liberated by neurons (neurotransmitters) or delivered by the circulation. These signals, in turn, result ultimately from the responses of specialized photoreceptor cells to light. **Example:** When young rats are kept under continuous light, photoreceptive cells in their retinas respond by liberating neurotransmitter substances that activate other brain neurons, these neurons in turn, transmit signals over complex neuroendocrine pathways that reach the anterior pituitary, where they stimulate the secretion of gonadotropin hormones that accelerate the maturation of the ovary. That the cells of the ovary are not responding directly to light can be shown by removing the eyes or the pituitary gland before placing the animals under continuous lighting, in such animals light no longer exerts any measurable influence on ovarian growth and function.

I. Light and Biological Rhythm

It is known that light is the dominant environmental input affecting rhythm. Rather than inducing the rhythm, the light cycle might simply entrain it, causing all animals in the same species to exhibit maxima and minima at the same time of day or night. The factor that generates the rhythmicity per se could be intrinsic biological clock. Placing the animal in an environment of continuous light or darkness should not extinguish the rhythm. But in the absence of cycling lighting input the rhythm became dissociated from each other. The rhythms free runs or become circadian, that is its precise period changes from exactly 24 hr to something more or less.

II. Light and the Mammalian Pineal Organ

The best-characterized indirect effect of light on any process other than vision is the inhibition of melatonin synthesis by the mammalian pineal organ. Light acting on the retinas send impulses via the sympathetic nerves to the pineal and inhibits melatonin

synthesis. This is a different route taken by the nerve impulses responsible for vision and unique for mammals.

If rats are maintained for several days under continuous light the activities of the enzymes responsible for melatonin synthesis decrease. This effect is absent in animals in which the eyes are removed or the nerve to the pineal is cut. It is an exaggeration of the normal daily response to light. Melatonin affect the secretion of various endocrine organs. Immature rats and hamsters kept under continuous light become sexually mature at earlier age than animals kept under 24 hrs light-dark cycle. This may be mediated by haptic inhibition of melatonin.

III. Light and Gonadal Function

The gonads of birds and many monoestrus mammals (ferret, hamster) mature in the spring time, in response to the gradual increase in day length. sexual maturity can be accelerated in these animals by exposing them to artificial long days. The annual period of gonadal activity in domestic (diurnally active, monoestrus species) occurs in the fall in response to decreasing day length. Exposure to “short day” to less than 12 hr of light per day causes bird’s testes to atrophy.

In birds, photoreceptors capable of mediating gonadal responses exists in the brain as well as the eyes. In adult mammals, however, only the retinas contain the photoreceptor cells necessary for stimulating gonadal responses.

Reproduction:

Environmental light is a major factor influencing reproduction in monoestrus mammals and birds. The reason of this is that naturally occurring changes in daylength are precisely the same from one year to the next and perform two major physiological functions: (1) Synchronizes various rhythmic activities, and (2) Induces hormone production. Both of these functions are essential for the normal reproduction function.

- (1) Synchronizer function: Environmental light is a particularly good synchronizer of physiological events as it is the only environmental factor which varies in precisely the same manner from one year to the next and thus changes in day length and season can be anticipated and used in a predictive manner. Since

seasonal breeders possess a natural annual rhythm of reproduction, they utilize the seasonal changes in day length in a predictive manner in order that the young will be born or hatched at an appropriate time of the year, when the weather is mild and food plentiful, i.e., early spring.

- (2) **Inducer function:** Normal reproductive performance is dependent on proper hormone levels. Light plays a very important role in stimulating and coordinating the production of hormone via a neuroendocrine reflex. This involves the brain, the pituitary and the gonads. Birds, unlike mammals do not require the presence of eyes in order to have a physiological response to light. *They have the ability to perceive light directly by the brain.* This means that light passes through feathers, skin and bone to reach the brain which subsequently influence hormone production.

Sheep

It is believed that in the ewe, reproductive activity, once begun continues until it is somehow inhibited. That is, it is temporarily inhibited during anestrus, instead of being temporarily stimulated during the breeding season. The inhibition of gonadotropin release may result from seasonal variations in release of neurohormones (e.g., melatonin).

Birds

Birds under short photoperiod have their gonads regressed and gonadotropin hormones are low. *When they are exposed to long photoperiod FSH and LH increase within 2 days.* Therefore, sexual activity in birds appears to be controlled by long or increasing photoperiod somehow increase gonadotropin release.

Photoperiod

Photoperiod is the most reliable indicator of season and as such is extensively used to control the important productive functions of animals, particularly growth and reproduction. This achieves both the synchronization of peak nutrient demands with peak availability and the preparation and synchronization of the animal's body for

reproduction at the optimum time, usually to produce a spring parturition. The synchronization of parturition is particularly important in species whose neonatal offspring 'follow' their parents rather than 'hide' (Rutberg, 1987) to avoid predation. Sheep may be classified as 'followers' and are strongly photosensitive, whereas cattle and pigs are 'hidiers' and are weakly photosensitive. Chicks, like pigs, have nests but usually spend a large proportion of the day 'following' the hen. Other possible reasons for the greater photosensitivity of sheep and goats than pigs and cattle are the greater seasonal variation in food availability for the smaller ruminants, which evolved in harsher conditions, and the increased selective breeding by man that cattle and pigs have been exposed to. There are strong genetic influences on photosensitivity. These are more pronounced between species and genera, but within a population variation is less pronounced so that synchrony of parturition can be achieved. In the wild this synchrony would produce a limited availability of neonates for predation, thus reducing the predator population.

Photoperiod can in essence be considered as a biphasic light intensity change. However, this change is relative rather than absolute, since the lunar cycle during the scotophase can have additional effects on reproduction. In artificially manipulated photoperiods aspects of the photophase such as light intensity colour (wave-length) and length of the transition between the photophase and scotophase (artificial dawn/dusk) affect the animal's response. Artificial biphasic sequences of more or less than the normal 24 hour day (ahemeral cycles) can also be used, as well as the replacement of part of the photophase with darkness (skeletal photoperiods).

In this review the effects of photoperiod on the production and reproduction of farm animals, the mechanisms involved and methods of artificial manipulation are considered. For more comprehensive reviews the reader is referred to papers by Terqui et al. (1984) and Ortavant et al. (1988) for sheep, Morris (1967) and Cavalchini et al. (1983) for poultry, Ortavant et al. (1985), Forbes (1982) and Tucker (1985) for growth, lactation and feed intake in farm animals, particularly cattle.

Photoperiod Perception

Photoperiod is perceived by the eyes in mammals and additionally also through the skull in poultry. The photic information is relayed to the hypothalamus and the pineal gland via the superior cervical ganglion – the pineal gland encoding the information by producing melatonin in higher concentrations in the dark than the light. Research in sheep has demonstrated that daylength is measured not by the total exposure to light but by the illumination of two special set points during the day about 16 hours apart (Ortavant et al., 1988). An animal can therefore be ‘tricked’ into giving a physiological long day response by being given, for example, a one hour burst of light 16 hours after a short day. This elementary mechanism may yet prove to be too simple, as it does not explain why 24 hours of light do not usually give a long day physiological response. This circadian rhythm of melatonin production entrains the animal to photoperiodism from an early age, in fact influence of the maternal melatonin rhythm begins the process in utero. As the rhythm becomes more firmly entrained into the animal’s biorhythm the animal builds up a resistance to photomanipulation, and residual effects lasting up to several months maintain the physiological response to natural photoperiod.

Perception of light intensity depends on the ratio of rods to cones in the eye and most farm animals appear rather more adapted to low intensity vision and less to visual acuity than man. For example, in cattle the ratio of rods to cones is 15:1 compared with 20:1 in humans, giving cattle optimum visual acuity at a light intensity as low as 120 lux (Dannenmann et al., 1984/5).

Milk Production

Cattle

Several long-term studies comparing cows given natural daylength of 8-10 hours and a period of supplementary light of 4-8 hours with cows receiving the natural daylength only have demonstrated that milk yield is increased with supplementary light by 7-16% (Peters et al., 1978, 1981; Bodurov, 1979; Stanisiewski et al., 1985; Phillips and Schofield, 1989). Level of milk yield of the cows does not affect this response (Peters et al., 1981; Stanisiewski et al., 1985), but in the application to commercial herds it has been found that the response is not uniform (Stanisiewski et al., 1985). Where the

effects of supplementary light have been examined using a short-term changeover experimental design, little or no response has been obtained (Murrill et al., 1969; Peters et al., 1978; Phillips and Schofield, 1989). The reason for this is not clear but may be related to temporary inhibition of prolactin elevation when supplementary light is applied (Eisenman and Chew, 1982) or may arise from a relative rather than absolute perception of photoperiod by the cows.

Perera and Hacker (1982) have reported that 6 hours' light during the day plus a 2 hour pulse at night administered during the last two months of gestation will increase yield persistency, compared to cow given 12-14 hours continuous light daily during two months. To be effective the light pulse had to begin more than 2 hours after the end of the daylight. Further research on this technique would seem worth while

Other species

Bocquier (1985) reported that ewes subjected to 16 hours light (16L) and 8 hours dark (8D) from day 100 of gestation to day 60 of lactation had heavier lambs and increased milk yield than ewes on 8L, 16D. Some of the increased milk yield could have been due to the ewes having heavier lambs at birth. However, photoperiod per Se appears to have had the dominant effect since crossing over photoperiod treatments at 60 days resulted in milk production levels crossing over within 20 days. The magnitude of the milk yield response to photoperiod (20%) appears greater than that usually recorded in cattle. This has implications for frequent lambing systems where ewes may be lactating in short daylength. Similar responses to long days have also been recorded in goats (Linzell, 1973; Terqui et al., 1984). However, some cyclicity is maintained in the absence of light and temperature cues, demonstrating the existence of a photoperiodic history.

In pigs, Mabry et al. (1983) reported increased nursing frequency and increased litter weights at weaning when sows were exposed to 16L, 8D compared with 8D 16L. However, Jones (1984) found no effect of these photoperiods, although a creep light was provided for the piglets in both treatments and the supplementary light intensity (100 lux) was low.

Milk Composition

Peters et al. (1978, 1981) reported that milk fat content of dairy cows was not affected by supplementary light, but in a more robust design of experiment Stanisiewski et al (1985) reported that milk fat content was reduced by 1.6 g kg^{-1} . A large reduction was reported by Phillips and Schofield (1989), but this was not statistically significant. The apparent reduction may not be related to the increase in milk yield since in a separate experiment Phillips and Schofield (1989) found milk fat content to be reduced by supplementary light in the absence of any effect on milk yield. In the only report on the effect of light on milk protein content the same workers found it to be reduced where the light was of high intensity (529 lux at cow eye level), but not at lower intensities (101 or 191 lux). In goats' milk the protein content was also found to be reduced in long daylength, but milk fat content was unaffected (Linzel 1973).

Growth and Carcass Composition

Cattle

Several experiments have demonstrated that an extended photoperiod of approximately 16L, 8D increases the growth rate of heifers by up to 10% compared natural photoperiods of 8-10L (Petitclerc, 1985; Zinn et al., 1986a,b). Others have found no effect (Hansen et al., 1983; Bourne et al., 1984; Petitclerc et al., 1984; Roc and Enright, 1988; Zinn et al., 1989). With steers similar results have been obtained some researchers finding that an extended photoperiod increased growth rate by up to 10% (Zinn et al., 1988; Johnson et al., personal communication), but other finding no effect (Roche and Enright, 1988; Zinn et al., 1989). Weiguo and Philling 1991). One reason for this dichotomy may be that the extended photoperiod reduces fat accretion relative to that of protein in both heifers (Petitclerc et al., 1984; Zinn et al., 1986b) and steers (Johnson et al., personal communication), especially on a high plane of nutrition (Petitclerc et al., 1984). The concomitant reduction in the energetic content of carcass gain would be expected to increase the growth rate slightly. In the wild it is expected that animals entering a period of short days in the autumn will divert nutrients from protein accretion (an increase in size) to fat accretion (an increase in body reserves to sustain them through the winter).

Skeletal long (6L, 8D, 2L, 8D) photoperiods have been tested with growing cattle but appear to have less benefit than a conventional long photoperiod (Zinn et al., 1986a). The major economic benefit of long photoperiods for growing cattle is the reduction in carcass fatness, allowing the producer to rear cattle to a heavier weight before slaughter. To a certain extent this could be offset in heifers by earlier puberty in light-supplemented cattle (Fauconneau and Gauthier, 1984; Hansen et al., 1983).

Pigs

In pigs no benefit of 16L, 8D compared with 8L, 16D has been found in the feed intake or weight gain of growing pigs (McGlone et al., 1988; Gooneratne and Thacker, 1990). Similarly an increasing daylength through the rearing period does not alter performance compared with a declining daylength (Wright et al., 1984). However, compared with 8L, 16D a skeletal photoperiod of 2L, 5D, 2L, 15D has been shown to increase growth rate by 3% and feed conversion efficiency by 2%, and reduce the electricity consumption for lighting by 48% (Melhorn and Dorn, 1985).

Poultry

Continuous light or 8L, 16D GR retards growth in the male compared to 14L, 10D (Leeson and Summers, 1985; Legare et al., 1986; Okamoto et al., 1989). The beneficial effect of 14L, 10D is most pronounced in the first 12 weeks and extending daylength above 8L after 12 weeks has little effect on growth rate (Leeson and Summers, 1985; Classen, 1990). However, increasing the photoperiod in the first 2-6 weeks of age from 6-14L to 23L has been shown to almost double the incidence of leg disease in broilers (Classen, 1990) and also to increase the incidence of sudden death syndrome.

Light intensity is usually kept low to reduce the activity level of the birds, counteract aggression and reduce the electricity cost. In this respect a blue light, which is perceived by the birds as less bright than a red or white light, is preferable to a white light to stimulate growth, at least in the first 16-18 weeks (Lavenick and Leighton, 1988), conceivably because the birds are establishing their dominance order. Thereafter white or red light acts as a better photostimulant than blue light (Lavenick and Leighton, 1988), conceivably

because the birds are settled in a dominance order but have a greater number of meals under the perceived brighter light.

Ahemerak skeletal photoperiods of 2Lm 2D have been shown to increase growth rate, compared with conventional diurnal, 12L, 12D, cycles (Lavenick and Leighton, 1988). A skeletal photoperiod of 1L, 3D is possibly too extreme initially because it does not allow sufficient feeding time in the light. However, the consequent reduction in initial growth rate has advantages of reducing leg disorders and other fast.

Growth problems, and the birds compensate in growth later on. Such a regime may therefore improve the health of the birds without compromising productivity.

Sheep and Deer

In growing lambs a long photoperiod, e.g. 16L, 8D has been shown to significantly increase live weight gain compared with 8L, 16D (Forbes et al., 1979, 1981). However, at least 50% of the increase is due to an increase in gut contents (Forbes et al., 1979, 1981), even in lambs fed at restricted intakes. Continuous light, as with cattle and poultry, is detrimental to the growth of lambs (Hulet et al., 1968). Like cattle, the carcass composition of lambs on long daylength tends to show increased protein and reduced fat content (Forbes et al., 1979, 1981).

As with most other species skeletal long photoperiods, e.g. 7L, 9D, 1L, 7D have been successfully used to replace long photoperiod (Foster et al., 1988) and achieved the same increase in weight gain.

In deer there is also clear evidence for effects of daylength on growth rate. Abot et al. (1984) reported faster weight gains with doe fawns exposed to 8L, 16D than 16L, 8D. The increased weight gain appears to be largely accounted for by increased lipogenesis (Verme, 1988).

Body Covering

Wool

In sheep photoperiod controls the timing of the moult, now confined largely to unimproved breeds, and the growth of wool, this being minimal in winter and maximal in summer (Fig. 3.1) (Story and Ross, 1960). This is mainly a difference in wool fibre diameter (Fig. 3.2)

(Story and Ross, 1960), which creates a weak point in the middle of the fibre in summer shorn sheep. Quality tests have shown that the single thread strength test is an average of 20% greater for winter whorn fibres, with an increase in the hank test of 24%. Much of the summer shorn wool therefore has to be used for carding in woollen manufacture, whereas winter shorn fibres can more often be used for combing for worsted production.

In the natural annual photoperiodic sequence is reversed, to give long days in winter and short days in summer, the periodicity of wool growth is reversed within two years. This gives further evidence for the strong influence of photoperiodic inertia in mature animals, seen also in milk production experiments.

Hair

In cattle the coat is normally thick and long in winter but short and sleek in summer. Extending the photoperiod artificially in winter prevents the growth of the winter coat (Bourne et al., 1984).

Feathers

In poultry the annual moult is photoperiodically determined but is reduced in birds intensively bred for high egg production (Meyer and Millam, 1986). In these animals the moult can be abruptly induced by reducing the photoperiod to 8Km 16D. After the moult the birds go through a photorefractory period of limited reproductive potential. Photosensitivity can be restored by subjecting photorefractory birds to several weeks of non-stimulatory short photoperiod (Meyer and Millam, 1986).

Antlers

In deer, antler growth is seasonally controlled, with most rapid growth during long photoperiods in summer and least growth in winter. The cycle can be accelerated to give up to three cycles per year with artificial photoperiod control (Goss, 1969).

Puberty

Photoperiod has a strong influence on the age at puberty of strongly seasonal breeders, such as sheep and deer, in order to time the first parturition to the rest of the adult population. In

farm animals without strong seasonal breeding patterns there are still some photoperiodic influences on age at puberty. Evidence suggests that in many species there is a photosensitive phase, usually at about one-half of the earliest pubertal age, when long days will stimulate early puberty.

Sheep

In the ewe lamb the timing of puberty is determined primarily by photoperiod and nutrition. The lamb must reach an adequate size before she is receptive to photo stimulation. Normally the spring-born lamb will enter puberty until 12 months of age, also in the following autumn.

The hormonal control of these events is shown in Fig. 3.3. The external cues are photoperiod and nutrition; if nutrition is adequate the GnRH (gonadotroph releasing hormone) pulse generator operates at a low frequency. Photoperiod is regulated by melatonin release from the pineal gland during the dark cycle. This release pattern takes up to 20 weeks to become established in the neonate, and it is the photosensitization to a short day period by the long day melatonin secretion pattern that triggers an increase in GnRH pulse frequency and the subsequent LH release that causes ovulation. The photosensitization, or refractoriness to long days, develops soon after the long day melatonin secretion pattern is established, as a long day period of as little as one week at 20 weeks of age is sufficient to induce short day receptiveness (Yellon and Foster, 1985). However, a lamb kept constantly in short or long days from birth will not enter puberty at the normal age of 6 months. Similarly autumn-born lambs do not enter puberty until they have experienced both the long days in the following summer and the shortening days in the autumn (Foster et al., 1985). The evidence is that the lamb develops a photoperiodic reference, using long days to photosensitize the lamb to enter puberty in the short days of autumn.

Cattle

In cattle, although reproduction is not limited to a particular time of year as it is in sheep, there is evidence of photoperiodic effects on puberty. Spring-born heifers are usually older than autumn-born heifers at puberty (Kamwanja, 1984). This is because the gonadotrophin

production develops later in the former than in the latter. In spring-born heifers extending the photoperiod artificially to 16L, 8D during the first winter reduces the time to puberty by about 20 days and reduces the weight at puberty by about 10 kg (Petitclerc et al., 1983) to 35 kg (Hansen et al., 1983) but may reduce conception rate (Hansen et al., 1983). Long photoperiod at this time also stimulates mammary parenchymal growth, and in postpubertal virgin heifers (Petit-clere, 1985), but has no effect on the mammary growth of pregnant heifers (Newbold et al., 1989).

Pig

In the pig, spring-born gilts have delayed puberty, which occurs at a later age and greater weight than pigs born in other seasons (Mavrogenis and Robison, 1976), but they have a reduced incidence of silent oestrus compared to gilts born at other times of the year. It is likely, therefore, that long days retard reproductive development. Most researchers agree that rearing gilts in the complete dark retards reproductive development (e.g. Ntunde et al., 1979), although Dufour and Bernard (1968) report accelerated puberty by 11 day under darkened conditions compared with natural light. The differences in age to puberty between artificial photoperiods of 10L and 18L appear small (Ntunde et al., 1979), although Klotchov et al. (1971) found an increased number and size of corpora lutea in pubertal gilts with long days. In spring-born boars extension of natural photoperiod (10L) to 15L in the first winter has been shown to advance puberty (Berger et al., 1980) but has little effect on semen quality (Mahone et al., 1979).

Poultry

In egg strain pullets it is generally established that long daylengths up to 16-17L will advance age at first lay up to 2 weeks (Morris, 1967) and result in smaller eggs (Leeson and Summers, 1980). Continuous light is detrimental in that it results in an unacceptable incidence of blindness (Payne, 1975). Not all researchers have found large effects of photoperiod on age at maturity (e.g. Leeson and Summers, 1985), while it has even been found to be delayed by long photoperiod with a corresponding increase in egg size in meat strain pullets (Payne, 1975).

In female turkeys a short photoperiod is required for 3-6 weeks prior to lay as a conditioning period to maximize subsequent egg production (McCartney et al., 1961). In male turkeys more rapid development of semen production occurs in similar short photoperiod conditions (Hocking, 1988).

Male and Female Reproduction

Sheep

Ewes normally confine their breeding season to the late summer/early autumn period, but there is a large variation between breeds, and less effect on sheep at low latitudes. The ovulation rate peaks in the middle of the breeding season but oestrous behaviour accompanies all ovulations equally. Reversing the annual photoperiod pattern will reverse the seasonality of ewe reproduction. It is interesting that the onset of oestrus in the autumn typically occurs at a considerably longer daylength (e.g. 14L in Suffolk ewes) than the onset of anoestrus in the spring (e.g. 11.5 h in Suffolk ewes; Robinson and Karsch, 1984). This suggests that the ewes cease breeding because they become photorefractory to short daylength, rather than, a limiting photoperiod for reproductive activity. Using contracted photoperiodic cycles the ewe can be induced to ovulate frequently, with ovulation starting 50 days after the transition from long to short days (Ortavant et al., 1988).

In the ram seasonal variation in reproductive activity is less pronounced than in the ewe, and the peak of activity precedes that in the ewe by 1.5 to 2 months, presumably to allow the rams time to find the ewes and stimulate them to enter oestrus early by pheromonal induction. In peak activity during late summer/early autumn rams normally have greater testes weight, greater spermatozoan output, better quality semen and increased libido (Ortavant et al., 1988), although low forage availability at this time and high seasonal activity rates can reduce testes weight (Masters and Fels, 1984).

The control of gonadal activity is both by photoperiod and gonadal steroid production, since long daylength is inhibitory to luteinizing hormone (LH) release in intact but not in castrated or ovariectomized sheep. Thus the gonadal steroid inhibits LH release in long, increasing daylength but not in short, declining day length. The hormonal mediator to monitor daylength from the photic cues and induce changes in gonadotrophin production is melatonin. Exogenous melatonin administration by oral or subcutaneous implant methods

will induce reproductive cyclicity in ewes and spermatogenesis in rams with increasing photoperiod (English et al., 1986). However, constant cyclicity cannot be induced by repeated melatonin or short daylength administration since, after a period, gonadal steroid production increases and LH declines. Alternating long days with melatonin-stimulated short days in two month cycles can induce almost constant fertility as the gonads are inactive. This obviates the need for lightproof buildings and is particularly useful to maintain functional rams for semen production for artificial insemination, or for a frequent lambing flock (Schanbacher, 1988). The administration of long days to sheep has also been shown to reduce the gestation length of sheep by about 1 day, independent of any effect on lamb birthweight.

Cattle

In cattle there are seasonality effects on reproductive activity in the female, but seasonal anoestrus does not occur. In autumn-calving cows the interval from calving to first ovulation is less than in spring-calving cows (Roche and Boland, 1980), this arising from photoperiod rather than nutritional cues (King and Macleod, 1983). However, the delayed period to first ovulation only occurs for early spring calvers, who traditionally would have been producing their calves during the most severe feed shortage in midwinter (King and Macleod, 1983). There is also evidence that the reproductive performance of dairy and beef autumn calving cows can be improved by extending the photoperiod during the winter breeding season to 16-18L (Sweetnam 1950). This is probably a combination of several factors, none of which has been extensively researched. The interval from calving to first ovarian activity is probably reduced under long daylength (Hansen and Hauser, 1984; Garel et al., 1987), oestrous exhibition may be reduced (Phillips and Schofield, 1989) but the herdsman can see cows displaying oestrus better in an extended lighting pattern.

Pigs

In the wild, pig reproduction is basically biphasic, with a primary breeding season in autumn and a secondary one in spring (Claus and Weiler, 1985). These differences occur in both the boar and sow with the latter being anoestrous in summer. They are present in the

domesticated pig too, but with less pronounced variation in gonadal activity than in the wild pig.

In the boar changes in ejaculate volumes and the number of motile spermatozoa per ejaculate show a maximum in November, a decrease in February, followed by a slight increase in April/May, and a nadir in June. In the sow, weaning to oestrus interval is longest in the summer and the oestrus is prolonged, making it difficult to time accurately mating or AI. Ovulation and conception rates are reduced, and the proportion of the litter lost either as embryos or aborted fetuses is greatest for sows mated in June to September. Artificially advancing the declining autumnal daylength to the summer has been effective in increasing boars' libido and spermatazoa production and reducing the sows' weaning to oestrus interval from 24 to 6 days (Claus and Weiler, 1985).

Behavior

Many of the effects on production and reproduction previously described are often assumed to arise from changes in the animals' physiology, stimulated by photoreception. However, particularly in the case of effects on production, the photic stimuli change the animals' environmental perception so dramatically that there are marked effects on behaviour, which could be partially responsible for observed effects. In dairy cattle a small increase in lying and a large reduction in walking has been recorded in 18L compared with natural (10L) daylength (Phillips and Schofield, 1989). The change in locomotion may be due to the ability of subordinate cattle to see dominant cattle for most of the day and avoid unexpected confrontation. Normally subordinate cattle have to move about frequently to avoid confrontation with dominant cattle. Similar, though less pronounced effects have also been observed with group-housed calves (Weiguo and Phillips, 1991) but no effect of photoperiod on daily lying time has been observed in bulls (Dechamps et al., 1989) or grazing cows (Phillips and Hecheimi, 1989). The reduction in activity observed for loose housed dairy cows, and hence their maintenance requirements, could account for at least one-half of the increased milk production observed under long daylength.

Additional benefit to production or welfare might accrue from a reduction in stress or fear in light supplemented, group housed animals. Reduced concentrations of cortisol in bulls (Leining et al., 1980) and β -endorphins in sheep (Ebling and Lincoln, 1987) suggest that

stress is reduced under long days. Some of the reduced stress could be a conditioned reflex as these animals are normally kept in a more benign environment (nutrition, space, etc.) in the long days of summer than the short days of winter. There is ample evidence from photoperiodic manipulation that animals develop a photoperiod memory, which can take up to two years to eradicate by photoperiodic manipulation, and the ability of a remembered visual stimulus to alleviate stress by conditioned response has been demonstrated by Willis and Mein (1983)

Within the changes in daily behaviour patterns supplementary light evokes specific responses during the period of supplementation. As farm animals are by choice diurnal, any increase in photoperiod extends the period of activity and lengthens the rests in between activity bouts. Housed dairy cattle under 18L have five meals a day compared to four in 10L (Phillips and Schofield, 1989), and in grazing cattle the number of grazing bouts is directly related, and the length of the grazing bouts inversely related, to photoperiod (Phillips and Hecheimi, 1989). Total daily feeding time is not significantly affected by photoperiod in housed or grazing cattle, at least in the short term. However, if production is increased under extended photoperiod it would be expected that feed intake might ultimately increase unless the maintenance requirement is reduced (by reduced activity) or the efficiency of digestion is increased. The latter has been observed in sheep (Forbes et al., 1979, 1981). An increase in digestive efficiency could arise from a more even flow of feed to the rumen. Normally cattle spread out their feeding bouts to attempt to cover the photophase and the most intensive feeding periods are seen at dawn and dusk. The reason for this is that on the one hand an even supply of feed to the rumen will allow more efficient fermentation, as the micro-organisms will have a more constant supply of substrates (particularly the rapidly soluble cell solutes), and on the other hand they prefer not to feed in the dark, probably because of a strong vestigial anti-predator instinct.

Light intensity also affects behaviour, with high intensities stimulating activity, especially social interactions, in calves (Dannenmann et al., 1984/5). The optimum light supplementation to stimulate production and reduce activity would therefore appear to be a long daylength (c. 16-18L) of low intensity, which is the pattern adopted in most commercial controlled environments for pigs and poultry.

PRINCIPLES OF TEMPERATURE REGULATION

In the preparation for considering mammalian responses to extreme heat and cold, we must first review the principles of temperature regulation as they apply to moderate corrective changes in body temperature of the animal.

Essentially the small corrective-events which keep the constant temperature of the animal are the responsibility of the hypothalamus which serves as the control tower of the negative feedback system.

The anterior and the posterior hypothalamus are the control centers. The anterior hypothalamus is responsible for heat dissipating events and the posterior hypothalamus responsible for heat conservation.

Principles: Constancy of Body Temperature

Most mammals are homeothermic which means that they can maintain a relatively constant body temperature which is independent of the environmental temperature. Another convenient term to apply to mammals and birds is "endothermic" meaning that they produce and control their own sources of heat. The remaining vertebrates (fish, frogs, reptiles) have body temperatures which fluctuate with changes of the external environment. Such vertebrates are called cold-blooded or ectotherms (external sources of body heat). There are exceptions among the mammals to the rule of maintaining a constant body temperature. The camel and the marsupials are considered to be thermally unstable. Some mammals become dormant at certain times. Animal also has a large multitude 24-hr body temperature variation.

A reversal of day and night by artificial means lead to the adjustment of body temperature. The variation of body temperature can also be modified by various routine factors of management.

Daily Fluctuations

The body temperature of homeotherms does not stay strictly constant. Even under normal conditions, it changes. Normally it is low in the morning and high in the evening. It has been suggested that the two types of human beings may be distinguished by the pattern of their temperature fluctuations during a day. The larger group are those who have difficulty in getting up in the morning and have unfriendly dispositions at least until after the first cup of coffee. Their body temperature is low in the morning but high at night. The early risers have a relatively high temperature in the morning and are cheerful before breakfast.

Seasonal Fluctuations

Body temperature changes as a function of the environmental temperature at different seasons of the year. Animals increase their body temperature at high environmental temperature but regulate it at higher level.

Topographical Variations

Complete uniformity of temperature of a body is only possible if no heat exchange occurs between the body and its environment. However, homeotherms constantly produce heat and lose it to the environment. Therefore, there is a thermal gradient from the warm interior (core) to less warm. The factors which determine the temperature of an organ or a tissue. Heat production, heat gain and heat loss vary from one location to another. The temperature therefore varies. Rectal temperature is also but a local temperature. The temperature of the brain, liver, heart and other active organs may be 1 to 2°C higher. Rumen temperature can exceed rectal temperature by as much as 2°C.

Normal Body Temperature

Normal body temperature of mammals ranges from about 36.2°C (96°F) to about 40°C (104°F), birds is about 41°C. There is no correlation between normal body temperature and body size. Normal body temperature is however affected by age. Body temperature declines with advancing age. Eventually attaining the level characteristic of the adult of the species. The approximate figure of this fall : pig 40.0 to 39°C; sheep 39.9 to 39.1°C; cattle 39.1 to 38.3°C; and horse 38.7 to 37.8 °C.

Body temperature is also affected by change in the reproductive stage. In cows, body temperature is lowest just before estrus, high on the day of heat and low again at the time of ovulation.

The Regulator of Body Temperature

The temperature regulating system consists of three basic components: sensors, a thermostatic control unit, and thermoregulatory effectors (heat producing and heat loss processes). The control of these thermoregulatory effectors is based upon the difference between the actual core temperature and the desired (set point) core temperature. Thus the system functions essentially as a thermostat with a "Set point".

Sensors

Information on body temperature is sensed by temperature-sensitive neurons-thermoreceptors are located throughout the body. Some are sensitive to increasing temperature, others to decreasing temperature. Change in temperature increase the frequency of impulses to the brain.

Thermoreceptors are located in the brain, spinal cord, the internal organs (intestine) and in the skin Information from all these sites is channeled via afferent nerve to the thermostatic control unit.

The Thermostatic Control Unit

The hypothalamus contains the animal's thermoregulatory center. The anterior hypothalamus is responsible for heat dissipating events and the posterior hypothalamus responsible for heat conservation.

How does the hypothalamic thermoregulatory go about integrating this information as it decides what thermoregulatory response is needed?

“Set-Point” Theory

Hypothalamic temperature is the controlled body temperature and hypothalamic responses are proportional to the difference between actual hypothalamic temperature and a certain hypothalamic “set-point” temperature.

The thermoregulatory center is similar to room thermostat which has a set-point and a temperature sensor, and compares these two temperature; ex., if actual hypothalamic temperature is lower than the set-point temperature, the hypothalamus might respond by calling for a decrease in heat loss or an increase in heat production. The magnitude of the response is proportional to the difference between actual and set-point temperature thus central nervous receptors are very important in temperature regulation.

The hypothalamic “set-point” is adjustable. The adjustments is made by information carried to the center from receptors in other parts of the body. If inputs from skin receptors report an increase in skin temperature, hypothalamic set-point would decrease, consequently actual hypothalamic temperature would not need to change. The thermoregulatory center would respond by calling for increased heat loss or decrease heat production.

Thermoregulatory Effectors

Signals from the hypothalamic thermoregulatory center travel to the thermoregulatory effector directly by a nervous link, and/or travel to another part of the CNS where they synapse to with efferent nerves which in turn carries the signals to the effector or cause the release of releasing factors and the release of hormones.

Tissue insulation: Some thermoregulatory center output affects the vasomotor center in the medulla oblongata. Increased impulse frequency cause vasoconstriction decrease frequency cause vasodilation.

Panting: The output of the thermoregulatory center also affects the function of respiratory centers in the medulla oblongata which control breathing. By this mechanism, panting and consequent heat loss are evoked in response to heat stress.

Sweating: Sympathetic nervous system.

Skeletal-muscle response: Some of the thermoregulatory center synapse with nerves in the primary motor center which control muscle contraction. Efferent travel to the skeletal muscle.

Hormonal response: It appears that some of the thermoregulatory center’s output changes the hypothalamus’ secretion of releasing factors which in turn act on the pituitary and change the release of tropic hormones which result in a change in thyroid hormone, growth hormone and glucocorticoid by the adrenals.

Sympathoadrenal Function: Nerve fibers arising in the hypothalamic thermoregulatory center synapse with sympathetic efferent which innervate the adrenal medulla—in cold this leads to increased norepinephrine and epinephrine.

Thermal Zones

Evaluation of the relationship between animals and their thermal environment begins with the thermoneutral zone (TNZ). The concept of thermoneutrality may have varied meanings depending on the view point of the describer.

There are several definitions:

1. The range of EAT over which metabolic heat production remains basal.

2. The range of EAT over which the body temperature remains normal, sweating and panting do not occur and heat production remains at a minimum level (this is referred to as the zone of minimum thermal regulation).

3. The range that provides a sensation of maximum comfort (this is also defined as the *thermal comfort zone*).

4. The EAT selected by an animal offered an unrestricted range is environment (this is called the preferred thermal environment).

5. The environment that promotes maximum performance and least stress for the animal.

The preferred definition is based upon one's interest or reason for describing the TNZ.

Subcommittee on Environmental Stress

In this report, TNZ is defined as the range of effective ambient temperature (EAT) within which the heat from normal maintenance and productive functions of the animal in nonstressful situations offsets the heat loss to the environment without requiring an increase in rate in metabolic heat production.

The effectiveness of various insulative and behavioral responses to cold stress are maximal at the lower boundary of the TNZ, a point called the lower critical temperature. Below this point in the cold zone where the animal must increase its rate of metabolic heat production to maintain homeothermy.

LCT = used to predict animal sustainability to cold

Measuring of LCT have proven to be quite useful in determining nutrient requirements in establishing design criteria for housing, and in guiding practical husbandry decisions, *particularly for cold-susceptible animals such as swine, sheep and calves.*

Critical Environmental Temperatures

The figure gives a simplified schematic representation of critical environmental temperatures and the zones embraced by them. Comfort zone is a range of environmental temperature within which body temperature is maintained constant with a minimal effort from thermoregulatory mechanisms, and within which the sensation of cold or heat is absent. This range is usually designated as comfort zone (A-A). This zone can be approximated by the following criteria: blood vessels of the skin over the whole body are neither all vasodilated nor all vasoconstricted, evaporation of moisture is minimal, *piloerection and behavioral responses to cold or heat are absent.* When moving outside the zone of thermal comfort towards cold or heat, the animal activates its defense mechanisms in a sequential manner. When environmental temperature falls below thermal comfort (A), general vasoconstriction and piloerection takes place which bring about some increase in heat conservation. With temperature falling further, beginning at point B (the lower critical temperature), the rate of heat production rises. At a certain, still lower, temperature (C) the extra heat produced is insufficient to balance the heat lost from the animal and body temperature begins to fall. Heat production, after having reached a peak, declines sharply, thereby accelerating the cooling process. Eventually, at the lethal level of temperature, the animal dies from cold (D). In all these events, time, *not considered in this simplified representation plays an important role.*

When environmental temperature rises above thermal comfort (A1), physical defense mechanisms against overheating come into operation: general vasodilation, sweating,

panting or both. With temperature rising further (B1) , sweating and panting are intensified, and may. Be a compensatory decrease in heat production. In response to "further rise" in heat stress (C1) sweating or panting or both are further increased, but cooling so derived is insufficient to maintain homeothermy so that body temperature begins to rise. This, in turn, brings about an increase in metabolic rate due to the Van't Hoff effect, thus setting up a vicious circle which eventually leads to death from heat (D1)

The Environment of Heat

Eatable soup	152°F
Potable coffee without cream	140°F
A very warm bath	113°F
A cool bath	99°F
Tolerated by humans	
for up to 25 min	240°F
Not tolerated by cattle	105°F
Upper limit for comfort zone for cattle	60°F

Responses to the Hot Environment

More mammals suffer from heat than from cold, partly because there are more physiological mechanisms for combatting cold than for combating heat. Furthermore, some simpler non-physiological mechanisms for warming up are available to all mammals ; these include huddling together. Escape from heat is not so easy. Essentially the physiological devices available for cooling the body are sweating , panting , and vasodilation.

Classification of Hot Climate

Hot climates can conveniently be referred to as hot-dry or warm-humid. The hot-dry climates are usually desert regions which are widespread over the globe and exist over large areas in southwestern United States. The warm-humid climates are typically represented by the tropical rain forest areas.

The characteristics of the hot-dry climate are :

1. high air temperature during the day
2. low humidity
3. increased solar radiation
4. wide day-night variation in temperature
5. scanty precipitation
6. vegetation scruffy or non-existent
7. the ground absorbs solar energy and heat to temperatures as high as 190°F
8. the ground radiates long-wave heat to cooler bodies in the environment such as animals
9. ambient air is at a temperature higher than the skin

10. the hot ambient air heats the body by convection instead of cooling it

The characteristics of the warm-humid climate air:

1. air temperature not excessive with an upper limit of 90-95°F
2. the average relative humidity is 75% or higher
3. high moisture content of atmosphere reduces its solar heat load on animals, direct solar heat is less a problem than in desert
4. there is little day-night or seasonal variation in temperature and dew point
5. precipitation is high, usually varying with season; vegetation is abundant, providing ample shade and a favorable radiation environment.

Now comparing the two areas in more detail we find that the input of solar energy is high in both areas but in tropical regions, solar energy is converted in water vapor and thus exists in the atmosphere as insensible heat. In the desert, where moisture is lacking, the solar energy directly or indirectly heats surfaces as well as ambient air and thus exists as sensible heat. Physiologically speaking in both areas, mammals experience heat stress: on being exposed to insensible heat of the tropics, his problem is how to promote more efficient evaporation of sweat, whereas, one being exposed to the sensible heat of the desert, his sweat evaporation is no problem. Its difficulty there is to maintain sweat production at a sufficient high rate to meet the requirement of body cooling.

Animal Physiology in the Heat

The mechanisms concerned with heat loss in animals are related to its ability to vasodilate the vessels in the skin, to store heat in the body, to take advantage of size, and to sweat. The latter is more important and complicated physiological mechanism. The mechanism of vasodilation is not considered an important factor in heat dissipation since it probably becomes maximum at an early stage in heat exposure. At an ambient temperature, lower than that cause sweating, the skin will be vasodilated and heat brought to the skin from the core will be lost, through radiation to cooler surfaces in the surrounding. When blood flow of the skin increases due to dilating of cutaneous vessels, the thermal conductance of the peripheral tissues may increase 5- to 6-fold. This increases the heat loss.

Mechanisms of Heat Loss

Heat Storage: The mechanism of storing body heat is illustrated in the extreme circumstances of animals being exposed to heat and dehydration at the same time; their body temperature begins to rise. Although some investigators consider this increase in body temperature is a failure in heat dissipation, others suggest that the rise in body temperature reduces the heat load in a hot environment because the difference in temperature between the environment and the cooler body is diminished. The heat flow from the environment is roughly proportional to the temperature difference and goes down as the difference gets smaller. They point out that this rise in body temperature has both advantages and disadvantages but it is better to avoid classifying it as failure of heat regulation.

Body Size: We must now consider the advantage of large body size under very hot conditions. If a small object and a large object made of the same material are exposed to the sun, after a time the small object will be burning hot while the larger object will still be partially cool. We say that the larger object has a greater "thermal inertia". This advantage which any large animal has over a small animal in the heat is expressed in the rule that any object has a surface area which, relative to its weight, increases if its linear dimension decreases. An illustration of the surface area relationship is as follows: inanimate objects gain heat from the environment in proportion to their surface, but the heat load on an animal in hot environment has two components; heat gain from the environment plus metabolic heat. The first component includes conduction from the over-warmed air as well as radiation from the sun and the substratum; since both types of heat exchange are surface processes, the environmental heat load will be directly proportional to the surface. It also happens that the second component, the metabolic heat production in mammals, is also nearly proportional to the surface. Therefore, the total heat load on the animal, metabolic and environmental, will also be approximately proportional to the surface. A small mammal with their larger relative surface are in much less favorable position for maintaining a tolerable low body temperature.

Reflectance: It is now necessary to consider the effect of animal coat color as a mechanism of heat gain or loss. The absorption and reflectance of solar radiation depend upon the color of the hair, the color of the skin and the type of radiation. Part of the radiation impinging on the integument is neutralized by being reflected from the animal's surface. The remaining part is absorbed; the depth to which absorption occurs increases with increasing wavelength. Ultraviolet penetrates only a little beyond the epidermis, visible radiation well into the dermis, and infrared radiation beyond the dermis. Reflection of visible radiation from the animal's surface varies with the color of their hair coat. Examining the infrared range from 900 to 1200 mn one notes that about 15% of the radiation is absorbed by the white rat but approximately 90% of the radiation by the black hair Holstein cattle.

Heat Balance: The overall heat balance under conditions of excessive dry-heat. In temperate climates about 50% of heat produced by the body is lost through radiation to cooler surfaces, about 25% is lost by convection to the cool air, and 25% by evaporation from the skin by insensible perspiration. The heat loss by radiation and convection becomes progressively less as ambient temperatures rise, it reaches zero at 95°F when air, water and skin are at the same temperature. Under these conditions, all heat produced in the body is lost by evaporation. At still higher temperatures, the body gains heat by radiation and convection. The environmental component is thus added to the metabolic component to give the total heat load. Evaporation is the only channel remaining for heat dissipation.

Thus far, we have considered only the circumstances of dry-heat. If we introduce high humidity into the challenge of the environment, an increase in humidity will result in a greater extent of sweating over the body surface to provide enough evaporation to maintain heat balance. In other words, to maintain the same rate of evaporation in tropical heat, it is necessary that a greater proportion of the body surface be covered with sweat than it is in drier climates.

Evaporation for the Skin: By the time heat stress becomes so severe that the animal needs to increase evaporative heat flux to achieve homeothermy, the rate of blood flow from the core to skin is relatively high. Heat used to evaporate water from the skin is replaced almost immediately by heat carried from the core by the blood. Thus, venous blood draining the tissues underlying evaporative surfaces is cooler than the arterial blood that supplies them. Water arrives at an evaporative site on the skin in 3 ways: (1) passive diffusion through the skin; (2) active sweating onto the skin surface, or (3) external application by wallowing behavior or sprinkling.

Passive diffusion: Water passively diffuses through the skin at all times in all species. It is in the vapor state as it passes through the epidermis. The animal has no control over such transcutaneous diffusion; it is a physical process. The direction of transcutaneous diffusion depends upon that of the vapor-pressure gradient. In the pig, for example, water vapor moves toward the environment when environmental vapor pressure is less than 25 millibars, but into the pig at environmental vapor pressures greater than 27 millibars.

The rate at which diffusion occurs is related inversely to environmental vapor pressure, but directly to skin temperature and to the rate of air flow over the skin. Water diffuses passively through the skin at a rate of around 10 gm/hr/m² in a thermoneutral environment and increases to a maximum of around 30 gm/hr/m² in a 40°C environment in mammals and birds.

Thermal Sweating: Cattle and sheep, respond to heat stress by actively secreting sweat onto the skin surface. Pigs' sweat glands do not respond to heat stress. There are no sweat glands in the skin of birds. In cattle and sheep sweat glands are part of hair-follicle units. Therefore, an animal's sweat gland population density is essentially the same as its hair population density. Further, just as hair-follicle population density declines as the animal grows, so does sweat-gland population density.

Sweat gland population density is also influenced by species and breed. It averages 250/cm² in the skin of adult sheep and around 25/cm² in adult swine. It is much higher in cattle. In zebu, sweat gland population density is around 1,600/cm² and in European cattle it is around 800/cm². Total follicle number in cattle is genetically determined.

Physiological heat tolerance is lowly directly related with sweat gland population density and sweating rate in cattle. Indeed, although zebu cattle have larger and more sweat glands, they have only slightly higher sweating rates than European-type cattle under comparable conditions of heat stress.

Maximal sweating rate is much greater in cattle than in sheep: 200 gm/hr/m² versus 30 gm/hr/m². This means passive diffusion of water across the skin (maximally 30 gm/hr/m²) is a small part of total skin evaporative flux in cattle, but about 1/2 in sheep.

In cattle, sweat is evaporated from the skin, per se. This is fortunate because in this way the haircoat may remain warmer and thus maintain various temperature gradients with the environment. In sheep, water vapor formed at the skin passes through the fleece along a vapor pressure gradient, but some may be taken up by the wool which is hygroscopic. Heat is given off as the wool absorbs moisture, and as a result, skin temperature sometimes actually rises. The fleece hinders the sheep in losing heat, especially during hot, rainy weather.

Wallowing Behavior: The difficulty faced by the pig in a hot environment is greater than that confronting other animals, since in addition to its inability to thermoregulate effectively by sweating, the pig has a higher thermal insulation and lower critical temperature.

Pigs wallow to apply moisture in the form of mud onto their body surfaces. Mud is a very efficient medium for evaporative thermolysis. Heat loss from an area smeared with mud is greater and more sustained than that from a comparable area thoroughly wetted with water alone. Evaporative flux from a pig's muddied side reaches 800 gm/hr/m². In fact, evaporative heat flux from the side of a pig that has wallowed in mud is greater than that from the side of a cow that is sweating maximally.

As pointed out by Lyman (Amer. Scientist 51: 127), if a mammal's body temperature were set at 85°F, it would be physically impossible for it to produce enough water to cool itself by evaporative water loss at an air temperature of 100°F. We must consider what evaporative cooling can be accomplished by animal, assisted by its high body temperature.

Sweating: The subject of perspiration was introduced earlier with a description of insensible water-loss, non-thermal sweat, and thermal sweat. The contribution of the first two types are rather subtle when extreme heat is concerned; no attention will be given to them here. The production of thermal sweat, however is a costly physiological event which might be predicted to be a factor to upset homeostasis completely. Consider for moment the quantities of water concerned on a hot day in the desert. Most men can produce 12 liters of sweat at a rate of 1 liter per hour. It is time that some could produce 0.5 liter/hr, while maximum capacities are given by several authors as 2.6 liters/hr and 4.2 liters/hr. These rates were not sustained of course. This mechanism is obviously a different type of process than those which are involved with warming the mammalian body in the cold. Shivering is primarily a muscular process not too much different from waving the arms or legs, or running slowly in place. The effect on homeothermic mechanisms will be those involved with exercise. On the other hand, maximum sweating removes from the body a high percent of body water. Although this water is taken from the blood as it passes through the capillaries of the sweat gland, indirectly the loss is replaced from other body compartments. Such a high loss of water cannot be sustained without replacement in the form of drinking water. Nevertheless, the rate of sweating is not altered by moderate dehydration. The rate is still adjusted according to the need for heat dissipation. Furthermore, drinking in excess does not increase the rate of sweating.

What environmental stresses cause the sweat glands to be activated? In a comfortable climate an animal loses metabolic heat partly by evaporation and partially by convection and radiation from the skin. In air temperature from 82-86°F (28-30°C) , temperature regulation results from changes in the amount of heat lost by convection and radiation from the skin controlled by changes in the vascularity of the skin. As the ambient temperature gets hotter, sweating is evoked in quantities nicely adjusted to the requirements of thermoregulation. The output of sweat increases 20 grams/hr for each 1 °C rise in air temperature. Once sweating begins, the skin blood flow must continue to increase as the heat load rises, to transfer more heat from the core to the periphery; here

it is dissipated to the environment by the evaporation of sweat. Undoubtedly, the skin blood flow becomes maximal soon after it begins to increase.

Sweat Glands: These remarkable glands, that can accumulate a copious quantity of body water in human subjects, are called eccrine glands. They lie deep in the skin and are open to the surface through twisted secretory coils. It is supposed that during secretion, cells in the wall of the glands lose glycogen, alter in content, and decrease in size. The precise route for the transfer of water and other solutes through the walls of the glands is unknown.

There are two forms of sweat glands among the mammals; almost all sweat glands in man are of the eccrine type, although he has a few glands of the apocrine type in specific location. Although it is an over-simplification, we may say that eccrine glands secrete copiously onto the furless skin, while the apocrine glands are associated with hair follicles and produce an oily skin (picture, Folk page 233). Some other mammals have no eccrine glands and are served entirely with apocrine glands; the horse is an example. Apocrine sweat is odorless but it contains sebum which is quickly attacked by bacterial action. Apocrine sweat droplets dry to form a glistening glue-like mass. This material is evoked in man from his few apocrine glands by pain or fear; these stimuli also produce some eccrine emotional sweating. Apocrine sweat is not evoked by heat. Apocrine material is milky. There is fat included that is represented by fatty acids, baldrin, capric and caprylic acids. There is doubt for the presence of fat in eccrine sweat.

The nerve supply to the sweat glands is sympathetic, but it is believed that there is no adrenergic component when sweating is induced naturally by heat. The reflex control of sweating seems to be partly related to the stimulation of peripheral receptors and partly to the temperature of the hypothalamus. One accepted theory is that the reflex act of sweating is initiated by the thermal receptors in the skin, while the degree of activity so induced may be potentiated by a rise in hypothalamic temperature. Another hypothesis is that sweat is solely affected by receptors lying deep in the skin, but the rate of sweating is determined by deviation from a set-point in hypothalamic temperature. Another theory is that temperature regulation is mediated through the release of E, NE and 5-HT in the hypothalamus. The core temperature may be the outcome of the balance between the release of the three amines.

Sweat Composition: The salt concentration in sweat is of considerable importance when exposure to extreme heat is concerned. Large quantities of salt are lost to the skin during the sweating process. The urinary output of salt may go down virtually to zero. Thus the salt output must be replaced in the diet. This means that water alone is not sufficient to make a successful desert dweller out of man; the price of salt is high in hot countries. "Salt is a main article of trade and taxation, it has caused wars and at times it has been weighed against gold". It has caused wars and at times it has been weighed against gold"

Sodium and chloride always seem to be present in lower concentrations in sweat than in the blood plasma. Most subjects have a chloride content between 0.2-0.3% , even a few at 0.1 or 0.6%. In another term, NaCl range from 5-100 mEq/L. There is a tendency for the salt concentration in sweat to decrease with acclimatization to heat and to increase with increasing sweat rate. Others believe that salt concentration increases with increased temperature of the skin.

Also, it was found that salt concentration in sweat depends on dietary salt intake. In absolute figures, we find that at high sweat rates the total loss of NaCl may be as excessive as 10-30 gm of salt per day. A person can lose about 25 gm in 2.5 hr. This high % of the estimated total salt in the body; 165 gm.

During sweating, the effects of salt loss are not apparent, but when water is consumed the body fluid becomes diluted and this may lead to heat cramps. Until 1929, it was assumed that it may be due to heating.

Increase in Evaporation From the Respiratory Passages: In defense against heat, an increase in ventilation is effected by an increase in frequency accompanied by a decrease in depth, the rate of this fast, shallow breathing (panting) is used as an indication of respiratory evaporation. Up to 15°C respiratory rate of cattle remains fairly stable at a level of 20 respirations/min. There is a general tendency for maximal respiration rate in panting animals to be inversely related to body size. It is about 200 in cows, 250 in calves, 350 in sheep and 440 in lambs. Under severe heat stress, in many species a change occurs in the type of breathing. The fast shallow breathing goes over in a slower deeper breathing, leading to a further increase in ventilation. High ventilation rates achieved in this way may have adverse secondary effects. Elimination from the lungs of an excess amount of CO₂ lead to respiratory alkalosis shown in cattle. Blood pH increases to 7.8.

Relation Between Cutaneous and Respiratory Evaporation: The sweating animals control the amount of H₂O, the panting animal the amount of air movement. The relative contribution made to total evaporation by cutaneous and by respiratory evaporation varies with the species. Sweating and panting are complementary in a sense that animals with a low capacity for sweating normally have a high capacity for panting. Birds, the dog, cat and the pig are non-sweating species. Sheep and goats can discharge small amount of sweat, cattle much larger ones. The horse, camel and in particular, man are truly sweating species. Heat loss through evaporation is most effective if environmental temperature is below the body temperature.

The importance of water evaporation in heat loss as the environmental temperature rises. This is true only when the effective environmental temperature (air temperature for convection and temperature of the walls and/or sky for radiation) is actually below the temperature of the body, because evaporation of water at the surface leads to a decrease in the surface temperature. If the surrounding temperature is the same as the body temperature, then this allows heat flow, not only from the inside of the body to the surface, but also a flow of heat from the environment (air and radiating surfaces) to the body surface. Therefore, in an environment with an effective temperature equal to the body temperature, the animal has to evaporate even more H₂O per day to take care of influx of heat from the environment to his cooled surface.

Unlike animals that sweat, dogs, chickens increase evaporation in the respiratory tract rather than at the body surface. This gives the dog, chicken a certain advantage because its surface temperature do not decrease as it does in sweating species. A dog chicken in hot environment with his high surface temperature, may still lose heat through by convection, whereas under the same circumstances man, with his cooled surface gains heat by convection and has to make up for this by additional evaporation.

Response to the Cold Environment

In this day of °F heated cars and American houses maintained at 75°F, the average American is not aware that his total physiological reserves for combatting cold may suddenly be drawn upon. In spite of the comfort and convenience-engineering of this age, some individuals die of cold exposure.

Wind Chill Chart

Equivalent Temperatures in Terms of 0 mph (in °F)

Actual Temperature	Wind Velocity				
	5 mph	15 mph	25 mph	35 mph	45 mph
32°F	29°F	13°F	3°F	-1°F	-3°F
23°F	20°F	-1°F	-10°F	-15°F	-18°F
14°F	10°F	-13°F	-24°F	-29°F	-32°F
5°F	1°F	-25°F	-38°F	-43°F	-46°F
-4°F	-9°F	-37°F	-50°F	-52°F	-60°F

Considering lower mammals, the tolerance to prolonged extreme cold presents more of a physiological challenge to a few animals than most. Many mammals can seek protection under the snow or in dens. This does not apply to some winter residence such as moose, caribou, Canada Jays and Chickadees which have not been known to seek enclosed shelter. The temperature regulation such animals as Caribou standing in deep snow at -60°F requires unusual adaptation, with a core temperature fixed at 100°F, these animals must find enough food to hold this temperature when the environment temperature is as much as 150°F lower. Yet these animals are abundant: In the Fairbanks area (record low at Tanana -76°F), there are 130,000 caribou and many moose. Both birds and mammals have a short day light period of feeding during the cold season (3 h 40 min) of sun light in Fairbanks, Alaska. Observation of chickadees at -50°F. There may be animals living in even more extreme cold in Siberia where temperatures range as low as -90 or 108°F

Types of Cold Exposure

You often hear a physiologist say that his animals have been "exposed to cold" This expression is inadequate for two reasons; first, there are several types of "cold air", and second, the cold-exposed animal does not necessarily experience a low temperature. The secondary factors which must be considered are the amount of moisture in the air, the amount of air movement, and the duration of the exposure to cold. It has been pointed out that wet cold has more meaning near 0°C than at a much cooler temperature.

Describing conduction of heat in different wind velocity is more straight forward than explaining wet-cold. By means of physical models it has been possible to show different amounts of heat transfer with different wind velocities.

Responses to Acute Cold Exposure

It will be convenient to consider the situation of an underclothed man or sheared sheep exposed in a cold room to -20°F and a wind velocity of 5 mph. Within a very few moments the following events will take place:

1. There will be a cutaneous vasoconstriction. This will permit the temperature of the skin and deeper layers under the skin to cool and the surface-to-environment heat loss will be lowered; in a sense this means the effective thickness of the body shell is increased and this decreases conductivity from the exterior. Essentially, this is accomplished by a shift of blood from the shell area to the core area. This means there must be an increase of blood in the viscera.

2. There is a paradoxical increase in heart rate, which is very evident. This response is paradoxical because of the massive vasoconstriction.

3. There will be an acceleration of respiration.

4. Pilo-erection in the skin will show itself as so-called goose pimples in the skin of man and be erection of hair in the skin of other mammals, a factor that tends to increase insulation.

5. This vasoconstriction may reduce heat loss 1/6.

Shivering: Shivering is involuntary muscle contraction that does not cause body movement and therefore does not disrupt the animal's boundary layer. By this means the temperature of muscles is raised to approach that of the core. Because the work function of this muscle contraction is zero, shivering is a very economical thermogenerator.

Man can raise his heat production 3- to 4-fold by shivering and raise core temperature over 0.5°C . This shivering may be prolonged over considerable time and during sleep.

Metabolic Rate: Thermogenic muscle tonus gradually give way to increased metabolic rate throughout the body, which is called nonshivering thermogenesis.

Hormonal Effect: Cold exposure will stimulate the sympathetic nervous system which will cause the adrenal medulla to release epinephrine and NE. Other hormonal pathways are activated during exposure to cold are the pituitary-thyroid system and the adrenal cortex and hypertrophy of the adrenals and thyroid as a result there is an increase in metabolic rate.

When the exposure is prolonged, the initial changes will normalize, while more stable and specific response will appear. After several days or weeks in the cold, nonshivering thermogenesis is markedly increased, where shivering is reduced. If the cold exposure is further prolonged for several months, the hypertrophy of the endocrine glands can decrease in spite of the continuous cold stressor.

The nonshivering thermogenesis is more specific and economical than shivering, as the former avoids heat loss caused by shivering and does not disturb voluntary movement.

Nonshivering thermogenesis is elicited by norepinephrine and epinephrine. This can elicit nonshivering thermogenesis by injection of epinephrine and epinephrine.

The locus of the highest percent of nonshivering thermogenesis originate from brown fat as a result of hibernation of norepinephrine. It is important that nonshivering thermogenesis is of minor importance in farm animals. The color of brown fat results from the many mitochondria present in the fat cells, which reflects the high metabolic capabilities of this tissue as compared to white adipose cells and with numerous blood vessels. Activation of brown fat by sympathetic inputs elicits heat production through pathways that allow the process of oxidative metabolism to be largely uncoupled from phosphorylation. The results is that stored lipids are catabolized, but very little useful work (ATP) is performed. The sole purpose of these cells is to rapidly generate heat.

Response to Chronic Cold Exposure

Non-shivering Thermogenesis: It has been shown that the liver and abdominal viscera contribute heat to the cold-exposed animal. It is this mechanism that becomes more efficient in the rat exposed continuously to cold at 5°C for 2 to 3 weeks. At the end of this period, shivering disappears so that it cannot be detected by electromyography. However total metabolism remains elevated by about 80% and body temperature is held near normal. If the animals are removed to a warm environment (30°C) the metabolism of the rats remains for some time 15-20% higher than the warm-acclimated rats. The locus of the highest percent of the non-shivering thermogenesis originates from the brown fat as a result of liberation of basal metabolic rate at 30°C for cold-acclimated rat is higher.

The maximum liver metabolism cannot be maintained at -40°C this has also been shown in birds.

The first factor of cold acclimation is the non-shivering thermogenesis. This is followed by a rise in total daily food consumption. Initially there is a transient decrease in body weight followed in the young adult by resumption in growth within a week. There is a hypertrophy of the thyroid and adrenal glands as heart, kidney, liver. These increases occur at the expense of skeletal muscle growth which become reduced relative to control.

Time Course of Acclimation

It can be generalized that the expression of cold acclimation are completed in 7-10 days, but some endocrine parameters may take as long as 4 weeks. As earlier expression that cold acclimation requires as long as 2 months does not seem justified.

Therefore the timing depends upon the measurement of oxygen consumption has leveled off in 2 weeks, but liver metabolism 4 weeks. When hematological and body fluid adjustment in rats were studied. On the whole there were large changes in 7 days, but very little change after that. Another measure of acclimation is heat production by direct calorimetry, this technique revealed that rats at 5°C showed the major part of acclimation by 10 days within minor changes occurring up to 20 days.

The deer mouse has shown a maximum response to cold in 8 days in the parameters of increased basal metabolic rate, total body water, and weight of the liver and in 3 weeks in case of nonshivering thermogenesis, food consumption. Other animal (mice) exposed

to -3°C showing first a marked drop in mean food eaten and then a steep rise, leveling off at day nine. This new level of feed does not bring the body weight back at first.

Change in Critical Temperature

It would be reasonable to postulate that as mammals become cold acclimated and increase the thickness of their insulation, there might be a change in lower critical temperature.

The change in critical temperature with season is amplified in sheep when the fleece grows.

Fleece length	Critical Temperature
0.1 cm	$28-30^{\circ}\text{C}$
2.5 cm	13°C
4.5 cm	8°C
10.0 cm	3°C
12.0 cm	-3°C

Cold Adaptations and Cold Acclimation

We must consider the technique of survival of large arctic animals. These mammals and birds have greatly extended the thermal limits within which their survival and activity are possible. These animals may be active indefinitely at temperatures of -40°C and below. The challenge of life in a 'heat hungry' environment has been met in a variety of ways.

- The cooling of the extremities of large mammals.
- Peripheral nerve conduction at low temperatures.
- Counter-current vascular heat exchange system.

Cooling of the extremities of large mammals

Let us consider the caribou and moose which spend long hours standing in extreme winter climate frequently as cold as -60°F .

There are two possibilities for the thermal regulation of these long extremities as it stands.

The leg and feet may be warm requiring a large amount of energy and fuel on the part of the animal.

Or these extremities may remain very cold.

The rule seems to be for arctic animals to solve the problem by cooling the extremities ; ex., on the reindeer when the air temperature is -31°C , the hoof was 9°C and the skin on the leg was also 9°C ; the rectal temperature was 38°C and the forehead temperature was 36°C .

Nerve Function

The caudal nerves were excised. Nerve conduction persisted but velocity was reduced 20- to 30- fold.

The Counter-Current Vascular Heat Exchange

This was first discovered in the fin of the porpoise.

When the question was asked, 'What prevents wails in the polar seas from being chilled to death from heat loss through their large thin fins?'

They found that each major artery was located centrally within a multiple venous channel. These bundles exchange heat between the arteries and the veins. The system is referred to as arterial-venous counter-current system, serving for heat preservation. In such arrangement the warm arterial blood is cooled by the venous blood which has been chilled in the fin. The result is a steep temperature drop in the appendage. Body heat is conserved at the expense of keeping the appendage cold.

The same adaptation for rewarming cold venous blood is found in both the arm and the leg of man.

The Bare-Skinned Animals

The adaptation of maintaining cold extremities as a response to cold environment and saving of heat has a parallel in adaptation of swine.

These animals tolerate the extreme cold down to -50°C with apparent ease. In young pigs, the metabolism increase at a critical temperature of 0°C . This is a low critical temperature for a naked animal. When they are exposed to cold, their skin temperature declined steadily until it was as low as 10 or 8°C .

The evidence that the cold skin is an economic biological adaptation is, that the critical air temperature is 0°C . It was remarked that as a consequence the cost of feeding pigs is not noticeable elevated in the cold Alaskan winter.

Air temperature is the most indicator of the thermal environment and determine the magnitude of animal-environment heat exchange. But there are other factors that play a major role in determining environmental heat demand; e.g., humidity, floor-wall temperature, air movement, rain.

- e.g., (1) Chickens, ventilation
(2) Temperature, humidity
Pigs, wallowing

Management--1 pig vs 10 pigs or straw vs non-straw.

Scientists tried to put all these factors together in on equation but they were not very successful.

ANIMAL REPRODUCTION AND THERMAL ENVIRONMENT

Reproduction is fundamental to food-animal production.- Factors that reduce reproductive efficiency increase the cost of production. The effects of thermal environment on Reproduction in food animals have undergone a great deal of study.

Reproductive Seasonality

Seasonal differences in reproduction are well recognized in all species of farm animals. Reproductive seasonality is controlled to a certain extent by daylength. In this way, evolution has generally favored establishment of breeding seasons in the various species that provide for birth of the young at times favoring their survival. For instance, the seasonally polyestrous ewe and the ram tend to have a season when mating is most frequent commencing as the days become shorter in the fall. The lambs are born, after a five-month gestation, in early spring.

Seasonal Breeders

Sheep. In the Midwest, the sheep's normal breeding season runs from August to December. Lambing rate (number of lambs born per ewe lambing) peaks in mid-season matings. The percent of ewes exposed which lambled tends to be highest early in the period, so there is little difference in lambing percent (number of lambs born per ewe exposed) during the breeding season.

Continuous Breeders

Other species are called continuous breeders, although they have seasonal variation in reproductive efficiency.

Cattle. Cattle naturally tend to mate most frequently in late spring and summer. The optimum period for fertility in cattle is in spring, perhaps because increasing daylength stimulates gonadotropin secretion. In lower latitudes and warmer climates, fertility level wanes in the summer, possibly due to heat stress. In high latitudes, where there is greater daylength variation, fertility level is lower also in winter, when the days are short. Thus, effects of photoperiod and environmental temperature on reproductive function are complexly interrelated.

The detrimental effect of hot weather on cattle fertility is confirmed in Arizona cows artificially inseminated with fresh semen. Percent cows bred on first service was 48 percent from July through September, while the average for the other months was 58 percent. In hot Arizona, the cow seems to be more responsible for the summer fertility slump than the bull. When fresh semen from bulls in moderately hot weather was used, summer fertility decline was noted in Arizona cows, but not in those in less hot climates.

On the other hand, in more temperate Ohio climates, the 30- to 60 day and 150- to 80-day nonreturn-to-estrus data for month of insemination indicated no time trend in cow fertility. There was no summer fertility slump in the cows. But semen collected in August and September resulted in lower conception rate. And the decline in fertility due to semen aging was greatest in semen collected from May through October. All this suggests that in these Ohio cattle, the bull was largely responsible for seasonable variation in fertility.

Swine. In swine, matings in the wild ordinarily occur from November through January. Conception rate is lowest in the months of hot weather. Swine, like cattle, breed the year round, but there marked seasonality in their reproductive efficiency.

Chickens. At environmental temperatures between -5°C and 10°C , if photoperiod is adequate, the fertility of chicken eggs was unaffected by environmental temperature. However both fertility and hatchability of hen eggs wane during periods of hot weather.

Turkeys. Seasonal decline in turkey fertility is due more to the hen than the tom. Age is another important factor in turkey fertility, and in production age is often directly correlated with environmental temperature.

How does thermal stress affect reproductive functions in males and females of the food-animal species?

The Male

Environmental temperature influences reproductive function in the male in two main ways: by altering spermatogenesis so semen quality and male fertility drop, and by reducing libido. Reduced sex drive is rather obvious, but the defective male which mates, but cannot settle, a female may go unnoticed for a long time and thus become very costly.

Testis temperature and sperm production in mammals. Certain semen quality characteristics are generally related to a male's fertility. Mammalian testes are extremely sensitive to heat. Warming them reduces sperm concentration and proportion of sperm that are normal.

The ram. In the ram, semen damage is directly related with subcutaneous scrotal temperature, which is closely reflected by --testis temperature, but not with changes in rectal or flank temperatures. The higher the scrotal temperature, the sooner semen damage becomes evident and the longer it lasts. Heat damage first becomes obvious two to three weeks after the exposure. There is great variation among rams in scrotal temperature, and consequently in semen damage, during heat stress. Rams able to keep testes cooler presumably are affected less.

Time heat damage becomes apparent. In another study, semen from rams whose testes were warmed to 40.5°C for 2 hours was similarly low in quality two and seven weeks after heating. Further, the number of sperm per ejaculate was reduced between five and seven weeks after heating. Fecundity was low between two and five weeks after, and nil between five and seven weeks.

These data accord with the finding that in the ram heating the testes is most damaging to type-B spermatogonia and primary and pachytene spermatocytes. The spermatogenic cycle in the ram is such that one would expect a greatly reduced number of sperm ejaculated about five weeks after heating, if these stages are most sensitive to high temperature. Dividing spermatogocytes and spermatids are also affected by testicular heating.

Metabolic and ultrastructural changes in ram sperm situated in the testes per se also result from heating. Hence, there appears to be some direct effect of heat on fully formed sperm, though the effect is probably greater in earlier stages.

The rate of flow of rete testis fluid (in which sperm pass from testis to epididymis) is reduced while heat is being applied, but returns to normal immediately after heating stops. When testicular temperature is so high that spermatogenic damage occurs, then

testicular hypoxia also occurs. But neither testicular blood flow nor testicular glucose metabolism is altered by high temperature.

The boar. Spermatogonia are resistant to high temperature in boars, but primary spermatocytes and spermatids are damaged by heat.

The bull. In the bull, also type-B spermatogonia, primary spermatocytes, and spermatids to be damaged by heat. Percent live sperm dropped a third and percent normal sperm by over a third two weeks after heat treatment of the bull's scrotum in another study. These parameters of semen quality had returned to normal by six weeks after heat treatment.

Because sperm are relatively resistant to heat damage, heating the testes leads to little reduction in semen quality and fertility during the first two to three weeks after heating. Inferior semen appears only when cells damaged in the spermatid stage, for example, are ejaculated.

Cooling the Testes

The testes are much less sensitive to cooling than to warming. Fertility of male farm mammals is affected very little by cold environment, except that vasoconstriction may lead to ischemia and its metabolic sequelae, including testicular degeneration. Perhaps testicular degeneration during cold exposure is due to reduced androgen production. However, until intratesticular temperature falls to 0°C or below, little or no cold damage occurs. Bulls with scrotal frostbite develop testicular adhesions and then show seminal degeneration.

Importance of Scrotal Thermoregulation

The importance of scrotal thermoregulation to semen quality was shown by results of an experiment in which rams were held for 3 hours in a hot, dry environment (40.5°C/8.5 mm Hg vapor pressure) and 2 days later for 3 hours in hot, humid environment (40.5°C/31.5 mm Hg). Half of the rams had water at 18 °C circulated around the scrotum, while the scrota of other half were left unprotected. Rams with unprotected scrota ejaculated a high proportion of abnormal sperm beginning about two weeks after first exposure. Semen quality in these rams was very low between days 18 and 25. Semen quality was unchanged in rams whose scrota were cooled during heat exposure.

Scrotal Thermoregulatory Mechanisms

G.M.H. Waites has masterfully discussed the mechanisms by which the scrotal male regulates testicular temperature. Testicular temperature is determined by the balance of the following factors: heat gain from blood reaching the testis, metabolic heat produced by the testis, heat lost by way of blood leaving the testis, and heat lost and gained by the scrotum itself.

Testicular Blood Supply and the Vascular Heat Exchanger

The scrotum contracts the outer surface of the testis. Thus, blood flow through superficial testicular blood vessels exchanges heat with, and quickly assumes a temperature near that of, scrotal tissues. In general, scrotal temperature is lower than body temperature, so blood is ordinarily cooled as it passes through the testis.

As the relatively cool blood returns to the body by way of the spermatic vein, it passes through the spermatic cord's pampiniform plexus. This structure is an important part of a counter-current heat exchanger. Warm spermatic-arterial blood loses heat (and is thus cooled) to the cooler spermatic venous blood (which is warmed). In this way, blood is pre-cooled before it reaches the testis.

In anesthetized rams, rectal, deep-testis, and subcutaneous scrotal temperatures averaged 39.8°C, 34.1°C, and 33.0°C, respectively, while aorta temperature averaged 39.6°C; arterial blood leaving the abdominal cavity and entering the vascular heat exchanger, 39.0°C; arterial blood leaving the vascular heat exchanger and entering the testis, 34.8°C; venous blood leaving the testis and entering the vascular heat exchanger, 33.0°C; and venous blood leaving the vascular heat exchanger and returning to the body, 38.6°C. The pampiniform venous plexus makes this remarkable precooling of blood entering the testis possible. It and the greatly convoluted spermatic artery form the bases of the vascular counter-current heat exchanger in the spermatic cord.

In the bull, ram, and boar alike, the spermatic artery is a tortuous mass. It is greatly coiled and convoluted in of the spermatic cord. These convolutions greatly increase the artery's surface area, and thus its heat-exchange potential. The spermatic artery is intermingled and in close contact with the pampiniform venous plexus. At some points, the incoming and outgoing blood streams are separated only by the thicknesses of the two vessel walls. R.G. Harrison noted: "It is difficult to conceive of any function for this structure other than that of providing for exchange of heat between the testicular artery and veins."

The length of the internal spermatic artery, and thus magnitude of the body-testis temperature gradient, varies among bulls. It was noted that British-breed bulls in South Africa attempt unsuccessfully to adapt by increasing the length of spermatic or testicular artery, and their testes hang further from the abdomen than do those of Afrikaner bulls in the same environment.

This vascular heat exchanger is in way autoregulatory. It works on simple physical principles. The amount by which the arterial blood supplying the testis is cooled below body temperature depends mainly on the temperature of the venous return. In other words, the temperature gradient in the vascular heat exchanger is the main determinant heat flow from spermatic arterial blood, and thus of blood temperature as it enters the testis. The difference between abdominal and testicular temperatures is about 4°C in bulls and rams and about 2.5°C in boars.

In recapitulation, the temperature of the blood as it enters the testis is a couple of degrees higher than the temperature of the blood leaving it, and the temperature of the blood leaving the testis determines the magnitude of the vascular heat exchange in the spermatic cord. Thus, blood is actually cooled a couple of degrees more as it passes through the testis. This cooling is very important to maintaining the necessary temperature gradient in the vascular heat exchanger.

Furthermore, the temperature of the blood leaving the testis is very close to that of the subcutaneous scrotal tissue. Subcutaneous scrotal temperature is related ultimately to vascular heat exchange in the spermatic cord, and scrotal temperature is extremely crucial to testicular temperature maintenance. Hence, the heat budget of the scrotum must be considered. As Waites and Moule pointed out: the vascular mechanism is not by itself regulatory but it rapidly transfers any benefit of scrotal thermoregulation to all parts of the testis". The scrotum can actively participate in its own temperature control.

The tunica dartos is largely responsible for the state of the scrotum relaxed and smooth or contracted and puckered. It determines the distance between testes and abdominal wall, and thus the magnitude of vascular heat exchange.

The tunica dartos is a coat, comprising smooth-muscle fibers together with connective tissue, which surrounds both testes and forms a partition (septum scroti) between the two halves of the scrotum. It lies between the scrotal skin and the tunica vaginalis, to which it is connected at the bottom of each scrotal pouch. When the tunica dartos contracts, the testes are drawn closer to the abdominal wall.

In rams, and probably bulls and boars as well, the extension state of the scrotum depends on scrotal-skin temperature, not air temperature. Thermal receptors initiating tunica-dartos responses are probably located in scrotal skin.

External cremaster. The external cremaster is a striated muscle attached to the tunica vaginalis, which envelopes each testis. Thus, when contracted it draws the testes-closer to the abdominal wall and inguinal region. However, because it is striated, it is incapable of the sustained contraction the tunica dartos can accomplish. Thus, the external cremaster is presumed to be of less importance as a thermoregulatory structure.

Scrotal-skin vascularization. Scrotal skin is highly vascularized. The rate of blood flow through the scrotal sac varies closely and directly with scrotal-skin temperature. Blood-flow rate more than doubles as scrotal-skin temperature rises from 34°C to 40°C. This increase appears to be due to an increase in blood flow through capillaries with relatively high resting blood-flow rate. Capillaries with higher rates serve, among other things, the large sweat glands in scrotal skin.

The scrotum also contains arteriovenous anastomoses that function to facilitate scrotal heat loss. They differ from those in other parts of the body in that they are direct communications between arteries and veins.

Sweat glands. Sweat glands are present in scrotal skin. In the boar, evaporative moisture loss from the scrotum does not increase much as environmental temperature rises, but it is higher than from its back. Hence, even though scrotal sweat glands are not thermally responsive in the boar, they do secrete sweat at a low rate and are important. Evaporative heat loss accounts for 20 percent of total heat loss from the boar's scrotum at moderate environmental temperatures, and an even greater proportion in the heat, since sensible fluxes are depressed by the narrowing of thermal gradients.

In rams and bulls, on the other hand, there is an active sweating response to high environmental temperature. When scrotal-skin temperature rises above 35°C, the apocrine sweat glands in the skin discharge sweat onto the scrotal surface synchronously. In the hot, when atmospheric vapor pressure increases, thereby narrowing the gradient, scrotal-skin temperature rises.

Scrotal sweat-gland function varies with season. Maximal scrotal-skin sweating rate in merino rams is around 100 gm m⁻²hr⁻¹ in winter, but as high as 200 in summer. These compare with around 30 gm, m⁻²hr⁻¹ for midside skin, and are higher than the 75 gm m⁻²hr⁻¹ found in boars. When the superior perineal nerves supplying the scrotum are anesthetized, thermally induced scrotal sweating stops and does not recur even when scrotal-skin temperature rises to 39°C. However, epinephrine or norepinephrine injected into the external jugular vein at this time elicits sweat discharge from the glands, hence they function even after anesthesia. It appears that scrotal sweat glands are stimulated by a reflex involving afferent information from scrotal-skin thermoreceptors that respond above 35°C and afferent fibers in the superior perineal nerves. Sympathetic adrenergic

nerves form the efferent side of the reflex. Adrenomedullary hormones secreted into the general circulation may play a lesser role.

Scrotal thermoregulation and general-body thermoregulation are intertwined in some interesting ways. Warming the ram's scrotum above 35.5°C reflexly elicits increases in respiration rate. When a similar amount of flank skin is warmed, a much smaller increase in breathing rate occurs. At scrotal temperatures of 40°C and above, marked thermal polypnea ensues. At the same time, rectal temperature starts to fall, presumably because respiratory heat loss increases. Conversely, when the anterior half of the ram's body was warmed, sweat appeared on the scrotum within half an hour.

Libido

Male sex drive may be reduced during summer. This is particularly so in rams, whose libido appears to be affected by both photoperiod and environmental temperature.

Androgen status. Cryptorchid males, in which testicular temperature is higher than normal, generally have normal libido. But when rams were exposed for 14 days to an average environmental temperature of 30°C, testis testosterone content (dry basis) decreased from 1.1 to .4 $\mu\text{g gm}^{-1}$ and spermatic-vein plasma content went from 8.2 to 1.9 μg per 100 ml. Further, cryptorchid boar testes' androgen concentration is only half as much as normal. In rams, the concentration of testosterone is the same in normal and cryptorchid testes, but as the latter are smaller, the total amount of testosterone in each testis is several times less.

N.T.M. Yeates concluded that high environmental temperature does not affect male libido by changing endocrine status. Rather, he suggested hot environments exert a secondary effect: interest is diverted from sexual pursuits by the discomfort or anxiety due to the heat. Hence, males held in the hot except at the time of service or semen collection may show no change in libido. Most rams have enough libido to serve a ewe any day of the year, but during hot weather they may not actively seek out estrous ewes.

Heredity. There are genetic influences on the libido-depressing effect of a hot environment. Merino, Dorset, and Border Leicester rams were held at progressively higher temperatures--27°C, 32°C, 38°C, and 43°C. During an 8-hour test at each temperature, each of the rams was given the opportunity at hourly intervals to mount an anestrous ewe for semen collection. The number of ejaculates collected declined as the environment became hotter for Dorset and Border Leicester rams, but not for Merinos. After being returned to a cool environment, Dorset rams regained normal libido, but Border Leicesters did not.

Rams also vary greatly in libido during the ewes' normal anestrous period, and again breed differences have been found. For instance, in one study, Kerry rams were responsible for all out-of-season matings, even though Hampshires and Suffolks had an opportunity to serve and ram preference by ewes did not seem to be a factor. Also, Kelly rams were "quickest off the mark" at the beginning of the breeding season.

Environmental temperature, semen quality and fertility. It is known that males may be temporarily infertile during and after periods of exposure to hot environments. The question remains as to how effective environmental temperature, semen quality, and fertility are related. At what environmental temperature are the male's elaborate mechanisms for regulating testicular temperature overwhelmed?

The Ram: The classic paper on environmental temperature and fertility is the one on the ram by R.M.C. Gunn and co-workers. They concluded that when maximum daily environmental temperature exceeds 32°C each day for 4 weeks or more, semen quality drops. Later, it was found that even a mean environmental temperature of 27°C was sufficiently high to reduce semen quality. It had observed even earlier that ram fertility was impaired when they were kept in a hot room.

Semen quality. Seasonal variation in semen quality in the Central Valley of California has been found to parallel variations in maximum daily temperature and photoperiod. Even in a locale with moderate climate, such as in Ireland, it was highest in fall and winter, lowest in summer.

Seasonal breeders have greater seasonal fluctuations in semen quality than continuous breeders. Furthermore, there are differences in heat susceptibility. When the rams most dominant sexually in a multi-sire mating situation all happen to be relatively susceptible to heat-induced infertility, flock fertility suffers greatly.

It has already been established that testis temperature influences semen quality, but the relation between environmental and testis temperatures has not yet been fully rams held for two days at 35°C temperature averaged only 38°C.

Severe seminal degeneration is thought by some to occur only when deep testis temperature exceeds 39°C for several hours, while others hold that 36°C is the critical testis temperature. Of course, during summer, effective environmental temperature frequently exceeds 35°C for several hours daily in temperate as well as subtropical and tropical areas. In other studies, seminal degeneration occurred after rams were continuously exposed to a 32°C environment for one week or 38°C for three days.

Furthermore, atmospheric humidity level is also a factor. Rams held at lower relative humidity during heat stress had lower testis temperatures.

Hence, we may conclude that when environmental temperature exceeds 30°C even lower if vapor pressure is high for a couple of hours or longer, the ram's deep testis temperature will become so high 36°C or higher that spermatogenesis will be deleteriously affected. Of course, effective environmental temperature frequently exceeds 30°C on summer days even in temperate climates.

Fertility. Rams with low quality semen resulting from heat stress also have low fertility. One ram was exposed to 40.5°C and 45 percent relative humidity for eight hours one day, another on each of three days, and a control ram was not exposed to the hot environment at all. Each ram was hand mated to ten ewes on days 8 to 16 post heatexposure. The results demonstrate that even a small amount of abnormal sperm morphology due to short-term exposure of rams to moderate heat is closely associated with depression in conception and lambing rates. In a similar experiment, rams were exposed for 8 hours to 40.5°C and 45 percent relative humidity on 1, 2, 3, or 4 days.

Amounts of sperm abnormality and heat treatment were directly related, and ram fertility followed the same pattern.

Alleviating heat stress. Methods of alleviating heat-stress effects on the ram's reproductive processes include providing cool quarters and shearing. At Kentucky, rams were held all the time either in a room at 8°C or in a room where maximum daily temperature during a 4-month period averaged about 30°C. Photoperiod was natural in both rooms. Rams entered the experimental environments on June 2, and the breeding period lasted from August 22 to September 25. Semen quality and fertility were much higher for rams kept in cool quarters. Estimated embryonic death loss was lower in ewes

mated with cooled rams. The several-fold improvement in lambing percentage was apparently due to keeping only the room cool; ewes were in essentially the same environment as the uncooled rams.

At Oklahoma, beginning 3 weeks prior to the start of breeding season, rams were kept either in a cool room (average maximum daily temperature was 25°C) or in a barn (average maximum daily temperature was 27°C, 31°C and 30°C on successive years of the study) between 0800 and 1700 hours each day. Natural mating occurred each night between 1700 hr and 0800 hours. Cooled rams mated more often and sired more lambs.. Shearing is another way of alleviating heat stress. At Kentucky, either newly sheared or unsheared rams were held for a week beginning January 12 at 32°C and 60 percent relative humidity. The unsheared animals were less able to maintain normal body temperature and semen quality. During the fifth week after exposure, unsheared rams had a lower percentage of motile sperm (<10 versus 80 percent) and a higher percentage of abnormal sperm (70 versus <10 percent).

At Wisconsin, yearling rams were sheared in April and either at monthly intervals thereafter or not again until the breeding season was completed in the fall. Sheared rams were more fertile than unsheared rams. Deep-testis temperature is 1°C or more higher in unsheared rams than in sheared ones in warm environments. Relief due to shearing is beneficial to reproductive performance.

"Skin folds" and fertility. An interesting effect has been noted in Australia, where some Merino sheep breeders have selected for "skin wrinkle" or "skin fold" to increase the wool-growing surface area. Net-reproductive rate in flocks with a high degree of skin fold is relatively low, probably partly because, rams- with many skin folds are more susceptible to heat induced infertility. Deep-testis temperature in rams with many skin folds is higher than in those with few folds when both are subjected to high environmental temperature.

The bull: Results of numerous studies indicate that, in areas where there is marked seasonability in environmental temperature, the bull's semen-quality tends to be low during summer.

Providing a cool environment during periods of hot weather is beneficial also to the bull. In Louisiana, 91 percent of the semen collected from bulls held at 27°C could be used in artificial insemination, whereas only 47 percent of those from bulls kept in a barn under normal summer conditions were suitable.

The classic study of the bull was conducted by R.B. Casady and coworkers. Ejaculate volume was not affected, but as environmental temperature rose, sperm motility fell. After exposure either for 17 days at 37°C and 80 percent relative humidity (12 hours per day), or for 36 days at 30°C and 75 percent relative humidity (24 hours per day), sperm concentration and total sperm output dropped markedly. Total percent abnormal sperm averaged 34 percent during heat exposure as well as the 6 weeks following treatment. Semen quality had not returned to normal within 3.5 months after the end of heat stress. In two bulls, motility was essentially zero at the end of the heat-stress period. Histologic examination of the testes revealed degeneration of the germinal epithelium. Despite the fact the stress was so severe that one bull could hardly arise and stand, libido was apparently unimpaired by the heat.

Zebu-type cattle are not only more heat-tolerant than European type, the semen of bulls with zebu blood is less affected by hot environment. In one experiment, zebu and European crossbred bulls suffered less loss of semen quality due to heat stress than did

purebred Holsteins and Brown Swiss. The stress comprised 7 days of a daily cycle of thermal environment between 40°C with 54 percent relative humidity and 28°C with 72 percent. Mean maximum and minimum daily temperatures during the 3 weeks prior to heat stress were 18°C and 5°C, and during the nine weeks after, 21°C and 8°C.

Fertility. Climatic differences within North America lead to differences in the seasonal effect on bull fertility. Indeed, at latitudes of 40°C or greater, it has been found that bull fertility is highest during summer and fall. The situation is different, however, in areas where effective environmental temperature is higher. For instance, at Baton Rouge, Louisiana--a subtropical region--both semen quality and fertility were lowest in summer, and presumably due to a carryover effect, fall. While the cow's contribution to infertility was not removed from these data, it was accounted for in a study of the fertility of Ohio bulls. From these it is clear that from semen collected during the hot Ohio summer weather, fertility dropped more quickly with aging in the frozen state than it did in semen collected during cooler weather. Again note in the Ohio data the lag between the time heat stress was greatest (July and August) and the time fertility was lowest (August and September).

The Boar: The boar's fertility is also influenced by the thermal environment. Boars which had been subjected to an environment at 33 °C and 50 percent relative humidity for 3 days had inferior semen as a result. Concentration, total output, motility, and morphologic integrity of the sperm were deleteriously affected, by heat. The effect was maximal about a month after exposure, but semen quality returned to normal within two months.

Results of another study confirmed the detrimental effect of heat stress (33°C for 3 days) on semen quality in the boar. It began to decline 2 or 3 weeks after heat stress, but had returned to normal by 8 or 9 weeks. The boars' fertility after heat stress paralleled semen quality. There was a 20- to 40-percentage-point reduction in conception rate with semen collected from boars during the period 2 to 7 weeks after heat stress.

Hence, boars appear to be much like rams and bulls: effects of heat on reproduction are evident 2 to 3 weeks after the stress, and persist for over a month. Also provision of cool quarters for the boar during hot weather helps reduce the heat-induced fertility slump. In southern France, where during summer maximum daily temperature under shade is commonly 35°C, farrowing rate in sows inseminated with semen from boars kept outdoors averaged around 35 percent from June through September, in contrast to 55 percent the rest of the year. On the other hand, boars kept in quarters where environmental temperature never exceeded 22°C during the summer had higher fertility during June through September: conception rate was around 50 percent.

Cold stress and boar reproduction. In Manitoba, semen quality in boars kept in straw-bedded wooden huts was compared with that of boars kept at 17°C inside. Outside average daily temperature during the study period of January through March was -18°C, -20°C, and -15°C for respective months. Corresponding monthly minimum temperature averages were -24°C, -27°C, and -21°C. The cold macroenvironment did not affect testicular development, sperm production, or semen quality.

Conclusion

There is sufficient evidence that protection against exposure to extremely high environmental temperature is effective in reducing summer infertility in male mammals. However, photoperiod probably plays a role in causing summer infertility! too. This,

along with another discussion of temperature photoperiod interaction in regard to male reproduction, will be discussed further in Part III.

The Male Bird

The bird's testes lie in the body cavity, not in a scrotum. They are partially surrounded by the posterior thoracic air sacs, and it was once thought they were cooled by contact with these. However, semen quality in the cock is unaffected by removal of the thoracic air sacs.

The bird's testes are normally warmer than those of the scrotal mammal. Scrotal mammals keep testis temperature below 36°C except during extreme heat stress, whereas the cock's is normally over 41°C. Does this mean that spermatogenesis is always suboptimal in the male bird? Is there a difference in critical testis temperature for spermatogenesis between mammals and birds? Is spermatogenesis at all sensitive to temperature in the bird?

The Cock: The chicken cock, in contrast to most birds, produces sperm the year around. Most evidence is that heat stress does not reduce the cock's semen quality. However, spermatogenic rate is affected by photoperiod, and so--ironically--semen quality tends to be higher during summer. Neither does a hot environment reduce the cock's fertility. Cold environments--down to the freezing point--are also without effect.

The Tom: In traditional turkey production, the breeding season starts in winter and lasts through the summer. There is typically a progressive reduction in fertility during such a breeding season. While the hen may be largely responsible for this trend, there is evidence that the tom's thermal *environment also* influences fertility in a turkey flock. Providing the tom a warmer environment before and during the early part of the breeding period increases fertility and hatchability. Protection from hot weather between 0900 and 1600 hours each day during May, June, and July resulted in a 10-percent higher fertility rate from mid-June through mid-July in another study. Thus, the tom appears to be temperature-sensitive in terms of reproductive performance in the cock.

Daily Spermatogenic Cycle: In many birds, spermatogenesis occurs at night when body temperature is lowest. This is so in the chicken cock, in which mitotic activity in tests peaks at 2400 hours and is minimal at 0600 hours. This daily periodicity in spermatogenesis may be an important mechanism of protection against thermal damage in the bird.

The Female

Low reproductive performance during periods of thermal stress is due to functional problems in females as well as males. For instance, data on conception rate in sheep mated during hot weather indicate the ewe's contribution to lowered fertility is as great as the ram's. When neither ram nor ewe was provided a cool environment, fertility was drastically reduced.

What is the nature of heat-induced fertility in the female mammal? Which stage in the critical sequence of functional events does hot weather interfere with: estrous cycle, ovulation, fertilization, implantation, embryonic and fetal survival, or parturition? The critical period for heat stress effects on fertility is the period from a few days before mating to the few days after mating.

The Ewe

The Breeding Season: Ewes of many breeds are seasonally polyestrous. They are short-day breeders (see Part III). However, shepherds have long suspected that the "cool nights of fall" also have something to do with the onset of the breeding season.

An early attempt to demonstrate this interaction between photoperiod and environmental temperature involved holding ewes in an iced cellar close to the beginning of the breeding season. It failed, but it was eventually found that holding ewes at an environmental temperature of 8°C from May 26 on caused them to come into estrus an average of 54 days earlier than their counterparts held in an environment comparable except that the temperature was higher. Furthermore, ewes summered at a location about 5°C cooler than another location came into estrus a week or two earlier than those at the warmer place. Still other data suggest that heat stress does not affect the ewe's estrous cycle, but that it does reduce the number of multiple ovulations. Finally, cold stress around mating time may reduce the ewe's ovulation rate.

Fertilization and embryonic survival: Failure of ova to be fertilized and early embryonic mortality account for much of the reproductive inefficiency in ewes mated during hot weather. Typical experimental results are displayed in Table 9-36. They show that already within 3 days after mating in a hot situation a relatively large number of ova are abnormal and a small number are fertilized.

Subsequent research pinpointed the critical period for heat-stress effects on fertility as the period from a few days before to a few days after mating. Further study revealed that, while unfertilized ova from donor ewes held at 21°C or 32°C from 3 to 5 days. Prior to estrus on were equally viable in recipient ewes at 21°C, fertilized ova from donor ewes at 21°C were less viable in recipient ewes at 32°C than in those at 21°C. Thus, it appears that high environmental temperature does not alter sheep ova prior to fertilization.

Mechanism of early embryonic death during heat stress: It has been shown that rectal temperature at mating time is related to the percent of ewes that eventually lamb. Fertility was lower in ewes with rectal temperature above 39°C at mating time. One possibility is that nucleic-acid metabolism is upset in ova subjected to a high temperature at a certain stage of development (for instance, the zygote).

The possibility that hormonal imbalance may be responsible for early embryonic death in the ewe has been explored. Progesterone, thyroid hormone, and the glucocorticoids have been ruled out as contributory factors in heat-induced infertility in the ewe. Similarly, age of the ewe--1.5 versus 6 years old--was without effect on the ewe's susceptibility to heat-induced infertility. Breed, on the other hand, does influence it, presumably because breeds differ in general heat tolerance.

Levels of embryonic death in constant-temperature, hot-room studies are higher than those generally found in hot natural environments. A daily cycle in effective environmental temperature is a conspicuous feature of the natural environment that is absent in most such studies, and the rate of embryonic mortality is not so high when ewes are exposed to a cycling thermal environment, in which they are provided a respite from heat stress.

Alleviating heat-induced infertility. Shearing the ewe shortly before she is mated during hot weather reduces embryonic mortality. Furthermore, holding her in a cool environment from 10 days before mating to 25 days after mating did increase lambing rate.

"Fetal Dwarfing": Lambs born to ewes that are pregnant during hot weather are often relatively small at birth. Typical data from Texas show that, in a lambing period beginning the third week of October, birth weight increased progressively with time. Of course, environmental temperature during gestation was lower for lambs born later in the lambing season.

Experiments conducted to further describe heat-induced fetal dwarfing in sheep have revealed that ewes exposed to a hot environment the last two-thirds of gestation give birth to lighter lambs than do those heat-stressed only the last third (3 versus 3.6 kg) and that those heat-stressed 24 hours a day have lighter lambs than those stressed 12 hours (2.6 versus 3.6 kg). Subsequent research indicated that heat stress for a month or more during the last two-thirds of gestation causes fetal dwarfing.

Several factors are believed to influence the ewe's susceptibility to fetal dwarfing. Breeds which are more tolerant of hot environments appear to be less susceptible to fetal dwarfing. Yearling ewes may be more affected than older ones.

Causes: The ewe's plane of nutrition during gestation may be a causative factor. The theory is that the ewe's voluntary reduction in feed intake during hot weather reduces the availability of nutrients for fetal growth. Further, forage quality generally drops during hot weather. It is known that low nutritional plane during pregnancy results in small lambs at birth. However, it has generally been concluded that low nutritional plane is at least not the only cause of fetal dwarfing in sheep. Neither does elevated body temperature per se seem to play a major role. Data on gestation length as affected by heat stress during pregnancy are conflicting, and thus premature parturition is an unlikely major determinant of birth weight of lambs born to heat stressed ewes.

Two possible mechanisms of heat-induced fetal dwarfing appear most likely at present: placental stunting or reduced placental blood flow. Either would reduce fetal nutrition, and it is known that surgical reduction of placental size reduces lamb birth weight.

Finally, it was noted in Scotland that pregnant ewes housed in January to lamb in April gave birth to heavier lambs if they were sheared at the time of housing (5.6 versus 4.5 kg).

The Cow

Age at Puberty: Season of birth affects growth rate in the heifer and thus because in heifers body size is the main factor governing its age at puberty. Heifers which grow during warm weather tend to reach puberty later:

Fertility: It is well recognized that conception rate in cattle is noticeably reduced during periods of hot weather. The effect in subtropical regions is at least partly due to the cow, as opposed to the bull. In temperate regions such as Ohio, on the other hand, the cow may contribute less to summer infertility than the bull. The Ohio data indicate that, if anything, reduced photoperiod during winter may reduce the cow's reproductive efficiency,

Estrous-cycle length: Several effects of heat stress on the cow's reproductive functions have been elucidated. Any or all may be responsible for reduced reproductive efficiency during hot weather. In hot regions of North America, the cow's estrous-cycle length may be longer during periods of hot weather than at other times, but in a temperate locale no such effect was found.

Estrus: Duration of estrus in the cow is markedly shorter during periods of hot weather than at other times, making it more difficult to detect behavioral estrus.

Furthermore, the intensity of the cow's estrous behavior is much lower during hot weather. In the ewe, at least, season influences the amount of estrogen required to induce behavioral estrus.

Conception: Conception rate in cows is related inversely with an average temperature-humidity index for the day of mating and the two previous days: In one study, the empirical relation was: conception rate = $61 - (3.7(\text{THI} - 70))$. Heifers exposed to 32°C and 65 percent relative humidity for 3 days beginning immediately after mating all failed to conceive, whereas those kept at 21°C and 65 percent during the immediate postmating period became pregnant. The heifers held in a hot environment after breeding had higher rectal temperatures during this period (40.0°C versus 38.5°C). In a Hawaiian study, conception rate declined from 66 to 35 percent as the temperature-humidity index rose from 68 to 78. The THI on the second day before mating was related most closely with conception. Available data on the effect of body temperature around mating time on conception rate in the cow are conflicting.

Hormonal influences: There has been the suggestion that during heat stress the cow's adrenal cortex secrete more progesterone, a precursor of gluco-corticoids as well as sex hormone. However, when heifers were exposed to a 21°C/34°C daily cycle in environmental temperature, plasma level of neither gluco-corticoids nor progesterone was affected by the environmental-temperature regimen. on the other hand, heat stress does reduce baseline and preovulatory-surge levels of luteinizing hormone in the heifer's plasma. It increases plasma concentration of prolactin.

Fetal development and survival: As in sheep, the problem of fetal dwarfing is directly related to the degree of heat intolerance possessed by the cow. For instance, -while indigenous cows were not affected, British-breed cows gave birth to calves weighing 20 percent less from summer gestations than from winter. Abrupt and severe heat stress in midpregnancy can cause the cow to abort. Uterine blood flow is reduced by heat stress in the cow, and this may be responsible for some of the effects observed.

The Sow

Summer infertility in swine has already been noted, and the boar's contribution discussed. It appears that the female also plays a role in heat-induced infertility in swine.

Conception rate: In one study, gilts were exposed to either at 16°C or a 32°C environment on day 10 of the estrous cycle. They were mated at the next estrus to boars kept at 16°C throughout the study. Three days after mating, half the gilts in each treatment group were switched to the other environment, in which they were held until embryo survival was determined 25 days after mating. The hot environment exerted a deleterious effect sometime later than three days after mating. An increase in the occurrence of silent estrus was observed in those gilts held at 32°C before mating, confirming earlier findings. In another experiment, bred sows were exposed to a constant 35°C environment for one day commencing 1, 5, or 20 days after mating. There was a tendency for reduced embryonic survival rate in sows heat-stressed beginning on day 1. In a subsequent experiment, bred sows were exposed to a constant 37°C with 50 percent relative humidity for 5 days commencing on day 1 or 20. This stress was so severe that eight of 22 sows suffered heat death during the experiment, yet embryonic survival was reduced only in the sows exposed to the hot environment beginning on day

1. Again, hot weather had a deleterious effect on sow reproduction very soon after mating. Results of the experiments just reviewed, together with those reported by others, lead to the conclusion that heat stress before and at the time of mating reduces the intensity of estrous behavior, but does not reduce ovulation rate, and that heat stress during the 2 weeks following mating reduces early embryonic survival.

Effects in late gestation and after parturition: There seem to be detrimental effects of heat stress on the sow's reproductive efficiency when it occurs in late gestation. Gilts subjected to heat stress daily from day 102 through day 110 postmating had poorer farrowing performance than control gilts held in a cool environment.

In warm climates, piglet-stillbirth rate is highest during hot periods. In one study, it was 11.2 percent during the two hottest months, and only 4.6 percent the rest of the year. Sow deaths, apparently due to heat stress, were most prevalent at the same time. Hypogalactia occurs most frequently in sows during hot weather, too. The mechanisms responsible for these unfortunate consequences of heat stress are still not understood. But it is known that peripartal behavioral activities and constraints on heat dissipation during parturition lead to very high body temperature, especially when the environment is warm or hot.

Summary: Gilts and sows seem quite tolerant of heat stress before and during the time of mating and mid-pregnancy. However, hot weather during the 2 or 3 weeks prior to mating increases the incidence of silent estrus, during the first 2 or 3 weeks of pregnancy reduces conception rate and embryonic survival, and during the last 2 or 3 weeks of pregnancy increases the incidences of stillbirth and sow death during farrowing. Further, peripartal heat stress may result in hypogalactia.

Cold weather: Cold weather is apparently without effect on female reproduction in swine. When both gilts and boars experienced extremely cold weather, there was no decline in conception rate.

The Female Bird

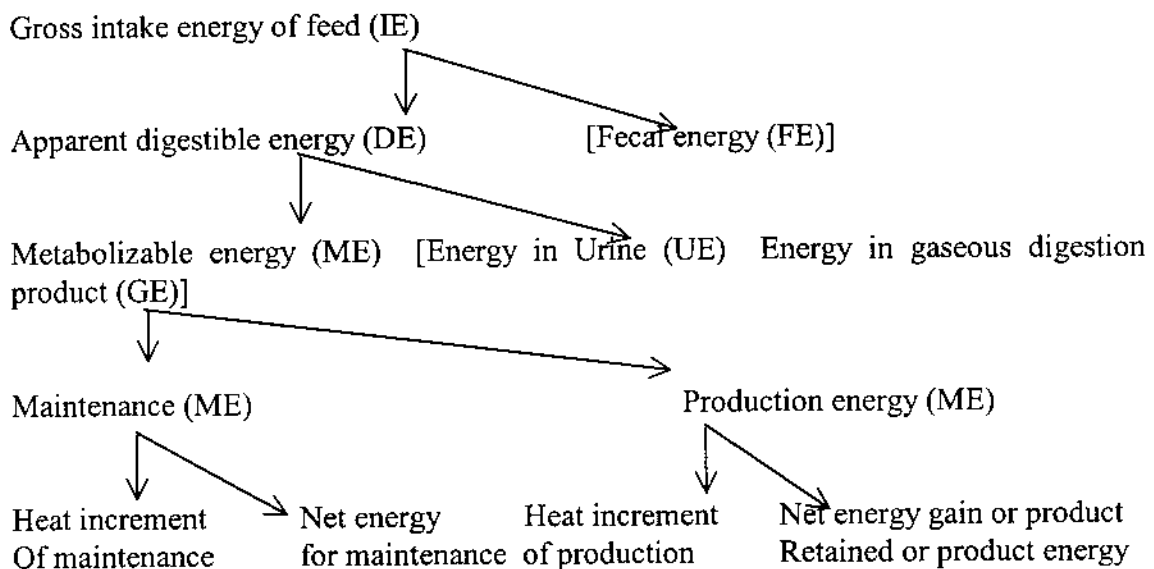
Chicken breeder flocks have a fertility (fertile eggs/total eggs) and hatchability (hatched eggs/fertile eggs) slump in late summer and early fall. Typical-results are displayed in Table 9-45. It is thought that reduced mating activity during hot weather may be responsible for much of this effect. Results of an experiment in which heat-stressed hens are artificially inseminated with semen from cocks held at thermoneutrality indicated that fertility of the hen per se was not impaired by the heat stress. Neither did hyperthermy in the hen affect the fertility or hatchability of the eggs. On the other hand, some results implicate the hen's reproductive *function* as the major factor in the summer reproductive slump in chickens. Reduction in the hen's voluntary feed intake below the level needed to support reproductive *functions* may be responsible for the effects that sometimes occur. Fertility in the chicken is unaffected by environmental temperatures as low as -5°C so long as an adequate amount of feed can be eaten. The well-known seasonal pattern in turkey fertility, already described, appears to be due at least as much as to the hen as the tom. However, this effect has not been associated definitely with seasonal changes in environmental temperature. Turkey hens held at an almost constant 10°C from January through May became broody, and thus their rate of lay fell.

ANIMAL ENERGETICS AND THERMAL ENVIRONMENT

Feed costs account for half to the total cost of animal production. Thus, factors that effect the efficiency with which animal convert feed to product have a major effect on the economy of animal production.

Under optimal conditions of environment and nutrition, the animal injects just as much feed energy as needed for maintenance and production. However, when an animal is kept under a sub-optimal environment, its feed intake might not meet its energy needs. When this happens, the overall efficiency of animal production declines.

How does an animal use the dietary energy?



Components of Animal Heat Production

Metabolizable energy is divided two ways: Heat production and animal product. The heat increment of both maintenance feed and production feed, together with the net energy for maintenance, combine to form animals' heat production. The rest of the metabolizable energy goes into animal product.

Heat increment of feeding: The heat increment of feeding is the heat produced by an animal during fermentation in the gastrointestinal tract and the use of nutrients by the body. It represents an inevitable inefficiency, unless the animal can use the heat to help keep the body warm in cool or cold environment.

Heat of fermentation: The heat produced anaerobically by microbes in the digestive tract is called the heat of fermentation. Of course, it is greater in ruminants than in nonruminants (the heat of fermentation of cattle rumina content 0.8 kcal/hr/kg of concentrate and 0.4 kcal/hr/kg of roughages). The heat of fermentation accounts for about 5% of a ruminant animal's total heat production.

Heat of nutrient processing: Ingestion, digestion, absorption, mastication, formation of urea or uric acid, require the expenditure of energy.

The energy cost of eating varies with the form of the diet. Example: Sheep spent 6 kcal eating 1 kg of dry matter as pelleted, dried grass, whereas it cost 57 kcal to eat an equal amount of dry matter as chopped, dried grass. To eat about 12 kg/day of a cattle weighing 400 kg spent 1.1 Mcal eating long hay, 0.7 Mcal chopped hay or 0.2 Mcal concentrates. Heat released during all these processes contributes to the heat of nutrient processing. In addition, heat is released during the metabolism of nutrients absorbed from the gut. Chemical transformations involved in productive and reproductive processes are not totally efficient, and thus they are accompanied by evolution of heat.

Heat increment of certain nutrients: The heat increment of feeding depends on species, diet quality, and the levels of feed intake.

The approximate heat increment of certain nutrients and mixed diets in pigs, cattle and sheep. Heat increment in various animal species are affected by class of compounds and mixture consumed.

Heat increment (kcal/100 kcal) of metabolizable energy at maintenance				
Species	Fat	Carbohydrate	Protein	Mixed Ration
Pig	9	17	26	10-40
Cattle	35	37	52	35-70
Sheep	32	32	54	35-70

It is clear that ruminants have larger heat increments than the nonruminant animals. This is one reason nonruminants are more efficient converters of certain low-fiber feedstuffs into animal products. Further the heat increment is larger for proteins than for fat and carbohydrates. It is also high when the diet is unbalanced in any nutrient.

The metabolizable energy minus the heat increment leaves the net energy. Thus for a constant level of metabolizable-energy intake, the greater the heat increment, the less the net energy available.

Net Energy

Net energy has two components: net energy for maintenance of the body and net energy for production. The ratio of these two net-energy fractions determines the animal's feed converting performance. In essence, animals perform maintenance function preferentially. Only the net energy remaining after all maintenance needs to have been met is available to conversion to animal product. As a consequence, when the maintenance cost is increased, animal product or at least the efficiency with which feed is converted to animal product is reduced. It is therefore important to understand the factors that affect animal's maintenance energy requirement.

Factors Affecting Maintenance Requirements

Stressful Conditions: In nonstressful circumstances, about 3/4 of an animal maintenance energy requirements supports vital functions; e.g., physical activity, cardiovascular, respiratory function and disease-resistance processes. The rest is released as heat to maintain body temperature. Any stress regime additional energy. Thus stress increases animal's need for net energy maintenance. As a consequence, it reduces either production rate or feed conversion efficiency or both. In particular, heat

to warm the body in a cold environment is part of the animal's net-maintenance requirement.

(1) **Metabolic body size and standard metabolic rate:** An animal's metabolic body size (MBS) is taken as body weight (in kg) raised to the $3/4$ power. The standard metabolic rate of farm animal is about 3 kcal/hr per unit of metabolic body size. This standard metabolic rate almost represents the maintenance energy requirement of the fasting, resting non-stressed animals.

(2) **Physical activity:** An animal carries out physical activities in addition to that involved in eating. It stands, walk, play and so on. All such activities require energy. They contribute to the animal's maintenance cost. It cost farm animals 0.02 to 0.03 kcal/kg to rise and similar amount to sit down. Once standing, 0.1 kcal/hr/kg is spent by sheep and cattle, pigs spend 10 times as much because they are more active. Thus, confinement of animals, because it generally reduces their activity, reduces maintenance energy needs.

Example: Sheep in a house had a maintenance requirement of 1400 kcal of metabolizable energy per day, while those in pasture required 2300 kcal. Cattle weighing 400 kg and foraging on flat land spend around 4.7 kcal per day. The same cattle in feedlot would spend only about 2.2 kcal per day if eating long hay, and still less 0.7 kcal per day if fed a concentrate diet.

(3) **Heat is required to warm feed and H₂O from their temperature as ingested to core temperature.** Water heat capacity is 1 kcal/kg/1 °C and feed is around 0.4. This can be very important in extreme cold.

Temperature in the digestive tract drops after an animal drinks cold liquid. Animals in cold environments may begin to shiver shortly after they drink a large quantity of cold water. Rapid body cooling in such a case causes an increase in heat production rate. In hot environment, of course, drinking cold water tends to help the animal achieve critical temperature. Example—In chickens, as body weight rose from 0.04 to 0.6, 1.6 and 2.4 kg lower critical temperature fell from 35°C to 32°C, 27 and 21°C, respectively. At the same time, the increase in heat production rate per 10°C decrease in effective environmental temperature (below the lower critical temperature) as expressed as its ratio to the thermoneutral rate, fell from 1.25 to 0.4, 0.28 and 0.24.

Net Energy for Production

The net energy for production is the same as the gross energy of the animal product. This can be estimated from its organic composition, because the approximate heats of combustion for protein, carbohydrate and fat are 5.7, 4.2 and 9.5 kcal/gm, respectively. Gross energy of some animal products are listed below.

Gross Energy Content of Animal Products

Product	Comment	Gross Energy Content
Cow milk	4%	750 kcal/kg
Egg		kcal/kg
Meat	Average across species and cuts	250 kcal/kg
Wool		6000 kcal/kg

Of course, the body does not convert metabolizable energy into product energy with 100% efficiency, the inefficiency appears as part of the heat of nutrient processing. Indeed, an animal's heat production rate is directly proportional to its rate of formation of any animal product.

The efficiency of conversion of metabolizable energy to animal product varies with the product. It is generally accepted that metabolizable energy is converted to milk energy at an efficiency of 60 to 70%. Hence for every 7 kcal of milk energy formed, 3 to 4 kcal of heat show up as heat of nutrient processing due to inefficiencies in the use of metabolizable energy for milk production. Similarly, growth is a 40-70% efficient use of metabolizable energy in mammals, 85% in chickens, egg production 85%.

Metabolizable energy is used more efficiency for maintenance than for production. About 75% efficiency in mammals and 80-90% in chickens. Variation in this efficiency owes largely to variation in heat of fermentation among diets.

Dairy cows sometimes call greatly upon body energy reserves to support milking production at certain stages of lactation, and body energy is converted with over 80% efficiency to milk energy.

EFFECT OF ENVIRONMENT ON NUTRITION REQUIREMENTS OF DOMESTIC ANIMALS

Nutrient requirements have been commonly established in an environment protected from climatic extremes. For that reason, such requirements are most relevant during optimum environmental conditions and less appropriate when animal are exposed to stressful environments. Despite the general awareness that energy demands are increased by cold and that the magnitude of those demands is moderated by total body insulation, few quantitative data exists relating environment, nutrient need and productive efficiency.

Digestibility and Metabolizability

There is evidence to indicate that the environment directly influences digestive and metabolic functions in animals. The ability of the animal to digest roughages increases with warmer temperature and decreases with colder ambient temperature. Although in severe heat stress, an animal's ability to digest feed may be depressed. The effect of ambient temperature on digestibility values. These changes do not depend on the feed intake.

Ambient temperature may effect rate of digesta passage in ruminants. During heat exposure rumen motility of cattle decreases and there is an increase in the retention time of digesta that should increase digestibility. Opposite responses obtained for cold exposed sheep and cattle; i.e., an increase in rate of passage and decrease digestibility.

This may be due to the thyroid. Thyroidectomized sheep had reduced rate of digesta passage that could be restored by thyroid therapy. That cold temperature increase thyroid activity and hot temperature decrease thyroid activity is documented. The effect of ambient temperature on digestion of feed stuff by growing hogs has indicated decrease in energy when animals are exposed to cold. There is a change in digestibility

value ranged from 0.12 to 0.48 digestibility units per 1°C change in ambient temperature. Poultry is not clear.

Feed Intake

The environmental condition effect levels of voluntary feed intake and the utilization of metabolizable energy ingested is well accepted.

Example: When lactating dairy cows are fed free choice of diet consisting of 60-65% roughage and 35-40% concentrates and exposed to constant temperature conditions. Feed intake will increase about 35% at -20°C over the level at 10-20 °C. Also, lactating cows under continuous heat stress begin to show a decline in intake at 25-27 °C with a marked decline occurring above 30 °C. At 40 °C intake is usually no more than 60% of the 18-20 °C levels. Efficiency of utilization of ME for production may actually rise at temperature down 5 °C to-10 °C but thereafter, efficiency declines due to high rate of heat loss. The rate of rise or decline in feed intake at extremes in temperature is influenced by level of milk yield and by the breed.

Feedlot Cattle

Feeding x temperature interaction is similar to that of dairy cattle. There is evidence that the appetite of crossbred cows is influenced less by summer heat stress than for purebreds. With the high use of crossbreeding in the beef industry, possible advantages of crossbreeds in feed efficiency during periods of stress.

Swine

The temperature at which intake rises or declines is approximately the same for light and heavy pigs. The absolute feed intake of young pigs (8 weeks) may be higher at 25 °C (1.82 kg/day) than at 20 °C (1.74 kg/day). Growth rate of young pigs is moderately reduced under cool (10 °C) and hot (30 °C) conditions; however, the percent of the energy retained by higher temperature (30 °C) may be higher (43%) than at 10 °C (34%)

Poultry

Under commercial conditions, where temperatures inside the house may range from 20-37 °C, the feed intake of laying hens will decrease 1.0-1.5 gm/day per 1 °C from 25-34 °C but by 4.2 g/day per 1 °C from 32-36 °C. Level of protein in the diet appears to have an interaction effect on feed intake of laying hens under thermal stress. For summer feeding in moderate temperature and throughout the year in hot climates, a crude protein of 25% or higher is recommended for good efficiency, whereas less than 25% CP is satisfactory at temperatures below 25 °C for laying hens.

Water-Environment Interaction

Water, a nutrient, is essential for life and intake is subjected to marked interaction effect with environment.

The water needs of livestock are filled from three major sources: (1) free drinking water, (2) water contained in feed, and (3) metabolic water produced by oxidation of organic nutrients. The catabolism of 1 kg of fat, carbohydrates or protein produces

1190, 560 or 450 gm of water, respectively. Metabolic water is important to all animals, particularly to those residing in hot arid environment.

Temperature and Nutritional Efficiency

Studies have shown that feed efficiency of swine decreases following exposure to either heat or cold stress.

Example: An environmental effect on rate of performance and energetic efficiency is shown (Table 11, page 53) for temperature ranging from cold stress (0 °C) to heat stress (35 °C). The energetic efficiency decreased during both cold and heat stress and was highest during TNZ. While temperature and efficiency values may differ from animals with different insulation, diet, etc. or for different species and products, the same general pattern for reduced energetic efficiency is consistent among animals exposed to stressful environment.

Specific climatic variables change total efficiency. No effect of 45, 70 and 95% relative humidity on hogs when temperature was considered optimum, but significant decline was noted during heat.

The impact of climatic environment on energy flow in terms of both energy intake and that available for growth may directly affect other nutrients. For example, protein efficiency ratio (gm grain/gm crude protein) is lowered during both heat and cold stress in sheep, swine and cattle. These examples emphasize the need to consider available energy in the light of environmental stress and to adjust rations to enhance efficient utilization of nutrients.

Approach for Practical Nutritional Management

Cold Stress

The extra feed required to compensate for the increased rate of heat loss and to (table 31, page 1001) keep body-warm. This is for below the thermoneutral zone and from the critical temperature. Of course, compensation for coldness by extra feed intake results in an average daily gain comparable to that at thermoneutrality.

If ME remain the same, body energy gain is reduced at environmental temperature below the lower critical temperature due to extra heat to keep the body warm. However, daily gain-even with extra feed intake may still not be the same in the cold as at thermoneutrality.

Another factor effect estimates of extra feed required by cold is the digestibility in cold stressed animals. Digestibility coefficient drop 0.1-0.4% per 1 °C has been shown. This for lambs and cattle but not for pigs.

Heat Stress

Various definitions have been used to describe the reactions of pigs to heat stress. From the concept of thermoneutrality, the upper critical temperature is defined as the effective ambient temperature above which total heat-production rate at a given feed intake will rise. Another; the upper critical temperature as that point at which a pig with dry skin can maintain maximum rate of heat loss. Compared with cold stress, much less information is available relating effects of heat stress on productive traits.

Pigs eat about 60 to 100 gm less feed each day per 1 °C of heat stress (32°C as opposed to 21 °C). This decline in feed intake resulted in a reduction in daily gain of 35 to 57 g/° of heat stress.

It is logical that adding fat to swine diet may be advantageous during heat stress, because fat had lower heat increment than either carbohydrate or protein. In addition, fat has a high caloric density that help offset lowered caloric intake during heat exposure. Feeding synthetic lysin is more advantageous than protein, which reduce heat increment in diet. Range of 18-21 °C is optimum for growing and finishing pigs. Adjustment for protein should be maintained.

Dairy Cattle

The efficiency of performance of dairy cattle is influenced to some extent by both high- and low-temperature conditions. The estimated range of temperature for highest efficiency of energy utilization is about 13-18°C. However, significant changes in feed intake or in numerous physiological processes will not usually occur within the range of 5-25°C. Below 5 or above 25, appetite will be influenced.

Feed Intake and Energy Requirements During_Cold and Heat Stress: (Table 21; page 79)

The relative changes in maintenance requirements and dry matter intake for 600 kg Holstein cow expected to produce 27 kg of milk with 37% fat. From -10 to 25°C, there is a gradual decline in feed intake. Decline decreases rapidly when the daytime temperature were 6 h or more above 30°C per day. The decline in feed intake to *minimized* heat production or shivering. Using 18-20°C as a base point of 100%, intake increases with decreasing temperatures, reaching 150% at -20 °C. The estimate DM intake to maintain 27 kg daily milk yield would increase from 18.2-21.3 kg. But because of the need to heat balance, coupled with lower palatability of food at -15 to -20°C, the expected dry matter intake will increase only to 20.4 kg/day. With rising maintenance requirements 20.4 kg or less intake will leave less ME available for milk resulting in lower milk production.

The maintenance requirements will rise when cows are exposed above 30°C. To maintain milk production, dry matter intake should increase from 18.2-20.2 kg when temperatures rise above 35°C. However, heat stress will suppress appetite; hence *reduced rather than increased feed intake is expected*. With reduced intake, increased maintenance, milk yield will decline by 33% at 35°C.

Poultry

Feed intake: The overall estimate for relating feed intake to temperature change appears to be 1.5%/1 °C with 20-21 °C as a baseline.

Performance: An improved growth performance may be observed upon a decline in ambient temperature as a result of an increase in feed consumption. Chickens in heated chambers lay smaller eggs with thinner shells.

Acclimation: Laying hens took 7 days to adjust to a shift in cyclic cold to cyclic hot. Chickens stabilized at a lower value of feed intake within 24 hrs, when shifted to warmer temperatures. However, 21 to 28 days were noted by other investigators for acclimation to occur. Turkey hens appear to be acclimated, based on feed intake, in 8 to 14 days when shifted from cold to hot environments or as long as 21 days, if the

temperature is as high as 37.8°C. If they are moved stepwise every two weeks into 5°C hotter environments starting at 20°C, each time there is a dramatic decline in productivity, feed intake, egg and shell quality with the move into 30 and 35 °C. Evidently, short-term exposure to warmer environment does not acclimate turkeys to a subsequently hotter environment. Unfortunately, we have not taken advantage in every day husbandry procedures of inducing acclimation or acclimatization as an approach to buffer an expected environmental impact.