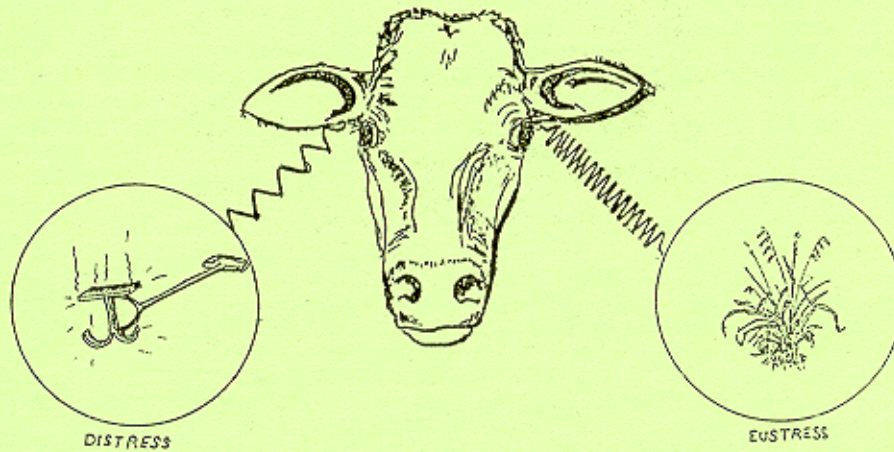
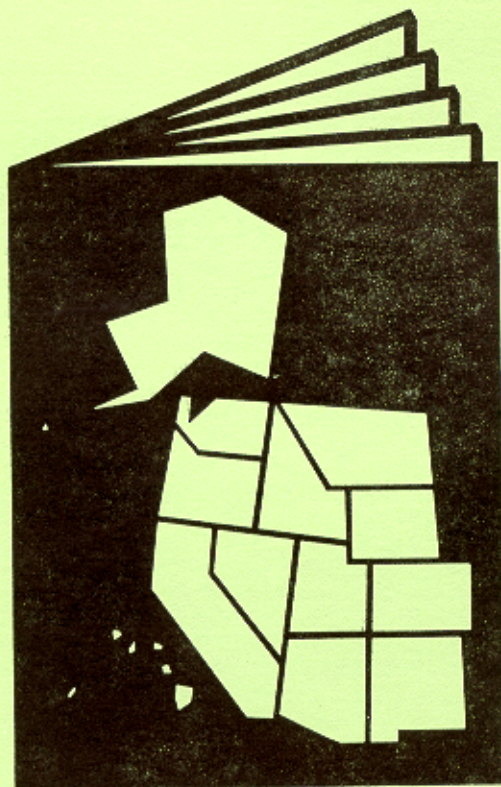


# Stress and the Free-Ranging Animal

A Western Regional Research Publication



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**STRESS AND THE FREE-RANGING ANIMAL**

Proceedings of a Symposium  
Sponsored by  
Western Regional Coordinating Committee on  
Utilization of Range Forage for Rangeland and Domestic Ruminant Production

W-151

Crystal Bay, NV

July 21, 1989

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## FOREWORD

Grazed forages provide basic nutrition for most ruminant livestock and substantial wildlife populations in the United States. Grazed forages are important economically because over 35% of the total nutritional requirements for United States beef cattle, sheep and goat populations are derived from this resource. Specific factors that effect productivity and health of domestic animals occupies the central focus of most management systems and form the basis of most current day research thrusts. These facts lend credence to the need for regional research focused on optimum and sustained production from rangelands.

One method to foster regional cooperation is through regional projects such as Western Regional Project W-151 in which both state and federal research is focused on questions which not only have local but also regional importance. Regional projects normally operate within a five-year time frame. Prior to the fifth year a decision is made by the participating members on whether the project should be revised, if a new project should be submitted or if the regional research should simply be conducted under the guidelines of a continuing committee.

In October 1983, the research locations participating in W-151 revised the then current project for the ensuing five-year period (October 1, 1984 through September 30, 1989). The new regional project was given the title "Utilization of range forage for rangeland and domestic ruminant animal production." Two main objectives formed the basis for this project. The first focused on activities of free-ranging livestock as they relate to livestock production efficiency and its impact on the standing crop. The second objective involved assimilating current knowledge into livestock production models for evaluating management strategies and identifying research needs.

In addition to the research focus encompassed in both objectives, it was the goal of W-151 to expand the knowledge base of the research community in applied animal behavior and other allied fields. One-day workshops or symposia held in conjunction with annual W-151 business meetings have provided this training.

The first workshop/symposium was held 29 August 1984 in Logan, Utah. Dr. David Balph, professor of Fisheries and Wildlife Sciences, Utah State University, Logan, Utah presented the participants with ethological concepts, terms and a brief overview of the historical evolution of ethology. The second workshop/symposium was held 7 January 1986 in Las Cruces, New Mexico. Dr. Scott N. Urquhart, professor of Experimental Statistics, New Mexico State University, Las Cruces, New Mexico and Dr. Mark Stafford Smith, research scientist in environmental ecology, Commonwealth Scientific and Industrial Research Organization, Division of Wildlife and Rangeland Research, Alice Springs, Australia addressed the topic of designing and evaluation animal behavior studies conducted under range conditions.

This research report is the final publication resulting from the five-year regional project which began in October 1984. The topics presented by three speakers represent the current information on stress, its measurement and importance in free-ranging animal production systems. In addition to this

publication the current interest in stress has prompted other recent publications on the subject of stress which the reader is encouraged to refer to when reviewing literature, three of which are:

Dantzer, R., and P. Mormède. 1983. Stress in farm animals: a need for reevaluation. *J. Anim. Sci.* 57:6-18.

Moberg, G. P., ed. 1985. *Animal Stress*. Amer. Physiological Soc., Bethesda, Md. 324 pp.

Moberg, G. P., ed. 1986. Limiting the effects of stress on cattle. *Utah Agr. Exp. Sta. West. Reg. Res. Pub. 009. Res. Bull.* 512.

Wiepkema, P. R., and P. W. M. van Adrichem, eds. 1987. *Biology of Stress in Farm Animals; an Integrative Approach*. Martinus Nijhoff Publishers, Dordrecht. 198 pp.

#### W-151 Subcommittee on Stress

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Workshops/symposia require the time of many dedicated persons and substantial resources including dedicated funds and expendable supplies in order to bring them to fruition. The members of W-151 especially thank the following sponsors who contributed materially to the success of this workshop:

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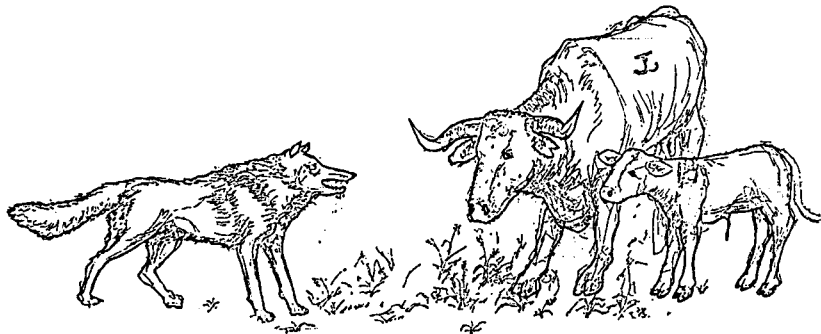
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**STRESS AND STRESSORS IN RANGELAND DOMESTIC RUMINANTS WITH  
EMPHASIS ON BEHAVIORAL STRESSORS<sup>1</sup>**

W.R. Stricklin and J.A. Mench<sup>2</sup>



**Key Words:**

Free-ranging livestock, Management, Social stress, Stress measurement

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<sup>1</sup> Published as Scientific Article No. A-5090, Contribution No. 8150, of the Maryland Agricultural Experiment Station.

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## **ABSTRACT**

Rangeland ruminants in western North America experience considerable variation in exposures to potential stressors. These stressors include weather, disease, diet, and interactions with other animals, both conspecifics and predators. Some management practices, including surgery, transport, branding, weaning, mixing, and restraint can also be stressful to animals. Assessing stress quantitatively in free-ranging animals, however, presents special problems. Even under controlled laboratory conditions there has been considerable controversy regarding the interpretation of physiological measures of stress, particularly since sampling can influence the parameters under consideration. Interpretation is further complicated in free-ranging animals because of the greater difficulties associated with sample collection. This can be overcome to some extent by the use of automated systems such as those used to collect liveweight data and physiological information. Although relatively insensitive, changes in liveweight gain and reproductive status can also be used as indicators of moderate to severe stress. Behavioral indicators (movement, spacing relationships, social interactions, and feeding patterns) can provide more subtle cues about animal stress. Multiple measures of stress are generally recommended, and are of even greater importance in investigations of free-ranging animals. Research leading to an understanding of stress in free-ranging animals has applications both to range production practices and to the understanding of stress in confined animals.

## **INTRODUCTION**

Stress is a topic which has received increasing attention from animal scientists, primarily as a result of the relationship between stress and animal well-being. Fox (1984) and others have contended that animals in intensive housing systems suffer because they experience behavioral deprivation, crowding, and increased aggression, all of which can cause stress. Animal welfare activists have thus focused their attention on intensive husbandry, which in turn has led to a greater welfare-related research focus on confined animals. Free-ranging animals, however, may also experience stress due to nutritional, social and management factors, health status and climatic extremes. Nutrition, disease and climate have been generally recognized as potential stressors and are discussed in detail in this publication (Parker 1990; Yousef 1990) and elsewhere (Ramanauskas 1988). The social and management stressors which impact range animals have not received as much attention.

The purpose of the present article is to briefly review current concepts of stress, and relate this information to the behavior and management of free-ranging livestock. Some research methodologies appropriate for the measurement of stress in free-ranging animals will also be discussed. A contention of this article is that research on stress and behavior of free-ranging animals is needed as a basis for comparison to stress monitored in animals that are housed in confinement.

## **CURRENT UNDERSTANDING OF THE CONCEPT OF STRESS**

Any prolonged or intense stimuli that are perceived by an animal as deviating from normal levels can be considered as stressors. Exposure of an animal to a stressor results in a series of physiological and behavioral responses which enables the animal to cope by eliminating the source of stress and/or by restoring homeostasis. The initial effect occurs via the sympathetic nervous system, and results in behavioral arousal, increases in respiration and heart

rate and redistribution of the blood supply to central organs, preparing the animal for "fight or flight". Within a few seconds, these effects are potentiated and prolonged by the release of the catecholamines (epinephrine and norepinephrine) from the adrenal gland. Shortly thereafter, hypothalamic corticotropin-releasing factor (CRF) stimulates the production of pituitary adrenocorticotrophic hormone (ACTH), which in turn induces the release of glucocorticoid hormones such as cortisol from the adrenal gland. Glucocorticoids act principally to increase blood glucose.

Stress responses are adaptive, and are therefore of benefit to animals. When stressors are persistent or extreme, however, the associated prolonged glucocorticoid secretion may have a number of deleterious effects. These effects include impairment of immune function, gastric ulceration, and perturbation of the secretion of the pituitary hormones which influence growth and reproduction, growth hormone releasing hormone and gonadotropin releasing hormone (Selye 1950; Kelley 1985; Moberg 1985b).

Some stress is inevitable and can in fact be beneficial. For example, injections of ACTH and glucocorticoids have been reported to improve learning and memory (Bohus et al. 1982; McGaugh 1983). Poultry housed in both high and low social stress environments show impaired immunocompetence, while those housed in a moderately stressful environment appear to respond optimally to immune challenge (Gross and Siegel 1973). Beneficial stress has been referred to as "eustress", while stress which has a negative physiological or behavioral impact on the animal has been referred to as "distress" (Selye 1976) or "overstress" (Ewbank 1973).

Even though stress has traditionally been defined in physiological terms, considerable controversy has arisen over the interpretation of physiological measures with respect to animal well-being, particularly basal hormone levels (Dantzer and Mormede 1983; Rushen 1986b). Basal cortisol levels fluctuate markedly as a result of normal diurnal variations in secretion and may vary greatly from one animal to another. Both cortisol and catecholamine levels are strongly affected by the stressors associated with blood sampling (capture, restraint, handling and venipuncture). In addition, cortisol levels may be found to be low not only when animals are not stressed, but when they have experienced such severe stress that the adrenal is no longer competent to produce enough hormone. Furthermore, since both "eustress" and "distress" cause a rise in cortisol, it is difficult to distinguish between the two using physiological criteria alone.

Pathological conditions such as decreased growth rates, reproductive suppression or increased disease susceptibility can be used as indicators of severe distress. Stressors that are intermittent or not severe enough to produce pathologies, however, may still be detrimental to the welfare of the animal. Moberg (1985a) suggested that measures such as impaired immune function can be useful indicators of distress when animals are in this "prepathological" state, although determining what constitutes impairment can be difficult. Behavior patterns such as stereotypies, increases in aggression, and abnormal behaviors are also suggestive of more moderate stressors (Fraser 1974).

The interpretation of both behavioral and physiological measures is further complicated by the fact that responses to stressors may vary among animals depending on each individual's perception of the stressor. For example, timid-acting kid goats show elevated cortisol levels during human-animal encounters, while non-timid kids do not (Lyons et al. 1988). Many intrinsic and extrinsic factors can affect the animal's perception, including genetic makeup, prenatal

effects, rearing experience, social status, the degree of previous experience with the stressor under consideration or with similar stressors, the controllability of the stressor, and the social context in which the stressor occurs. The effects of these factors have been investigated primarily in rodents and primates (see Moberg 1985a; Levine 1985; Kaplan 1986).

### **STRESS MEASUREMENT**

Because of the confounding effects of sampling previously discussed, obtaining accurate and sensitive physiological stress indicators in free-ranging animals can be particularly difficult. It is essential in range animals, therefore, that multiple measures of stress be utilized.

The confounding effects of sampling stress for physiological measures can be overcome to some extent by the use of special techniques for physiological sampling. De Waal et al. (1986), for example, constructed a remote blood-sampling device for horses which consisted of a harness apparatus containing a radio receiver and a venoject tube attached to a cannula inserted into the jugular vein. Sample collection was triggered by a pulse from a radiotransmitter, which operated a lever and valve system to release the pressure in the tube. Radiotransmitters for the measurement of catecholamine-influenced physiological parameters such as heart rate, blood pressure and body temperature are available commercially (Kenward 1987). Some disadvantages of automated remote sampling devices include their cost and sensitivity to extremes in temperature and harsh environmental conditions.

Animal behavior can be an indirect indicator of stress (Duncan 1974). Because animals use behavior as one means of trying to maintain homeostasis, deviations from normal patterns of activity or changes in social activities or spatial patterns can provide useful information regarding low-level or moderate stressors. Automated recording devices can increase the amount of information collected and in some cases can be used under range conditions. Pedometers have been used to measure total distance traveled (Williams et al. 1986; Anderson and Urquhart 1986), and vibracorders have been modified to provide an indirect measure of the amount of time spent eating (Stobbs 1970; Adams et al. 1986). Automated systems to monitor free-ranging cattle liveweight, water consumption and weather variables have been developed based upon electronic animal identification, and as such these systems can also be used to monitor activity patterns (Anderson et al. 1981; Adams et al. 1987; Anderson and Weeks 1989). Direct observation and recording of behavior is also quite practical under some conditions (Dwyer 1961; Gonyou 1984; Stricklin and Kautz-Scanavy 1984; Anderson et al. 1987).

### **BEHAVIORAL STRESSORS EXPERIENCED BY FREE-RANGING ANIMALS**

Livestock management is a process by which one group of animals (humans) manipulate other animals to a useful endpoint. Humans also use other animals, horses and dogs, in their management of herding animals. Through the contact with other animals and humans, behavioral stressors associated with management practices may be of great importance to range animals. Fear and/or anxiety are thought to be major causes of behavioral stress in animals (Duncan 1974), and range animals may experience these states at different phases of their lives. Predators, or even perceived predators such as dogs (Hulet et al. 1987; Anderson et al. 1988) or humans, may cause fear in animals. The presence of humans has been shown to evoke stress responses in both goats and swine, particularly when there is rough or unpleasant handling associated with that human contact (Gonyou

et al. 1986; Hemsworth et al. 1987; Lyons et al. 1988). The presence of dogs may also be stressful, particularly when the dogs are inexperienced herders (Thurley and McNatty 1973).

Artificial selection of domesticated animals has resulted in a decrease in the expression of those genes which cause fearful behavior in the presence of humans (Hale 1969). The ease with which animals can be captured, restrained and transported, referred to as tractability, is a behavioral trait of considerable economic importance. Relative to domestic cattle, some wild ruminants are more efficient utilizers of certain plant foodstuffs (Hawley et al. 1981). Because they are less tractable, however, raising these species is less economically viable and more stressful to the animals. In fact, the stress response of some wild animals to restraint may be so severe that they die, a response referred to as "capture syndrome" (Hediger 1969).

Tractability or docility may be influenced by the amount of human contact experienced, particularly during ontogeny. In range cattle tractability is probably selected for most intensely at weaning age and older, the time when cattle have the most contact with humans. *Bos indicus* and the more recently imported and so-called exotic breeds such as Chianina, on the other hand, generally experienced much more early contact with humans when raised under European conditions. In Italy the cattle were often housed in the same building as the owner, the cattle occupying the downstairs and the caretakers living upstairs. Thus, Chianina were probably selected for their "imprinting" response to humans in a critical period during the first few days of life. Because of the lack of human contact during the early life of range calves, breeds such as Chianina may show greater resistance to restraint under range conditions than the traditional European breeds, and thus a greater stress response. Animals born and reared in confinement are also typically more tractable than animals born and reared under range conditions and then confined later in life (Price 1985).

Because range cattle have comparatively less contact with humans than do more intensively-reared animals, they are likely to react more strongly to routine management practices. A number of management practices including surgical procedures, transport, restraint, branding, roping, vaccination, dehorning and slaughter may cause anxiety in animals:

**Surgical Procedures.** Both painful stimuli and the administration of anesthetics have been shown to result in increased glucocorticoid levels (Selye 1950). In lambs, tail-docking, castration and surgical removal of wool and skin from the breech to prevent blowfly strike (mulesing) result in increases in cortisol and changes in behavior (Shutt et al. 1987; Fell and Shutt 1989).

**Restraint.** Restraining calves for venipuncture causes an elevation in heart rate, whereas a considerable reduction in living space for 14 days causes only a transient elevation of corticosteroids and heart rate (Stephens and Toner 1975). Chute restraint of cows causes a doubling of catecholamine concentrations (Rulofson et al. 1988) as well as elevation of a variety of other physiological parameters indicative of stress (Mitchell et al. 1988). Electro-immobilization appears to be particularly stressful. Electro-immobilized sheep show a greater aversion to the location in which they were immobilized than do sheep that were only physically restrained (Rushen 1986a).

**Transportation.** Transportation has been reported to cause elevations in serum catecholamines (Rulofson et al. 1988), heart rate (Stephens and Toner 1975) and corticosteroids (Stephens and Toner 1975; Pearson et al. 1977; Fell et al. 1985) in both cattle and sheep. Elevated levels of corticosteroids may persist for 3 to 4 weeks after transport in cattle (Shaw and Nichols 1964). Transportation of calves for only 1 to 4 hours has been reported to elevate corticosteroid levels more than either castration, dehorning or 48 hours of water withdrawal (Johnston and Buckland 1976). It may be possible to mitigate the stressing effects of transportation in range animals. Housing sheep for short periods prior to transport, for example, decreases the corticosteroid response (Reid and Mills 1962).

Management stressors in domesticated animals are reviewed in greater detail by Stephens (1980), Phillips (1982), and Ramanauskas (1988).

### **SOCIAL STRESS**

Within animal groups, social interactions can result in stress (McBride 1968). The degree of stress an individual experiences probably depends both on the social organization of the group and the relative social position the individual holds within the group. For example, the mere presence of a more dominant conspecific can produce endocrine changes in subordinates (Dantzer and Mormede 1983).

**Social Organization.** The basic patterns of social organization in farm animals have been reviewed by Syme and Syme (1979) and Stricklin and Mench (1987). It has been suggested that studies of the wild and/or feral relatives of farm animals can provide a basis for understanding farm animal social behavior (McBride 1984).

There are no wild relatives of cattle, but studies of feral groups of cattle indicate that the social organization is matriarchal (Hall 1986). Reinhardt and Reinhardt (1981) found that among semi-feral Zebu cattle the nuclei of the herd were mother cows associated with their descendants, the latter of which also formed cohesive social units. The social behavior of feral and wild sheep and goats has been reviewed by Shackleton and Shank (1984).

**Social Dominance.** A feature of many groups of animals is that relationships exist among pairs of animals such that one animal is socially dominant to the other. Dominance relationships are established and maintained through aggressive and submissive social interactions of pairs of animals (Schein and Fohrman 1955). Social hierarchies are presumed to function to confer priority of access to resources such as mates and food to more dominant individuals.

Within beef cow herds, social dominance is highly related to age and weight, and within cow families mothers are dominant to daughters (Reinhardt and Reinhardt 1981; Stricklin 1983). Sheep grazing normally on pasture display little aggression, and dominance relationships, when present, are often bidirectional (Dove et al. 1974). Dominance hierarchies may be more pronounced, however, during supplementary feeding (Arnold and Maller 1974), intensive housing conditions (Ewbank 1974), or in ram groups introduced to ewes during the breeding season (Hulet et al. 1962).

Within small groups of cattle, the dominance rank order tends to be linear (Schein and Fohrman 1955; Wagnon et al. 1966). Genetic factors, such as breed, can be related to the amount of aggression experienced by an individual and thus influence dominance rank. Wagnon et al. (1966) reported that Angus cows were dominant to Hereford and Hereford were in turn dominant to Shorthorn. Similar results (Table 1) among Angus and Hereford cows on summer pasture were found by Stricklin (1983).

**Table 1.** Percentage of variation ( $R^2$ ) in social dominance value explained by age and liveweight in groups of beef cows composed of extended maternal families. (Source: Stricklin 1983).

Item	Age	Liveweight	Age and Liveweight
Group I			
Angus	87**	56*	89**
Hereford	52*	66*	73**
Combined	38*	21*	36*
Group II			
Angus	71**	90**	90**
Hereford	84**	55*	86**
Combined	38**	43**	45**

\* $P < 0.05$ ; \*\* $P < 0.01$ .

**Social Spacing.** Under range conditions, there is probably a tendency for cow families to form social units, and this may be reflected in spatial patterns. In fact, the relationship between social organization and spacing in social animals is so close that the use of the term socio-spatial has been suggested (Syme and Syme 1979). McBride (1968) proposed that, because of the relationship between social behavior and spacing, measuring spacing relationships between animals is a possible method of determining social stress.

**Separation.** Because of the strong social tendencies among domestic ruminants, individuals will experience conflicts between the "need" to be with the group and the "need" to maintain distance so as not to induce aggression. As a result of forage distribution, group composition of cattle under range conditions is different from that of improved pasture production systems, with range cattle typically in smaller groups and individual cattle sometimes experiencing separation from a group. Bobek et al. (1986) found that cortisol levels in sheep rose to maximal levels 1 hour after isolation from the flock.

**Resource Competition and Mixing.** Mixing cows during the calving season and the crowding that is associated with calving or feeding during overwintering can create an increase in the amount of social stress within the group. Competition between cows at the time of feeding during overwintering has been

investigated by Wagnon (1965) and Schake and Riggs (1972). Cows tend to be competitive when trough space is limited (Bouissou 1970). Other management factors such as the amount and distribution of feed also influence the amount of stress experienced by the group members. Schake and Riggs (1972) reported that cows lower in social rank weighed less, produced less milk, had lower conception rates and weaned calves with lower weights. Cows added to a group are at a social disadvantage. In a recent study (Mench et al. 1990), Angus cows from an outside farm were mixed with Angus and Hereford purebred and crossbred cows from the University of Maryland farm. The cows were overwintered in drylot paddocks each containing ten animals. The introduced cows were the most socially subordinate group, and their basal cortisol levels increased during the 84 days of housing, suggesting cumulative social stress (Fig. 1). The Hereford cows were also low in social rank and their cortisol levels followed a trend similar to that of the introduced Angus cows.

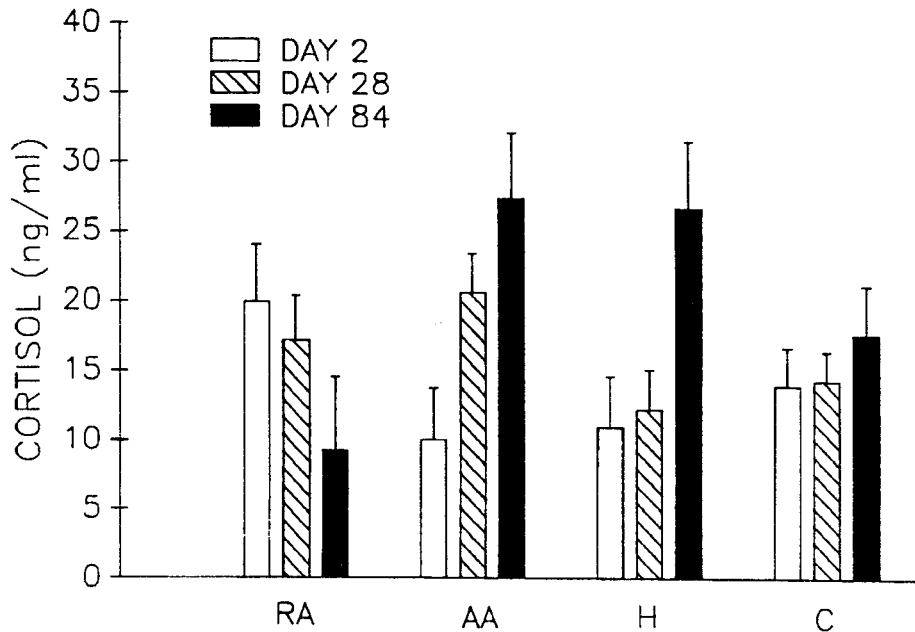


Figure 1. Cortisol levels of late-gestation beef cows 2, 28 and 84 days after mixing. Angus cows from an outside herd (AA) were mixed and overwintered with resident Angus (RA), Hereford (H) and crossbred cows (C). Cortisol levels in AA and H increased significantly over the sample days (Source: Mench et al. 1990).

**Social Stress and Animal Well-being.** Confinement animal production systems have resulted in considerable concern among some members of the public. Animals in confinement are thought to experience social stress largely because they are crowded, mixed, held in large groups, and in general cannot choose their own social environment (Stricklin and Mench 1987). Animals under conventional range management, on the other hand, are able to position



themselves at great distances from other animals. Because their social environment is thus "more natural" than a confinement environment, many animal welfare advocates would contend that these animals experience little social stress.

Social stress in range animals, however, is probably more important than these contentions and current research publications and funding levels would indicate. Short duration grazing systems, because they can involve moving cattle every 1 to 10 days as well as employ greater stocking densities (Savory and Parsons 1980; Savory 1983), may contribute to increased social stress. Therefore, management systems and grazing conditions can change other behaviors such as distance travelled and grazing time (Anderson and Kothmann 1980; Heitschmidt 1986) and may also influence stress levels. In a review article, Vavra (1982) suggested that changes in livestock behavior can also occur as a result of the presence of wildlife. Loewer (1989) listed social behavior as one category where there is a void in the essential data needed to adequately develop appropriate models for grazing strategies.

Among free-ranging livestock, competition for resources and rates of aggressive behavior directed against subordinates encroaching on resources are probably greater than is currently recognized by researchers. In summary, social stressors which may be experienced by range animals include separation from conspecifics, crowding (at least for short periods of time), and aggression as a result of resource competition and the periodic introduction of new group members.

### CONCLUSIONS

Although stress has traditionally been defined physiologically, physiological samples can be difficult to collect under range conditions as a result of methodological problems. These problems can be overcome to some extent by the use of implanted radiotransmitters to collect information regarding heart rate, blood pressure and body temperature. Transmitters can also be modified to permit remote blood sampling for the measurement of basal cortisol levels. In situations in which animals must be restrained to collect samples, measurement of cortisol in saliva or urine may be preferable, since levels rise more slowly than plasma levels in response to handling stress. We contend, however, that greater research activity is also needed in the area of animal behavior to determine its relationship to stress. Capitalizing on free-ranging animal behavior would provide the opportunity for gathering unobtrusive information. Similar techniques to those employed in automatically gathering liveweight data could be employed to obtain physiological parameters using appropriate transponders. Behaviors could then be more readily monitored in free-ranging animals and could thus provide valuable indicators of stress in animals.

An additional reason for emphasizing behavioral research is the growing awareness among the general public about farm animal welfare. Questions are being asked about the well-being of animals housed under conditions of confinement in regard to restricted movement, crowding, and large group sizes. Physiological studies are being conducted with confined animals to determine endocrine profiles associated with different housing conditions. However, the questions being asked by the animal welfare activists and some of the general public relate to animal behavior and not physiology. To address these questions, we believe that research should be conducted that has animal behavior as the

primary variable and physiological measures as supporting variables.

The public's concerns about animal well-being will likely continue to be directed primarily toward confinement animal agriculture. Research, however, should be concerned with unconfined as well as confined animals. Measurement of stress, especially behavioral stress, among range animals under various conditions would be an extremely useful comparison for determining appropriate or acceptable levels of stress among confined animals.

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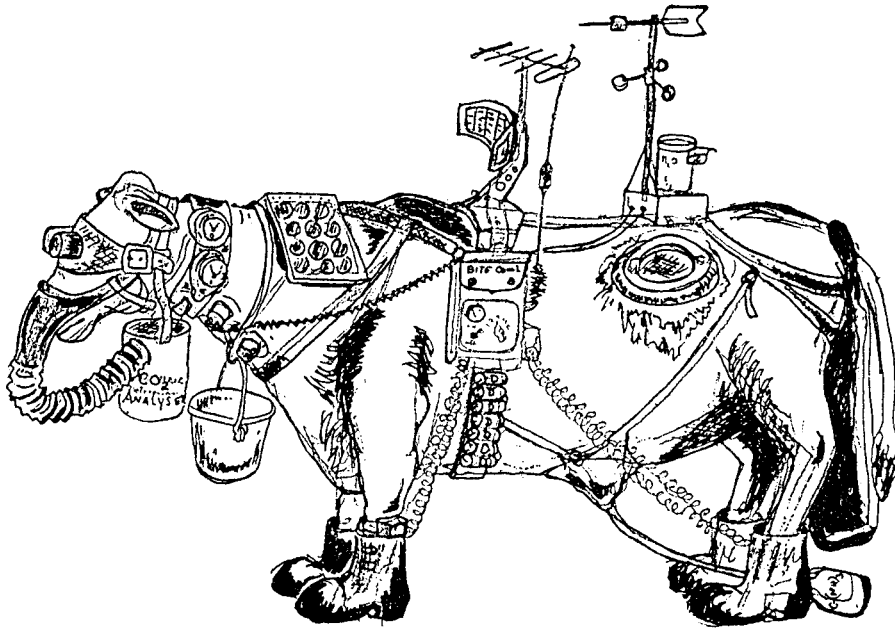
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## IMPORTANCE OF FIELD STUDIES IN STRESS PHYSIOLOGY

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**Key Words:**

Globe temperature, Thermoregulation, Panting, Sweating, Energy expenditure, Cost of locomotion

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## ABSTRACT

Traditionally studies in stress physiology have followed two approaches. In one instance, questions are submitted for examination in climatic chambers where the thermal environment is rigidly controlled and animal responses are precisely monitored. In the other instance, questions are submitted for investigation under naturally-occurring field conditions, where the impact of the "total" environment is evaluated. Although each approach has its shortcomings and limitations, both are needed to provide a better understanding of the complex interactions of weather and climate on animals.

Voluminous data sets have been obtained under laboratory conditions, but relatively few studies have been conducted under natural field conditions. In this review some evidence is presented to question the validity of extrapolating laboratory data to free-ranging animals. Therefore, it is hoped that increased emphasis will be given to studies under natural field conditions in future years. Time is now right for field studies since many physiological responses can be measured simultaneously and continuously under field conditions using available microcomputer data loggers.

Measurement of ambient air temperature alone to assess warmth of the environment, especially under arid land conditions, must be abandoned. Evaluation of the environmental thermal environment must include measurements of air temperature, humidity, wind and radiant heat.

## INTRODUCTION

An animal is never independent of the environment in which it lives. The study of interrelationships of animals and their environment is commonly termed stress or environmental physiology. Historically, two approaches have been used to study the adaptive capacity of animals for meeting the extreme climatic challenges in their surroundings. In the first approach, physiologists have sought to define and reveal the controlling mechanisms of adaptations in laboratories, supposedly simulating natural conditions, in climatic chambers. In the second approach studies are conducted outdoors under complex natural environmental conditions. Both approaches have limitations and shortcomings. Although the climatic chamber studies have yielded much valuable information, extrapolation of these data to natural conditions ignores the fact that all thermal elements of the environment-dry bulb air temperature ( $T_{db}$ ), relative humidity (RH), air movement and thermal radiation - are synergistically influencing the various adaptive responses. Therefore, these four thermal elements must be considered in conjunction, and must all be included in any study of the animal/environment relationships to convey an accurate meaning especially to those interested in free-ranging animals.

This review is not intended to lessen the importance of climatic chamber studies. However, it is confined to some aspects of thermoregulation which have been investigated under both laboratory and natural climatic conditions to demonstrate that extrapolation of the findings from one study approach to another may be inappropriate and perhaps misleading. The natural climatic conditions to be emphasized hereon are limited to arid lands. The thermal environment in arid lands includes momentous radiant heat exchanges, a condition that is quite difficult to simulate under laboratory conditions. Thus, the unfortunate common practice of simulating the thermal environment of arid lands in climatic chambers by increasing  $T_{db}$  is improper and has led to confusion in understanding the avenues of evaporative heat loss in some animals. Additionally, studies in climatic chambers have been done almost exclusively on resting animals, a

situation that seldom mimics the normal daily activities of free-ranging animals.

#### EVALUATION OF THE THERMAL ENVIRONMENT

Except for radiation, other elements of the thermal environment are measured by simple and commonly available instruments; (i)  $T_{db}$  is commonly measured manually using a dry bulb mercury-in-glass thermometer while thermocouples or thermistors are usually used with automated recorders, (ii) RH can be obtained from concurrent wet bulb ( $T_{wb}$ ) and  $T_{db}$  measures, (iii) air movement is measured by using a thermoanemometer, and (iv) radiant heat may be estimated by the Vernon globe (black body) thermometer ( $T_g$ ) which provides a practical and inexpensive means for measuring this component of the environment. Measurement of  $T_g$  provides an indication of the combined effects of radiant energy,  $T_{db}$  and air movement. The theory and physical characteristics of the black body thermometer have been reported by Kuehn et al. (1970). Also the  $T_g$  practical application have been considered in human (Bedford 1946) and animal (Bond and Kelly 1955; Hahn et al. 1961) studies. The conventional  $T_g$  consists of a thermometer with its thermally sensitive element located at the center of a hollow copper sphere about 10 cm in diameter and painted flat black (Fig. 1).

An acceptable single index to describe the four elements of thermal environment is not presently available. However, a few simple indices have been suggested and are summarized in Table 1. Each indice has its advantages and limitations. Studies in arid lands must include a measure of radiant heat in any index to be used for evaluation of the thermal environment. Perhaps the measurement of  $T_g$  in arid lands may provide a better indication of the environmental warmth since it indicates the combined effects of radiant heat,  $T_{db}$  and air velocity. Bond and Kelly (1955) concluded that  $T_g$  offers a practical and inexpensive means of separating, and quantitatively evaluating the radiant energy component of the environment.

#### EVAPORATIVE HEAT LOSS: CLIMATIC ROOMS VS NATURAL ENVIRONMENTS

When animals are faced with an increased environmental heat load, the primary avenue to prevent an explosive rise in body temperature is evaporative water loss (EWL). Cutaneous (sweating and/or moisture diffusion) and/or respiratory (panting) are the two modes used by animals for EWL. Numerous studies have examined the relative importance of cutaneous and respiratory EWL in many animals (Bianca 1968; Robertshaw 1985). Most studies were conducted in climatic rooms and have led to the conclusion that for cattle, sheep and goats, sweating and/or cutaneous moisture diffusion represents a minor component of the total EWL. This established dogma was seriously challenged when studies were conducted under natural climatic conditions. Borut et al. (1979) compared the avenues of EWL of the desert black goat during rest and exercise under both climatic chamber and natural desert conditions (Table 2). It is evident that under laboratory climatic room conditions, total EWL was made up of 65-75% respiratory and 25-35% cutaneous sources. However, when using the same animals and identical techniques under natural desert conditions, the relative importance of respiratory EWL was reduced and the primary avenue for EWL was cutaneous. The importance of sweating as an important route of EWL under natural conditions was confirmed in sheep studied in western Queensland, Australia where the mean monthly maximum temperatures exceed 35°C for 6 mo of the year with high solar radiation loads (Hopkins and Knights 1984). In this study, the Peppin strain Merino had a sweat rate of 219 ml/h (= to 74% of Total EWL), a value that is several times higher than has been reported for sheep under laboratory conditions (Mount 1979; Yousef 1988).



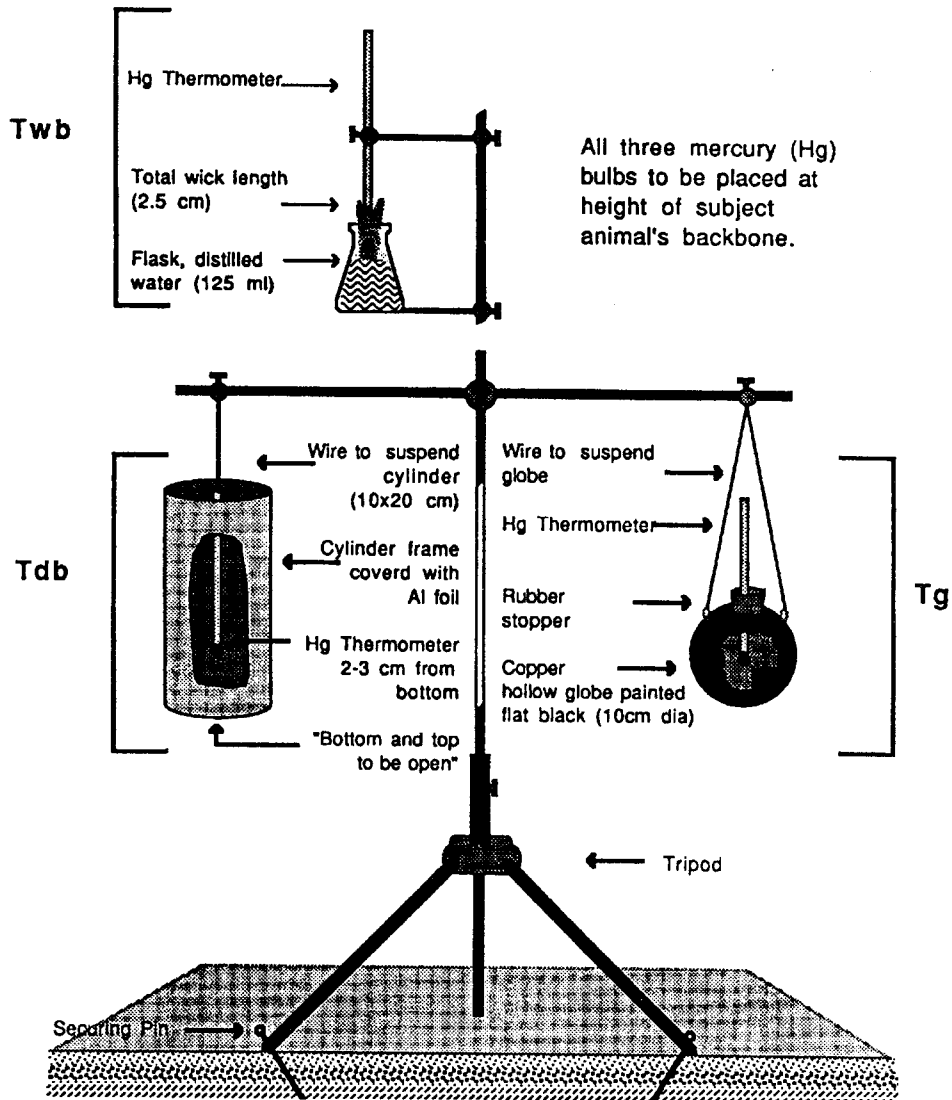


Figure 1. Instrument for measurement of wet bulb globe temperature (WBGT) under field conditions from wet bulb temperature ( $T_{wb}$ ), dry bulb temperature ( $T_{db}$ ) and blackglobe temperature ( $T_g$ ).

In a study on heat balance of a *Bos indicus* cow standing in the sun at noon on the equator, sweating was found to be the major avenue of EWL as shown in Table 3 (Robertshaw and Finch 1976).

Why does the avenue of EWL change when a heat load is imposed in different modes? In other words why does solar radiant heat trigger sweating whereas high  $T_{db}$  stimulate panting? This question was addressed in a study by Dmi'el and Robertshaw (1983) on the desert black goat. Various physiological measurements were made on goats under natural desert conditions and in a climatic chamber where the heat load of both conditions resulted in an equal total EWL. For the same total EWL, there was a higher cutaneous EWL in goats exposed to solar radiation as compared with the climatic room (Table 4).

Table 1. Meteorological indices for measurement of environmental warmth.

Index <sup>a</sup>	Meteorological Measurement <sup>b</sup>	Equations/ Nomograms	Source
THI	T <sub>db</sub> , T <sub>dp</sub>	THI=T <sub>db</sub> + 0.36 T <sub>dp</sub> + 41.2	Thom 1959
WBGT	T <sub>wb</sub> , T <sub>g</sub> <sup>a</sup> , T <sub>db</sub>	WBGT=0.7 T <sub>wb</sub> + 0.2 T <sub>g</sub> <sup>a</sup> + 0.1 T <sub>db</sub>	Minard et al. 1957
BGHI	T <sub>g</sub> , T <sub>dp</sub>	BGHI=T <sub>g</sub> + 0.36 T <sub>dp</sub> + 41.2	Buffington et al. 1981
CET	T <sub>db</sub> , T <sub>wb</sub> , V	Appendix Fig. 1 calculation*	Bedford 1946
ET	T <sub>db</sub> , T <sub>wb</sub>	Appendix Fig. 3	Yaglou 1926

<sup>a</sup>THI = Temp.-humidity index  
 WBGT = Wet bulb globe temp., °C  
 BGHI = Black globe-humidity index  
 CET = Corrected effective temp., °F  
 ET = Effective temp., °C

<sup>b</sup>T<sub>db</sub> = dry bulb temperature, °C, °F  
 T<sub>wb</sub> = wet bulb temp., °C, °F  
 T<sub>dp</sub> = dew-point temp., °C  
 \*T<sub>g</sub><sup>a</sup> = black globe temp., °C, °F  
 V = air movement (wind velocity), kmph  
 T<sub>g</sub><sup>a</sup> can be used to calculate radiant heat as shown in Appendix Fig. 1., °F.

Table 2. Partitioning of mean ± (Standard Error) evaporative water loss (EWL) in desert goats: comparison of climatic room and natural desert conditions (adapted from Borut et al. 1979).

Experiments <sup>a</sup>	Climatic Room		Natural Desert	
	26°C	40°C	Morning <sup>b</sup>	Noon <sup>c</sup>
<b>Rest</b>				
Total EWL	41.9 ± 3.6	86.7 ± 2.7	48.9 ± 6.9	170.3 ± 14.6
Respiratory EWL	29.6 ± 2.7	57.0 ± 3.7	12.5 ± 1.1	56.6 ± 8.3
Cutaneous EWL	12.5 ± 1.1	29.7 ± 4.5	36.4 ± 7.7	113.7 ± 19.3
<b>Walking</b>				
Total EWL	35.8 ± 4.8	94.6 ± 5.8	48.5 ± 5.0	143.1 ± 10.6
Respiratory EWL	20.4 ± 2.4	70.8 ± 9.4	15.4 ± 1.9	45.4 ± 5.0
Cutaneous EWL	15.3 ± 1.2	23.7 ± 3.2	33.1 ± 5.5	98.5 ± 10.9

<sup>a</sup> Values are expressed as % of heat production

<sup>b</sup> T<sub>db</sub> = 26.8°C ± 0.9; RH = 54.5% ± 0.7; total radiation = 12.0 Kcal/m<sup>2</sup>-h ± 3.1.

<sup>c</sup> T<sub>db</sub> = 35.7°C ± 2.2; RH = 24.5% ± 0.9; total radiation = 486 Kcal/m<sup>2</sup>-h ± 62.

Under natural conditions, the greater rise in dorsal skin temperature resulted in preponderate sweating, whereas in the climatic chamber, the higher hypothalamic temperature led predominantly to panting. In other words, the mode of evaporation seems to be appropriate to the thermal stimulus: higher blood temperature evoked panting, and higher skin temperature resulted in a predominant sweating.

Table 3. Heat balance of *Bos indicus* measured in equatorial noon sun (adapted from Robertshaw and Finch 1976).

Partition of heat balance	Heat exchanges, $Wm^{-2}$
Gain	
Metabolic heat	50.7
Radiant heat	638.0
Loss	
Non-evaporative	470.6
Sweating	146.2
Panting	36.1

$Wm^{-2}$  = Watts/ $m^2$

#### SWEATING AND NUTRITIONAL STATUS OF FREE-RANGING ANIMALS

In arid lands free-ranging animals are daily exposed for many hours to high levels of radiant heat, thus, it is expected that these animals may lose a volume of sweat to prevent an explosive rise in body temperature. If the solids in sweat contain protein and/or electrolytes in measurable quantities, then such losses must be considered in the nutritional status of these animals. Unfortunately, very little data are available on sweat composition of various large animals (Joshi et al. 1968; Jenkinson et al. 1974). Considering the limited available data, protein and phosphorus losses in sweat were calculated by Hutchinson (1977) for a grazing black Boran cow (*Bos indicus*), weighing 380 kg during the end of the hot dry season in the semi-arid region of Australia (Table 5).

The calculation presented in Table 5 clearly demonstrates that enough protein is lost in sweat to be considered important. This loss would be insignificant under good pastoral conditions. However, in arid-lands, low crude protein values are typical in forage plants during the dry season (Conrad et al. 1982). Therefore, with little protein digested and high loss of protein in sweat, grazing animals would lose weight during the dry season.

These calculations are based on little available data, thus their validity should be tested in future experimental work. Future research is necessary to establish the role of sweating on the nutritional status of grazing animals.

#### LESSONS FROM STUDIES UNDER NATURAL CLIMATIC CONDITIONS

The thermal environment in arid lands involves significant radiant heat exchanges which impinge a heat load on animals that can reach up to 9 to 12 times that of the normal metabolic rate (Table 3). Under these conditions, it is possible that sweating and not panting becomes the predominant avenue for EWL,

thus contributing to the possible loss of large amounts of proteins and electrolytes. To alleviate the intensity of radiant heat under natural conditions, provision of shade is recommended. A practical approach would be to emphasize planting of native trees and/or shrubs in areas where free-ranging animals graze. Studies on behavioral thermoregulation clearly document that shade seeking behavior is a feature of heat stressed animals (Ingram and Dauncey 1985).

Table 4. Effects of exposure to solar radiation and high ambient air temperature on mean evaporative water loss and various mean body temperatures of desert goats (adapted from Dmi'el and Robertshaw 1983).

Physiological Measurement	Heat Load	
	46°C (Climatic room)	30°C + Solar radiation (Natural desert)
Evaporative Water Loss		
Total (g/m <sup>2</sup> -hr)	288 ± 16	285 ± 17
Cutaneous	144 ± 18	193 ± 18
Respiratory	144 ± 16	92 ± 17
Temperature (°C)		
Dorsal skin	39.4 ± 0.2	40.1 ± 0.5
Arterial blood	39.6 ± 0.1	39.0 ± 0.1
Hypothalamic	39.3 ± 0.2	38.8 ± 0.1

± Standard deviation

Table 5. Sweat production together with protein and phosphorus losses in a 24 hr sweat from an animal grazing the semi-arid region of Australia.

Parameters	Calculated Values
Sweat (g/m <sup>2</sup> -24 hr)	
Sweat production	2,128.00
Protein (a)	3.40
Phosphorus (b)	0.32
Digestible protein	10.00
Sweat Protein (%)	
Digestible	34.60

(a) Protein concentration taken from Jenkinson et al. 1974.

(b) Phosphorus estimate from Joshi et al. 1968.

### HEAT PRODUCTION: LABORATORY VS NATURAL STUDIES

Resting and/or standing rate of oxygen consumption,  $VO_2$ , as an indirect measurement of metabolic heat production has been measured on various domestic and wild animals (Yousef 1988). Heat balance studies in the laboratory have been carried out almost exclusively on resting animals. The validity of such experimental data for free-range animals living under natural conditions is questionable at best since these animals spend a significant part of their time in unrestrained activities.

Grazing and walking locomotion occupies from 30 to more than 50% of cattle's 24 h day (Anderson and Kothmann 1980; Boyd et al. 1989). Distance livestock travel is influenced by many factors including the thermal environment, availability of food and water and the physiological state of the animal. The energy cost for this movement varies and very few studies have examined the energy cost of these activities under natural field conditions (Yousef and Maloiy 1985). These data are necessary for calculation of the daily nutritional requirements of free-range animals. Fancy and White (1985) using published data from various sources estimated the daily cost of locomotion as a percent of standard fasting metabolic rate (Table 6). It is evident that the total daily locomotion costs for animals are largely independent of body weight but are strongly dependent on the distance traveled. Although these calculated values do not take into consideration such factors as terrain surfaces, and walking uphill, they clearly make-up a substantial component of the total daily energy expenditure.

Most available data on the energy cost of locomotion in various ungulates were obtained from animals walking on treadmills under laboratory (Taylor et al. 1982) or natural (Borut et al. 1979) conditions. The extrapolation of laboratory data to predict the energy cost of walking under natural conditions must be made with extreme caution. Data obtained from animals walking under natural conditions showed the energy cost of walking on different terrains at the same work rate not to be the same (Fig. 2) (White and Yousef 1978; Fancy and White 1987). Energy cost of locomotion when animals move on soft surfaces such as snow and/or tundra is much higher than when they move on hard packed surfaces. Moreover, the predicted values for cost of locomotion from the interspecies equation developed by Taylor et al. (1982) in several large mammals are significantly higher than the actual measured values for some animals, i.e. the donkey (Yousef and Dill 1969), the camel (Yousef et al. 1989), the barren-ground caribou (Fancy and White 1987), and the wildebeest (Taylor et al. 1982). The measurements of energetic cost of walking in the donkey (burro) and camel are compared to that of man in Fig. 3 when the three species walked side-by-side at the same rate and under the same natural conditions (Yousef et al. 1972, 1989).

The low energy cost of locomotion for some animals suggests that selection for locomotion efficiency may have occurred as an adaptive mechanism for survival in harsh environments where food and water availability are unpredictable or where long migrations are undertaken.

There is an obvious need to develop a practical and easy method for measuring energy cost of locomotion for various free-ranging animals. Moreover, studies are needed to consider the effects of additional factors on muscular efficiency of these animals, such as age, sex, nutritional planes and climatic conditions. Without such data, the total daily energy requirement for these animals will remain poorly quantified.

Table 6. Calculation of daily cost of locomotion as a percent of standard fasting metabolic rate (SMR) for animals of different body weights traveling different distances (adapted from Fancy and White 1985; p. 156).

Body Weight Kg	Locomotion <sup>a</sup>	
	Distance Km/day	Energy Cost % of SMR
50	5	23
	10	45
	15	68
100	5	22
	10	43
	15	65
200	5	21
	10	42
	15	62

<sup>a</sup> Calculations were made assuming a mean walking speed of 3.6 Km/hr.

#### CONCLUSIONS

The limited available literature is testimony to the many gaps in our basic knowledge on stress physiology of free-ranging animals in arid lands. Studies on heat-balance under natural climatic conditions suggest that extrapolation of findings documented under climatic chamber conditions may be misleading. Investigators must abandon the use of  $T_{db}$  as a measure of environmental heat load. Measurement of radiant heat load must be given first priority in evaluation of the thermal environment. Accurate measurements of the relative importance of panting and sweating and the energy cost of locomotion in free-ranging animals remain largely unknown. The question of whether or not sweat losses of proteins and electrolytes are important enough to affect the nutritional status of free-ranging animals must be addressed to better assess the optimum productivity of these animals, especially those grazing on marginal pastures. The practical importance of shade planting of native trees and shrubs should be considered to reduce the intensity of radiant heat.

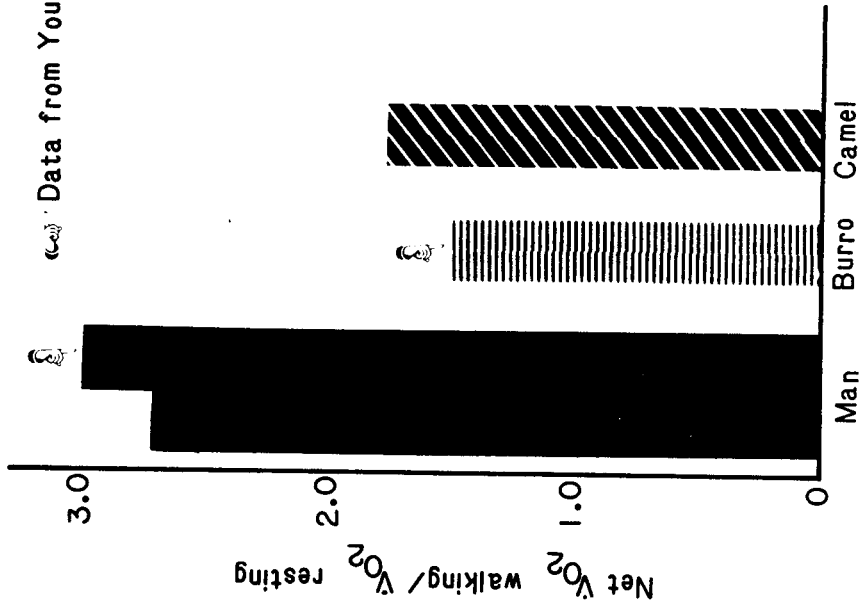


Figure 3. The energy cost of locomotion (Net VO<sub>2</sub>) for man as compared to the donkey and camel walking side-by-side in two different studies (adapted from Yousef et al. 1972; 1989).

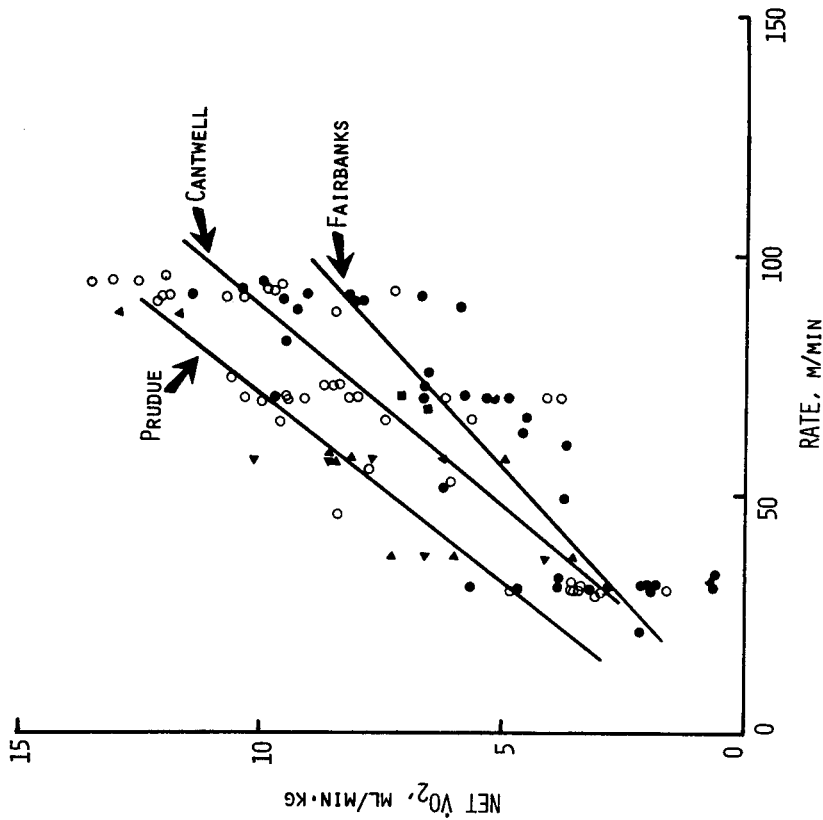
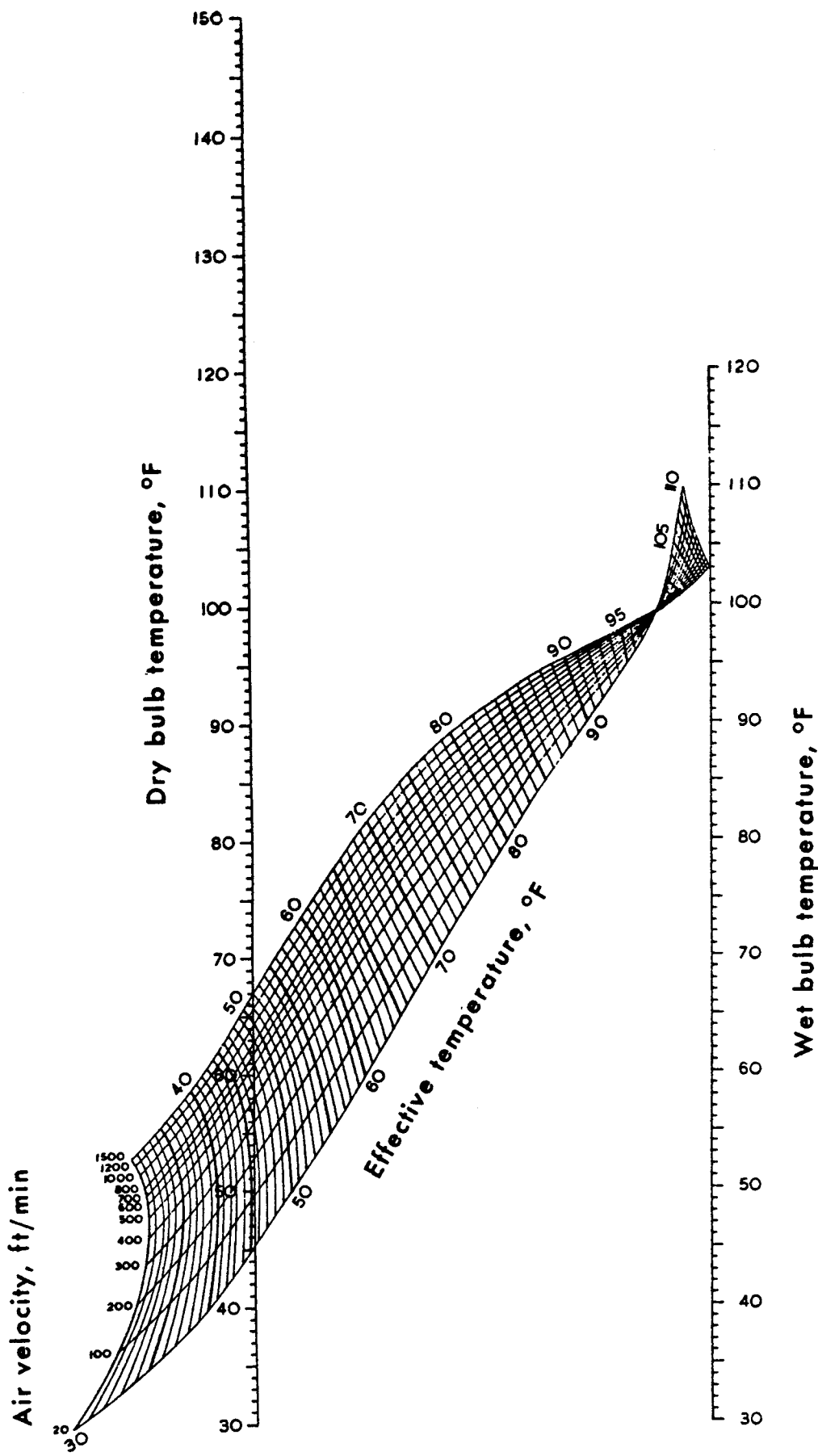


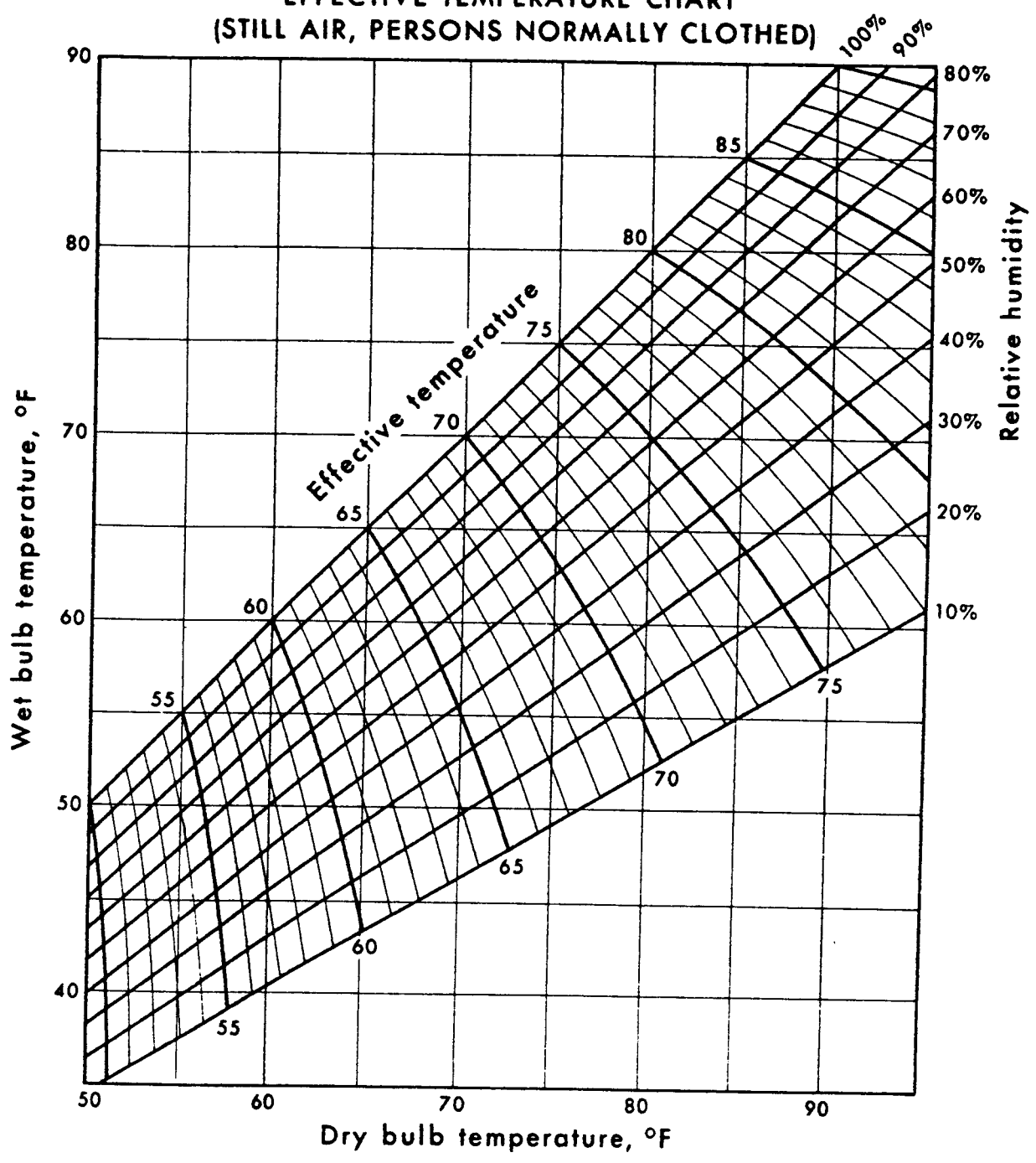
Figure 2. Energy cost of locomotion (Net VO<sub>2</sub>) for reindeer as influenced by rate of walking on various terrain surfaces in Alaska. Prudue Bay represents wet tundra, Cantwell represents dry tundra and Fairbanks represent hard-surfaced roads (adapted from White and Yousef 1978).



Appendix Fig. 2. Nomogram for determining corrected effective temperature (CET).



**EFFECTIVE TEMPERATURE CHART  
(STILL AIR, PERSONS NORMALLY CLOTHED)**



Appendix Fig. 3. Nomogram for estimating effective temperature (ET).

#### **ACKNOWLEDGEMENTS**

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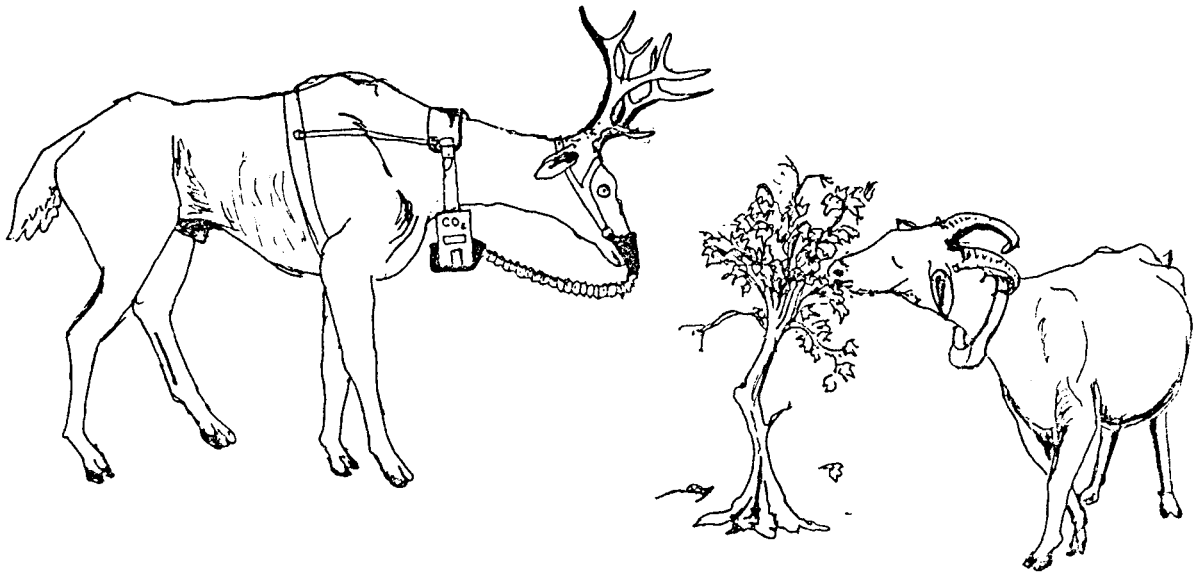
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**ASSESSMENT OF ENERGETIC STRESS IN FREE-RANGING UNGULATES:  
A BRIEF REVIEW**

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**Key Words:**

Foraging efficiency, Locomotion, *Odocoileus*, Standard operative temperature, Thermoregulation

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## ABSTRACT

Stress is limited to conditions in which an animal's energy losses exceed its energy gains. Recent advances in the determination of energetic constraints and requirements of wild ungulates are reviewed.

## INTRODUCTION

The concept of stress will be limited in this discussion to the energetic constraints that affect activity patterns and foraging strategies. Hence, it may, but not necessarily, be a relatively short-lived phenomenon that does not affect milk or meat production, the overall population, or even animal fitness in terms of reproduction. An animal is considered stressed if its energy losses exceed its energy gains, and the energy balance is, therefore, negative. Although energy may not be a limiting factor during all seasons of the year, it is of particular importance in the survival of many ungulates during adverse conditions especially in winter. Deep snowpack may raise locomotory costs substantially, thermoregulatory expenditures may increase below critical temperatures, and forage quality and quantity are often reduced. To assess the magnitude of energetic demands, the costs of the individual components must be analyzed in controlled experiments with captive animals. These results provide some insight into why animals use their environment as they do. Free-ranging animals, however, use a trade-off process of perceived costs and benefits, relating to energetic requirements, behavioral preferences, and food resources. Following a free-ranging animal in its daily routine enables an investigator to better understand these interactions. In this paper the objective is to present an overview of the recent advances in quantifying energy expenditures and energy intake for wild ungulates and to briefly introduce a current study that is evaluating foraging efficiency and energetic stress in free-ranging black-tailed deer (*Odocoileus hemionus sitkensis*). Therefore, most of the examples are limited to deer.

## ENERGY EXPENDITURES FOR ACTIVITY

Energy costs for specific activities, when combined with field observations of animal behavior, greatly improve our understanding of the ecology of wild ungulates (Fancy and White 1985). Most studies of energy expenditure have emphasized locomotion because it is the most costly activity. These expenditures depend on the animal's speed of travel, slope steepness, and surface substrate. Metabolic costs of horizontal locomotion by mule deer (*Odocoileus hemionus hemionus*) on bare ground are not different from interspecific regressions for other species (Parker et al. 1984; Fancy and White 1985). Expenditures by cervids increase linearly as a function of speed (Fig. 1).

The net cost, or energy expended per kg per km, declines exponentially with increasing body size. It costs relatively more for a smaller animal to travel a km than it does for a larger animal (Fig. 2). Compared to horizontal costs, energy expenditures are greater for upslope travel and less for downhill movement (Parker et al. 1984). In general, wild ungulates tend to have lower net costs of walking than do domestic animals (Fancy and White 1985).

Metabolic costs of transport are even higher for wild ungulates moving across soft surfaces such as wet tundra (White and Yousef 1977) or travelling through snow (Parker et al. 1984; Fancy and White 1987). Energy expenditures for walking in snow by deer (*O. hemionus*, *O. virginianus*), elk (*Cervus elaphus*), and caribou (*Rangifer tarandus*) increase exponentially with sinking depth (Mattfeld 1974; Parker et al. 1984; Fancy and White 1987) (Fig. 3).

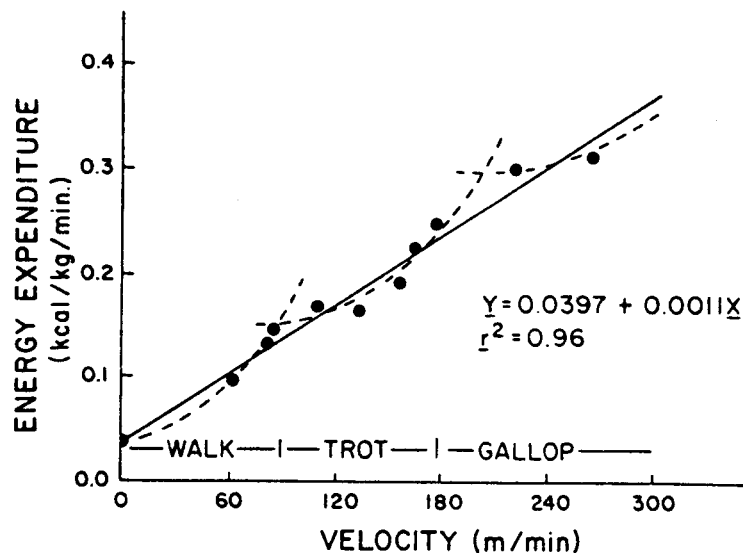


Figure 1. The energy cost of different gaits for a 42-kg elk calf (From Parker et al. 1984).

Metabolic rates are much greater in dense than light snows and may exceed eight times the costs of walking on bare ground when snow depths are equal to the animal's brisket height (Parker et al. 1984). Energy expenditures further increase when sinking depths are greater than brisket height and animals resort to exaggerated bounding gaits or when the snow pack is very crusted (Fancy and White 1987).

Estimates of energy costs for other daily activities have also been determined for wild ungulates and extrapolated to energy budgets of deer. The incremental cost of standing over lying averages 20%, which is much higher than the 9% reported for cattle and sheep, and may be attributed in part to a greater level of alertness in wild ungulates (Fancy and White 1985). The energy cost of eating over standing is approximately 26% (Wickstrom et al. 1984) and rumination costs are 2% of lying costs (Fancy and White 1985).

#### ENERGETIC COSTS OF THERMOREGULATION

Adaptive physiological mechanisms that allow wild ungulates to cope with climatic stress have been identified for a variety of wild ungulates (Parker and Robbins 1985). The importance of thermal constraints in modifying or determining activity patterns and habitat selection is recognized in the management concept of thermal cover (Black et al. 1976; Bunnell et al. 1986). Thermoregulation is an animal's ability to regulate body temperature within acceptable limits despite large variations in ambient conditions. Beyond upper and lower limits of a range of thermoneutral temperatures, metabolic rate is elevated and associated with thermal stress.

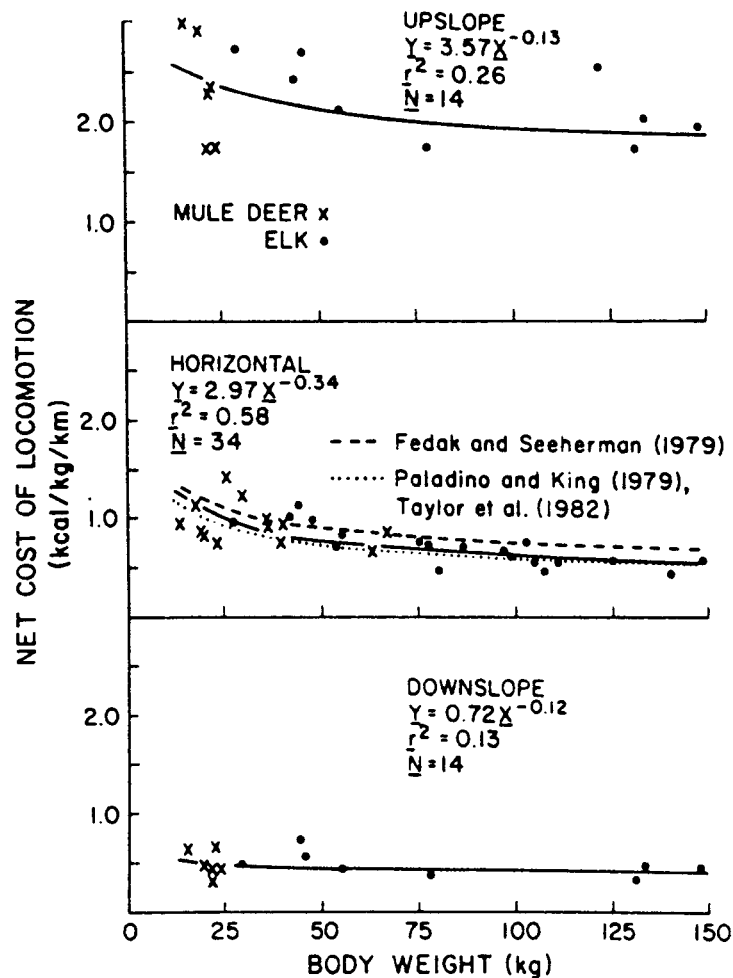


Figure 2. The net cost of upslope, horizontal, and downslope locomotion as a function of body weight for mule deer and elk. Energy expenditures for horizontal movement are compared with interspecific regressions for birds, mammals and lizards (Fedak and Seeherman 1979; Paladino and King 1979; Taylor et al. 1982). The lines generated from the two latter equations are not discernibly different and are, therefore, represented by one line (From Parker et al. 1984).

Most commonly, air temperature alone has been used to describe the thermal environment encountered by free-ranging animals. Standard operative temperature ( $T_{es}$ ; Campbell 1977; Bakken 1980; 1981), however, more appropriately describes the effective environment experienced by animals outdoors and integrates the effects of air temperature, wind speed, and incident radiation into a single variable. An animal's metabolic response to a given  $T_{es}$  is the same irrespective of habitat. Energetic requirements and the limits of thermoneutrality have been determined using indirect calorimetry for mule deer outdoors and directly related to simultaneous micrometeorological measurements (Parker and Robbins 1984) (Fig. 4).



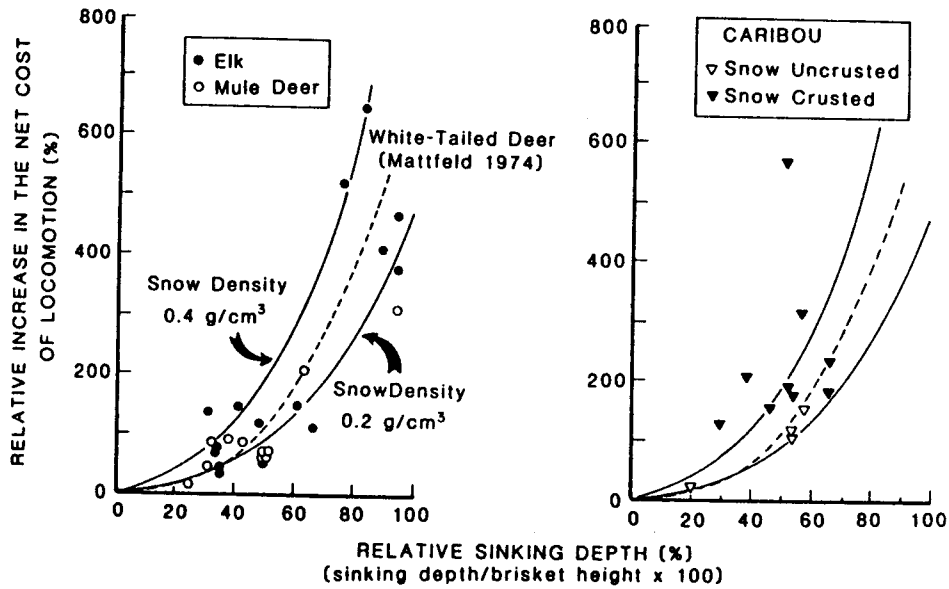


Figure 3. The relative increase in the net cost of locomotion with increasing sinking depth in snow. The effect of increasing snow density on the cost of walking is shown in the left figure (Parker et al. 1984); the effect of a snow crust which does not support the animal's weight is shown in the right figure (Fancy and White 1987).

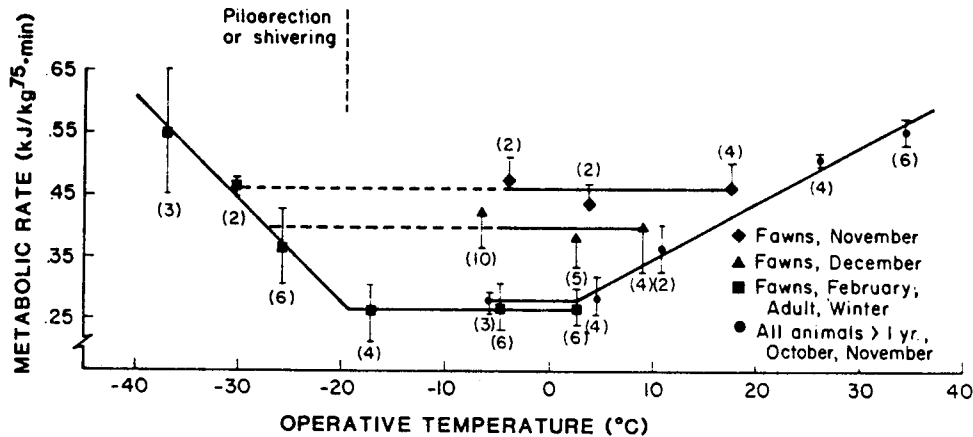


Figure 4. Energy expenditure of standing in winter as a function of operative temperature for mule deer. Lower critical temperature is  $-19^{\circ}\text{C}$  for adult animals; upper critical temperature is  $+2.5^{\circ}\text{C}$ . Values in parentheses are number of samples (From Parker and Robbins 1984).

As a means of comparing the thermoregulatory value of different habitats for deer, a model has been developed to estimate critical thermal environments based on  $T_{es}$  and metabolic responses for habitat-specific weather variables (Parker and Gillingham 1990) (e.g., Fig. 5). In general, high solar radiation levels with minimal wind raise operative temperatures  $10^{\circ}\text{C}$  above air temperature in winter; under snow conditions with high solar reflectance or in summer when incident solar levels may be twice as high as in winter, standard operative temperatures approach  $30^{\circ}\text{C}$  warmer than air temperature. High wind speeds (15 m/s), however, can eliminate most of the thermal effects of maximum solar levels and decrease the width of the thermoneutral zone for deer by  $10^{\circ}\text{C}$ . Therefore, the use of air temperature alone to describe the thermal environment as experienced by an animal has minimal utility in assessing whether an animal is stressed from a thermoregulatory standpoint.

In coastal areas where major snow events and temperature extremes are rare, rainfall may increase thermoregulatory costs for deer at temperatures just above freezing in winter (Parker 1988). Of even greater importance is the elevation in metabolic rate induced by rainfall at temperatures less than  $10^{\circ}\text{C}$  in summer; thermoregulatory expenditures after 5 h in moderate rainfall are greater than during heat or cold stress (Fig. 6).

### ENERGY INTAKE

A knowledge of the efficiency with which an animal harvests a food resource and extracts energy from its environment is vital to our understanding of the significance of foraging in the life strategy of wild ungulates (Wickstrom et al. 1984). Energy intake by *Odocoileus* is determined by dietary composition and total intake of dry matter. The digestibility of the forage has a profound effect on the amount of grazing time that is necessary to meet minimum energy requirements (Wickstrom et al. 1984). Dry matter intake is in turn affected by gut fill, rumen turnover rate (Spalinger et al. 1986; Baker and Hobbs 1987), and ingestion rate. Intake rates by deer are an asymptotic function of food biomass with the asymptote occurring at relatively low levels of biomass (Wickstrom et al. 1984; Spalinger et al. 1988). Because the effects on net energy assimilation are greatest when forage biomass and digestibility are low, winter is a critical time relative to energy balance for wild ungulates. Relationships between forage quality/quantity and energy intake/expenditure have been compiled by Hanley et al. (1989).

### FORAGING EFFICIENCY: A FIELD TEST

Currently, we<sup>2</sup> are evaluating the concept of foraging efficiency (energy intake relative to energy expenditure) in black-tailed deer. Particular interest is given to the concept of whether energy is the most limiting nutritional factor for deer and whether animals maximize foraging efficiency year-round or only when they are energetically stressed.

Data on activity patterns and forage intake are monitored intensively. Energy budgets are calculated from observed activities and extrapolated to the rest of the 24-h period using telemetry data. Precise estimates of energy expenditures

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<sup>2</sup>The study is a cooperative effort by K.L. Parker, M.P. Gillingham, T.A. Hanley, C.T. Robbins, and D.E. Spalinger. It is being funded by the U.S.D.A. Forest Service Pacific Northwest Research Station in cooperation with Washington State University.

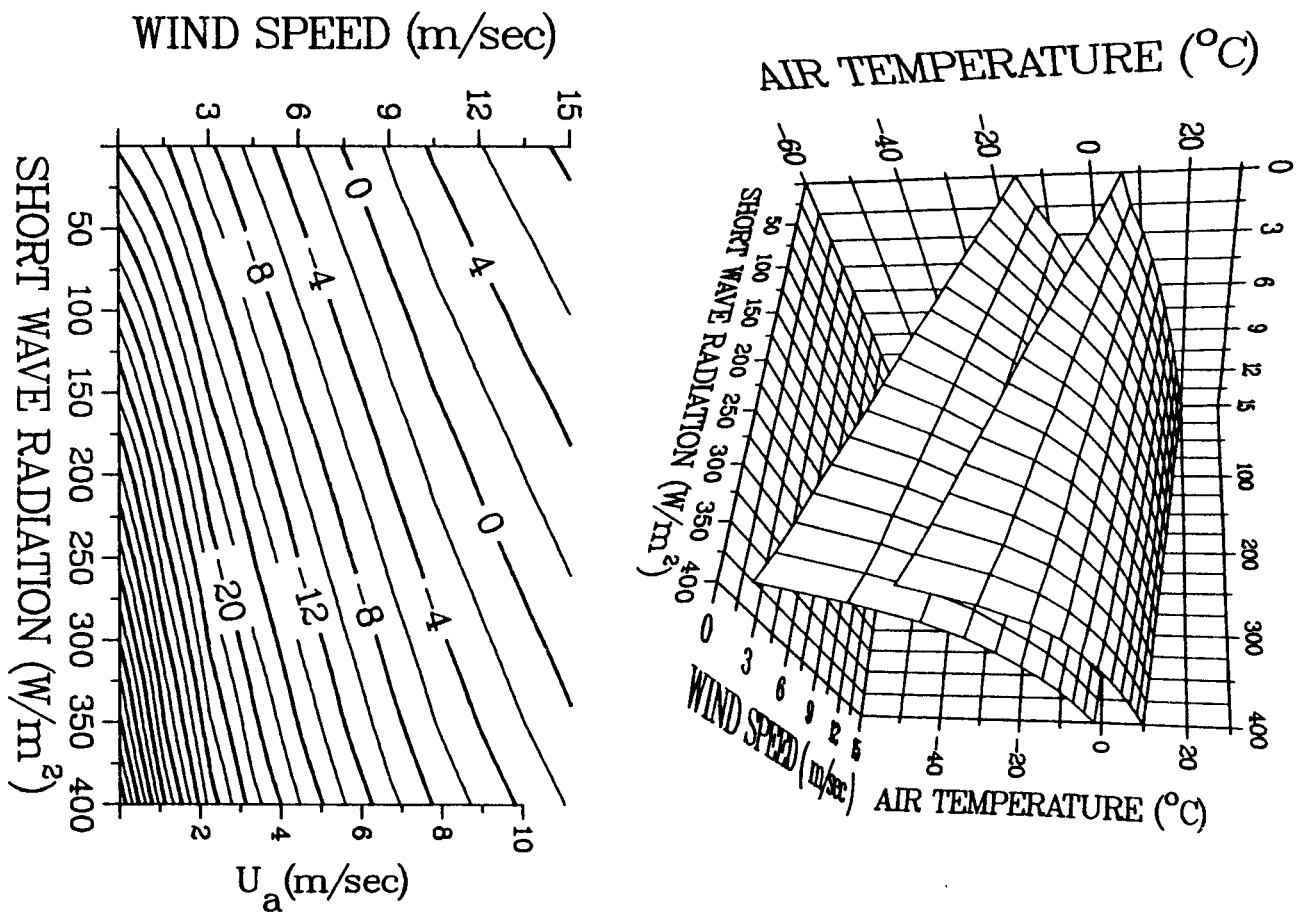


Figure 5. The upper figure shows three-dimensional surfaces of predicted upper ( $T_{es} = 2.5^{\circ}\text{C}$ ) and lower ( $T_{es} = -19^{\circ}\text{C}$ ) thermally critical environments for full-fed, adult mule deer standing in snow-covered, open habitats in winter. For any environmental conditions above or below these critical limits, the animal is thermally stressed. (From Parker and Gillingham 1989). The lower figure shows the temperature clines, which in combination with short-wave radiative input and wind speed ( $u_a$  = wind speed at animal height), result in a lower critical temperature ( $T_{es} = -19^{\circ}\text{C}$ ) for mule deer in winter.

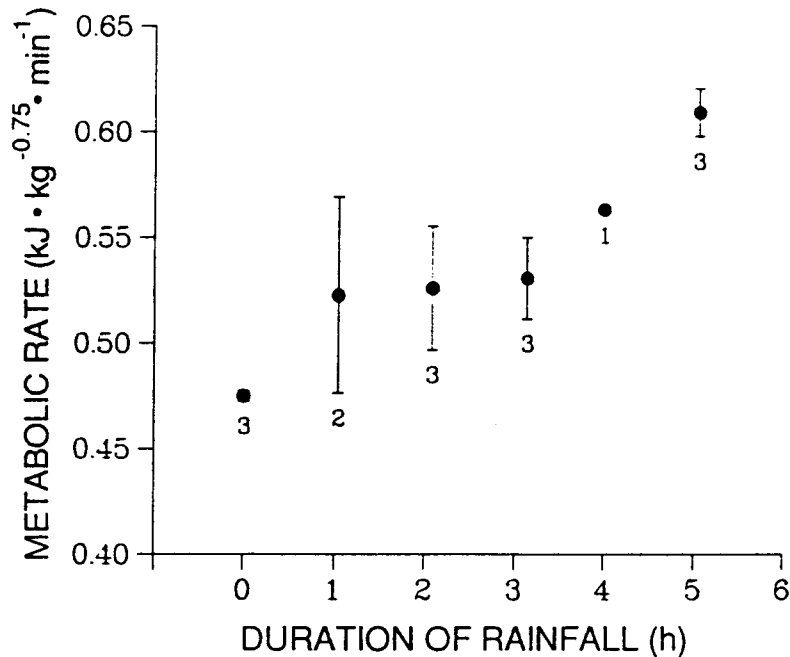


Figure 6. Metabolic rate ( $\pm$  Standard Error) of standing relative to duration of rainfall (4.5 mm/h) for a yearling black-tailed deer in summer at 10°C. Sample sizes are shown (From Parker 1988).

are determined using the doubly-labeled water technique with oxygen-18 and tritiated water (Lifson and McClintock 1966). Isotopically-labeled water, although very expensive when working with large animals, is currently the only available method for directly determining energy expenditures of free-ranging animals (Nagy 1983; Fancy et al. 1986). Both isotopes are lost from the body via water; oxygen is also removed via respiratory CO<sub>2</sub>. The difference in the fractional turnover rates of oxygen and hydrogen is a measure of the rate of CO<sub>2</sub> production, thereby enabling a calculation of O<sub>2</sub> consumption and energy expenditure. Body condition of all animals is monitored using tritium estimates of body water (Holleman et al. 1982) and calculations of body fat (Robbins et al. 1974; Torbit et al. 1985). This index tracks the contribution of the animal's body reserves to its overall energy balance.

The study has been designed to test several hypotheses about foraging energetics and energetic balance in free-ranging deer. Additionally, data from this study will be used to determine if and when animals are energetically-stressed relative to body weight changes, body condition, calculations of net energy based on forage intake and activity budgets, and precise estimates of energy expenditure using doubly-labeled water. They will provide insight into the strategies that individual animals employ for survival and contribute to models that predict the implications of those responses for deer populations (Hobbs 1989).

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HOW THE FORMULA WORKS

IN 1983, THE PUBLIC LAND GRAZING FEE WILL DROP \$0.46, FROM \$1.86 TO \$1.40 PER AUM. THE REASON FOR THE DECLINE IS A DROP IN THE PRIVATE GRAZING LAND LEASE RATE FROM \$8.83 TO \$8.36 (WHICH DECREASED THE FORAGE VALUE INDEX FROM 242 TO 229) AND A DECREASE IN THE COMBINED INDEX. BEEF CATTLE PRICES DECREASED FROM \$59.10 TO \$57.70 PER HUNDRED POUNDS, CHANGING THE BEEF CATTLE PRICE INDEX FROM 268 TO 262. THE INDEX FOR PRICES PAID TO PRODUCE BEEF INCREASED FROM 359 TO 378.

THE 1982 GRAZING FEE WAS DERIVED BY INSERTING THESE NUMBERS INTO THE PRIA FORMULA AND COMPARING IT WITH THE 25 PERCENT LIMIT ON AN INCREASE OR DECREASE:

$$\text{ECONOMIC VALUE} = \$1.23 \times \frac{229 + (262 - 378)}{100} = \$1.23 \times 1.13 = \$1.39$$

THE MAXIMUM 25 PERCENT DECREASE IN THE FEE WOULD RESULT IN A FEE OF \$1.40 ( $\$1.86 \times .75 = \$1.40$ ). SINCE, THE 25 PERCENT LIMIT IS EXCEEDED BY THE \$1.39 DETERMINED BY THE FORMULA, THE NEW FEE IS \$1.40.

HOW GRAZING FEES ARE COMPUTED:

THE PRIA (PUBLIC RANGELANDS IMPROVEMENT ACT) FORMULA

GRAZING FEES FOR USE OF PUBLIC LANDS ADMINISTERED BY THE FOREST SERVICE AND THE BUREAU OF LAND MANAGEMENT (BLM) IN THE 16 WESTERN STATES ARE COMPUTED ANNUALLY USING THE TRIAL FEE FORMULA ESTABLISHED BY CONGRESS IN THE PUBLIC RANGELANDS IMPROVEMENT ACT (PRIA) OF 1978. THE PRIA FORMULA IS:

$$\text{ECONOMIC VALUE} = \$1.23 \times \frac{\text{FVI} + (\text{BPI} - \text{PPI})}{100}$$

WHERE:

ECONOMIC VALUE = THE FEE TO BE CHARGED, WHICH REPRESENTS THE ECONOMIC VALUE OF THE USE OF THE LAND TO THE USER, AND WHERE ANNUAL INCREASES OR DECREASES IN THE FEE ARE LIMITED TO PLUS OR MINUS 25 PERCENT OF THE PREVIOUS YEAR'S FEE.

\$1.23 = THE BASE FAIR MARKET VALUE ESTABLISHED BY THE 1966 WESTERN LIVESTOCK SURVEY.

FVI = FORAGE VALUE INDEX

BPI = BEEF PRICE INDEX

PPI = PRICES PAID INDEX