The Energy Expenditure of Heifers Grazing Crested Wheatgrass Rangeland in West-Central Utah

Kris M. Havstad
Utah State University

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THE ENERGY EXPENDITURE OF HEIFERS
GRAZING CRESTED WHEATGRASS
RANGELAND IN WEST-CENTRAL UTAH

by

Kris Mark Havstad

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
Doctor of Philosophy
in
Range Science

Approved:

UTAH STATE UNIVERSITY
Logan, Utah
1981
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Kris Mark Havstad
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The free-roaming ruminant requires energy for the demands of grazing, traveling and thermoregulation that are not required by its confined counterpart. Literature estimates of these additional costs range from 10 to 170 percent above maintenance. The uncertain magnitude of this increased demand and the factors that contribute to it impede the ability of the rangeland ruminant nutritionist to establish guidelines for the energy requirements of the free-roaming herbivore. This study was designed to estimate the energy expenditure of yearling Angus heifers while grazing a declining supply of available crested wheatgrass forage (*Agropyron cristatum*) on rangeland in west-central Utah.
Free-ranging energy expenditure was estimated twice for four heifers during each of five ten-day periods during June, July August and early September, 1979. These estimates were obtained using the carbon dioxide entry rate technique. In addition, total fecal output, dietary crude protein and dietary in vitro organic matter digestibility were estimated for animals grazing the 20-hectare crested wheatgrass pasture. From these data, daily forage intake was calculated. The level of available forage during each period was estimated using the ocular weight-estimate technique applied on forty 1 m$^2$ circular plots.

Energy expenditure was estimated as 161 (with a confidence interval of ±43) kcal·kg body weight$^{-0.75}$·d$^{-1}$ (n=10), and was independent of the decline in available forage from 880 to 284 kg dry matter·hectare$^{-1}$ that occurred over the course of the grazing season. Daily intake was 54.5 grams (organic matter basis) per unit body weight$^{0.75}$ for the 305 kg heifers. Daily intake was independent of the supply of available forage.

During early July, 1980, crested wheatgrass was harvested as hay and fed to 260 kg yearling Angus heifers in metabolism stalls in a thermoneutral and constantly illuminated laboratory. Daily feeding levels were set at 54.5 grams (organic matter basis) per unit body weight$^{0.75}$. Energy expenditure under these conditions was estimated as 111 (±12) kcal·kg body weight$^{0.75}$·day$^{-1}$, 6 kcal per unit body weight$^{0.75}$ greater than the mean estimate of the fasting metabolism rate. The latter estimate was obtained following a
48-hour fast. These estimates of maintenance and fasting metabolism were combined to provide a mean estimate of 110 (±10) kcal·kg body weight\(^{-0.75}\)·day\(^{-1}\) (n=14).

Of the 45 percent (51 kcal·kg body weight\(^{-0.75}\)·day\(^{-1}\)) increase in the estimated energy expenditures by heifers under free-roaming conditions, 50 percent was attributed to the energetic cost of grazing. A daily average 9.2 hours were spent in this activity. The energetic cost of grazing was assumed as 0.82 kcal·kg body weight\(^{-1}\)·hour\(^{-1}\) spent grazing. Daily travel was estimated as 3.9 km at an assumed energetic cost of 0.58 kcal·kg body weight\(^{-1}\)·km\(^{-1}\). This accounted for a 20 percent estimated increase in energy expenditure. Average daily temperatures were generally between 12°C and 30°C and thermoregulatory demands were not considered as a substantial energetic expense. The remaining 30 percent (12 kcal) of the additional increment due to free-roaming conditions could not be explained.
STATEMENT OF THE PROBLEM

Introduction

The productive performance of domestic livestock is dependent upon the flow of nutrients from the feed to the animal and the prevailing efficiency with which those nutrients are utilized. Typically, the classical approach to animal nutrition has been to determine both the nutrient content of the feed and the animal's requirements, and supplement this flow with nutrients that are deficient (Harris 1968). The plethora of information on nutritional quality of feeds and nutritional requirements of domestic livestock allow this classical approach to be a successful one when managing the needs of housed or confined livestock.

The productive performance of domestic livestock on rangelands is also dependent on the flow of nutrients from the feed source to the animal. Yet, the complex interactions between the grazing animal and its forage resource is poorly understood (Rittenhouse and Vavra 1979). The variability of the grazing animal's requirements and the variability of the diet it selects severely restricts the classical approach in analyzing nutritional needs and solving nutritional deficits (Harris 1968). It becomes necessary to study the interactions between the plant resource and the free-ranging animal so that the mechanisms which generate the animal's response can be understood (McDonald 1968).
Much of the research in the range animal nutrition field of study has been devoted to developing techniques applicable to investigation of these interactions. Use of these varied methodologies has provided some insight into this plant-animal interface. Application of this understanding then becomes the rangeland approach to animal nutrition, an approach that is still probably as much an art as it is a science.

Delineation of the Problem

The nutrient requirements of animals include varying proportions of proteins, minerals, vitamins and nutrients which supply energy. Of this diverse group, those components which supply energy represent the category of nutrients required in the largest amounts (Knox 1967). Satisfying these energy needs of the confined animal is the basis for all ruminant feeding standards (Church and Pond 1974). Energy is required for the processes of maintenance, growth, lactation and reproduction. For the growing heifer these processes will demand an estimated daily intake of 5.2 Mcal for the net energy of maintenance (NEₘ) (NRC 1976). Any significant reduction in this level of energy intake can reduce performance.

The range animal requires additional energy inputs to meet the demands of grazing, traveling and thermoregulation. For example, 40 percent of the energy expended by grazing sheep has been attributed to the activities of standing, walking, ruminating and eating as compared to 10 percent for a housed animal (Graham 1964). Young
(1975) reported a 15 percent increase in maintenance energy requirements when previously confined cattle were confined outdoors where the ambient temperature was 17°C. There was an additional 12 percent increase when the ambient temperature declined to 12°C. There may be a 10 percent increase in the energy expended by sheep while grazing (Graham 1964), and a 2 percent increase for each hour of grazing by cattle (Holmes et al. 1978). Moderate activity by pronghorn antelope increased energy expenditure by 58 percent over maintenance levels (Wesley 1971). In the final analysis, fulfilling these additional demands upon the range animal may require an increase of 10 percent to 270 percent in the daily intake of metabolizable energy above that required by a housed counterpart (Young and Corbett 1968).

The uncertain magnitude of this additional energy demand impedes the ability of the range animal nutritionist to establish guidelines for energy requirements of the free-roaming herbivore. Furthermore, the ruminant's rate of metabolism is set not only by its body size, but also by the temporal and spatial quality and quantity of its forage resource (McNab 1980). Thus, for the animal whose forage resource shows a decline in quantity and quality, there is a resulting change in its metabolic rate and energy requirements for maintenance. Much of this increase in energy expended would result from an increased time spent foraging (Lambourne and Reardon 1963). Nastis (1979) reported an increased daily grazing time of 4.6 hours for yearling heifers grazing crested
wheatgrass rangeland as forage availability declined from 919 kg/ha to 144 kg/ha. Scarnecchia (1980) reported similar results from a comparable study. Using 0.54 cal·BW$^{-1}$·hr$^{-1}$ as the energetic expense of grazing (Graham 1964), the 300 kg animals in Nastis' study would have expended an additional 0.75 Mcal as forage availability declined to its lowest level. This value represents nearly a 10 percent increase in the energy expended by the foraging animal. Other workers have suggested similar conclusions (Lambourne and Reardon 1963, Coop and Drew 1963), but their estimates of energy maintenance requirements were based on conversion of digestible organic matter intake to Mcal of metabolizable energy expended.

Young and Corbett (1972b) demonstrated no differences in energy expended by sheep grazing pastures with levels of available forage of 1880, 460 and 270 kg/ha. However, these data were confounded by significant differences in the body weights of the animals grazing the three different forages. It is apparent that the effect of alterations in the availability of forage upon the energy requirements of the grazing ruminant has yet to be adequately quantified.

**Purpose of the Study**

This study was designed to elucidate the effect of declining forage availability upon the energy expended by free-roaming cattle grazing crested wheatgrass (*Agropyron cristatum*) rangelands. The quantification of this energetic relationship would provide a basis
for further clarifying the rangeland plant-rangeland animal inter­
face. Furthermore, these data could aid in the revision of present
feeding standards so as to be more appropriate for the rangeland
ruminant.

Objectives

The central objective was to determine the energy expenditure
of heifers grazing a crested wheatgrass pasture in west-central
Utah. The research objectives originating from the central ob­
jective were:

1. To determine the energy expended by heifers grazing a
variable supply of available forage during the summer grazing season.

2. To determine the differences in energy expended by heifers
grazing seeded rangelands and penned cows consuming a diet of similar
quantity and quality.

3. To develop a table of energy requirements for a heifer
grazing crested wheatgrass rangeland during the summer grazing season.

Hypothesis

The first objective was accomplished by testing the following
hypothesis:

The energy expenditure of the free-ranging heifer is a
function of the amount of available forage. This function will
include three relationships dependent upon that amount of forage.
These relationships are:
1. A linear positive relationship over a range of low amounts of available forage.

2. A linear negative relationship over a range of moderate amounts of available forage.

3. An independent relationship with high amounts of available forage.

Limitations

One of the most significant limitations associated with range­land animal nutrition research is the statistical variation of estimates of dietary quality, quantity and rates of energy exchange. Cordova et al. (1978) have reviewed the literature on animal variability and numbers required for sampling intake, diet quality and fecal output. Most intake studies reviewed reported coefficients of variation of 10 to 16 percent. It was suggested that at least six animals are required for six-day sampling periods for estimating fecal output within 15 percent of the mean. Sample size and duration recommendations were reduced for diet quality determination.

For non-chamber methods of determining energy exchange Brockway (1978) suggested that acceptable techniques must have an accuracy of 1 to 10 percent of chamber methods. The carbon dioxide entry rate technique (CERT) has not continually exhibited this degree of accuracy. Whitelaw et al. (1972) reported an accuracy of \( \pm 12.5 \) percent as compared to the \( \pm 7.9 \) percent reported by Corbett et al. (1971). These values represent the general range of variability.
associated with estimates of energy exchange of sheep in confined and controlled laboratory settings. Also, in the one report of the use of CERT with cattle in a field setting, Young (1970) listed mean estimates of energy expenditure that had an associated coefficient of variation of 15.5 percent. It becomes apparent that estimates of voluntary intake and energy exchange will be limited by associated coefficients of variation of at least 15 percent.

**Definitions**

**Available forage**

The amount of forage which can be potentially consumed per unit area at any given period of time (kg·ha⁻¹).

**Energy expenditure**

The number of kilocalories spent per unit metabolic body weight per 24 hours (synonym: energy exchange) (kcal·BW⁻⁰·⁷⁵·d⁻¹).

**Entry rate**

The ratio of infusion rate to specific activity (gCO₂carbon·min⁻¹).

**Infusion rate**

The number of nanocuries subcutaneously infused into the animal per minute for a 24-hour period (nCi·min⁻¹)

**Intake**

The number of grams of organic matter consumed per unit metabolic body weight per 24 hours (gOMI·BW⁻⁰·⁷⁵·d⁻¹).
Metabolic body weight

The live body weight (kg) raised to the 3/4 power (BW$^{0.75}$).

Specific activity

The number of nanocuries per gram of $CO_2$ carbon extracted from animal urine samples (nCi·g$CO_2C^{-1}$).
REVIEW OF THE LITERATURE

Introduction

Since the publication of "Experiences sin la respiration des animaux et sur les changements qui airwent a l'au en passant par leur poumons", by A.L. Lavoisier in the Mem. de l'Academie de Science (1777, p. 185), as cited by Brody (1945), animal nutritionists have continually developed and redesigned calorimetry equipment and techniques. From Armsby to Brody to Kleiber to Blaxter several successive generations of researchers have worked to develop the concepts and explore the complexities of the energy metabolism of ruminants. For the uninitiated, their combined legacy in the forms of textbooks, symposia, agricultural experiment station bulletins, journal articles and lectures is overwhelming. Fortunately this historical ground has been plowed and several excellent reviews have been assembled. These include reviews which deal with techniques (Flatt 1969, Pullar et al. 1969, Whitelaw 1974), terminology (Gessaman 1973, Brody 1945, Kleiber 1961) and processes (Blaxter 1969, Bartholomew 1972, Smith 1971).

It will be the purpose of this review to provide a brief overview of this information on the bioenergetics of domestic livestock and the calorimetry techniques used to provide this information. This review will provide the framework from which the methodology of this study and derived results can be comprehended and discussed.
Energy is defined as the ability to do work. Physicists recognize energy in several forms including electrical, chemical, potential, kinetic, mechanical and radiant. For the animal nutritionist, the actions, forms, and transformations of energy within the animal are termed bioenergetics. Based on the first and second laws of thermodynamics and dependent upon the Law of Hess (the law of constant heat sums) for the ability to quantify energy transformations, bioenergetics deals with energy in the form of heat. An excellent comprehensive review of the theoretical basis of bioenergetics can be found in Brody (1945, p. 12-36).

Blaxter (1971) has formulated ruminant bioenergetics as:

\[ F = aW^n \]

where: \( F \) = fasting metabolism, \( a \) = constant, \( W \) = live body weight, 
\( n = 0.811 \pm 0.08 \). This formula, and specifically the value of \( n \), has been and still is a subject of much discussion. This relationship originated from the so-called surface law (Rubner 1883 as cited by Poczopko 1979) which states that the fasting animal produces 1000 kcal per square meter of surface area and from the surface area (S) formula:

\[ S = kW^{2/3} \]

where: \( k \) = constant (9.41 for 18-month-old cattle in moderate condition) (Armsby 1930), \( W \) = live body weight (Meeh 1879 as cited by Poczopko 1979). However,
though evidence does suggest that metabolism is roughly proportional to surface area, Bartholomew (1972) has listed several reasons why $n \neq 2/3$. Included in this reasoning are that the effective surface area of a live animal is continuously changing and that there is no mechanism for the physiological control of metabolism by the surface area. Kleiber (1961) reviewed this subject and presented strong evidence for $n = 0.75$. This value was reaffirmed four years later (Kleiber 1965), and has been corroborated by more recent reviews (Poczopko 1979, Economos 1979, McMahon 1973).

Though the value of this exponent has attracted much attention, the real question for the bioenergeticist is what is the value of "a" (Bartholomew 1972). For calculation of basal metabolism $a = 70$ has been commonly used since first suggested by Brody (1945). This value has been further supported by several investigators (Kleiber 1961, Poczopko 1971). However, the standard deviation of this value has been estimated as ±15 percent (Blaxter 1971). For cattle, $a = 81$ is frequently encountered in the literature and has been used by Cook (1970) in calculating the energy budget of range livestock.

The cost of maintenance above that of basal metabolism varies widely with species, age and environmental conditions. Brody (1945) suggested a range of 1.3 to 4.0 times the "a" value for maintenance conditions. This range brackets values reportedly used by several investigators (Gessaman 1973). For domestic livestock the conditions of maintenance are 1.15 to 1.4 times more costly than basal metabolism demands (Blaxter 1971, Ledger and Sayers 1977). For
a mature cow this range represents a difference in daily energy expenditure of 1.7 Mcal. Table 1 presents values of basal and maintenance energy expenditures for a variety of ruminant species determined under a variety of conditions.Compilation of this information required the assumption that all investigators had similar definitions of basal and maintenance conditions, an unlikely condition. Also, liberties were taken in converting some data to the standard units of kcal·BW^{-0.75}·d^{-1}. This table shows that generalities concerning basal and maintenance requirements for energy will have to be broad ones.

Free-roaming conditions may increase requirements above maintenance 1.1 to 2.7 times (Young and Corbett 1968), though more moderate increases of 1.25 to 2.10 are typically quoted (Young and Corbett 1972a, Coop 1962, Ledger 1977). For a mature cow this range represents a difference in daily energy expenditure of 7 Mcal. Osuji (1974) estimated a 1.3 fold increase in grazed as compared to housed sheep, but this estimate was derived from summation of energetic costs of activities according to time spent or distance travelled. The energetic costs of these individual activities are well-established and thoroughly reviewed in the literature (Graham 1964, Osuji 1974, Malechek and Smith 1976, Ribero 1976, Toutain et al. 1977, Vercoe 1973, Holmes et al. 1978, Webster 1972). Yet, estimates derived in this manner are typically lower than those derived from calorimetry techniques (Blaxter 1971).

Table 2 lists the results from several studies on the increased energetic costs associated with free-roaming conditions.
Table 1. Some examples of basal and maintenance energy expenditure (kcal·BW$^{-1}$.d$^{-1}$) of several ruminant species.

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<tr>
<td></td>
<td>70</td>
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<td></td>
<td>70.5</td>
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<td></td>
<td>107.0</td>
<td>steer, 2-year-old</td>
<td>Reid and White 1979</td>
</tr>
<tr>
<td></td>
<td>102.0</td>
<td>steer, 2-4-year-old</td>
<td>Reid and White 1979</td>
</tr>
<tr>
<td></td>
<td>100.0</td>
<td>steer, mature</td>
<td>Reid and White 1979</td>
</tr>
<tr>
<td></td>
<td>157</td>
<td>calf @ +10°C</td>
<td>Christopherson et al. 1979</td>
</tr>
<tr>
<td></td>
<td>156</td>
<td>calf @ 0°C</td>
<td>Christopherson et al. 1979</td>
</tr>
<tr>
<td></td>
<td>198</td>
<td>calf @ -30°C</td>
<td>Christopherson et al. 1979</td>
</tr>
<tr>
<td>sheep</td>
<td>57.4</td>
<td></td>
<td>Dejen and Shkolnik 1978</td>
</tr>
<tr>
<td></td>
<td>60.2</td>
<td></td>
<td>Dejen and Shkolnik 1978</td>
</tr>
<tr>
<td></td>
<td>141</td>
<td></td>
<td>Poczopko 1979</td>
</tr>
<tr>
<td></td>
<td>101</td>
<td></td>
<td>Poczopko 1979</td>
</tr>
<tr>
<td></td>
<td>66</td>
<td></td>
<td>Poczopko 1979</td>
</tr>
<tr>
<td></td>
<td>56.3</td>
<td></td>
<td>Langlands et al. 1963a</td>
</tr>
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</table>
Table 1 (continued).

<table>
<thead>
<tr>
<th>Species</th>
<th>Energy Expenditure</th>
<th>Comments</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Basal</td>
<td>Maintenance</td>
<td></td>
</tr>
<tr>
<td>sheep (cont.)</td>
<td>76.4</td>
<td>yearling</td>
<td>Toutain et al. 1977</td>
</tr>
<tr>
<td></td>
<td>60.7</td>
<td>old, thin</td>
<td>Toutain et al. 1977</td>
</tr>
<tr>
<td></td>
<td>52.8</td>
<td>old, fat</td>
<td>Toutain et al. 1977</td>
</tr>
<tr>
<td></td>
<td>104.5</td>
<td>71 kg ewe (CERT)</td>
<td>Young and McEwan 1975</td>
</tr>
<tr>
<td></td>
<td>95.8</td>
<td>15-month-old</td>
<td>Reid and White 1979</td>
</tr>
<tr>
<td></td>
<td>87.9</td>
<td>42-month-old</td>
<td>Reid and White 1979</td>
</tr>
<tr>
<td></td>
<td>78.5</td>
<td>32°C</td>
<td>Yousi et al. 1977</td>
</tr>
<tr>
<td></td>
<td>82.2</td>
<td></td>
<td>Russel et al. 1977</td>
</tr>
<tr>
<td></td>
<td>63.8</td>
<td>summation of activities</td>
<td>Graham 1964</td>
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<tr>
<td>bison</td>
<td>223</td>
<td>calf @ +10°C</td>
<td>Christopherson et al. 1979</td>
</tr>
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<td></td>
<td>171</td>
<td>calf @ 0°C</td>
<td>Christopherson et al. 1979</td>
</tr>
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<td></td>
<td>171</td>
<td>calf @ -30°C</td>
<td>Christopherson et al. 1979</td>
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<tr>
<td>caribou</td>
<td>96.5</td>
<td>115.7</td>
<td>McEwan 1970</td>
</tr>
<tr>
<td></td>
<td></td>
<td>144.4</td>
<td>Young and McEwan 1975</td>
</tr>
<tr>
<td>reindeer</td>
<td>144.2</td>
<td>CERT</td>
<td>Young and McEwan 1975</td>
</tr>
<tr>
<td>elk</td>
<td>150.6</td>
<td>40 kg calves</td>
<td>Robbins et al. 1979</td>
</tr>
<tr>
<td>horse</td>
<td>107</td>
<td></td>
<td>Brody 1945</td>
</tr>
<tr>
<td>bighorn sheep</td>
<td>85</td>
<td>lowest level of year</td>
<td>Chappel and Hudson 1978</td>
</tr>
<tr>
<td>pronghorn sheep</td>
<td>76</td>
<td>adult</td>
<td>Wesley 1971</td>
</tr>
<tr>
<td>whitetailed deer</td>
<td>96.3</td>
<td>winter</td>
<td>Silver et al. 1969</td>
</tr>
<tr>
<td></td>
<td>143.9</td>
<td>summer</td>
<td>Silver et al. 1969</td>
</tr>
<tr>
<td></td>
<td></td>
<td>winter</td>
<td>Ullrey et al. 1970</td>
</tr>
</tbody>
</table>
Table 2. Some examples of the increase in daily energy expenditure (DEE) above maintenance attributable to free-ranging conditions.

<table>
<thead>
<tr>
<th>Species</th>
<th>Increase in DEE</th>
<th>Comments</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>sheep</td>
<td>1.47</td>
<td>DOMI&lt;sup&gt;1&lt;/sup&gt;/</td>
<td>Coop and Hill 1962</td>
</tr>
<tr>
<td></td>
<td>1.4</td>
<td>DOMI&lt;sup&gt;1&lt;/sup&gt;/</td>
<td>Corbett 1963</td>
</tr>
<tr>
<td></td>
<td>1.24</td>
<td>DOMI&lt;sup&gt;1&lt;/sup&gt;/</td>
<td>Langlands et al. 1963b</td>
</tr>
<tr>
<td></td>
<td>1.16</td>
<td>abundant forage, DOMI&lt;sup&gt;1&lt;/sup&gt;/</td>
<td>Lambourne and Reardon 1963</td>
</tr>
<tr>
<td></td>
<td>1.33</td>
<td>scarce forage, DOMI&lt;sup&gt;1&lt;/sup&gt;/</td>
<td>Lambourne and Reardon 1963</td>
</tr>
<tr>
<td></td>
<td>1.4</td>
<td>summation&lt;sup&gt;2&lt;/sup&gt;/</td>
<td>Graham 1964</td>
</tr>
<tr>
<td></td>
<td>1.57</td>
<td>MIC&lt;sup&gt;3&lt;/sup&gt;/, CERT&lt;sup&gt;4&lt;/sup&gt;/</td>
<td>Young and Corbett 1968</td>
</tr>
<tr>
<td></td>
<td>1.3</td>
<td>summation&lt;sup&gt;2&lt;/sup&gt;/</td>
<td>Osuji 1974</td>
</tr>
<tr>
<td></td>
<td>1.6-1.7</td>
<td>not influenced by level of forage&lt;sup&gt;2&lt;/sup&gt;/</td>
<td>Young and Corbett 1972b</td>
</tr>
<tr>
<td>cattle</td>
<td>1.6</td>
<td>CERT&lt;sup&gt;4&lt;/sup&gt;/</td>
<td>Young 1970</td>
</tr>
<tr>
<td></td>
<td>1.5</td>
<td>DOMI&lt;sup&gt;1&lt;/sup&gt;/</td>
<td>Wallace 1956</td>
</tr>
<tr>
<td>pronghorn</td>
<td>1.6&lt;sup&gt;5&lt;/sup&gt;/</td>
<td>RE&lt;sup&gt;7&lt;/sup&gt;/</td>
<td>Wesley 1971</td>
</tr>
</tbody>
</table>

<sup>1</sup> DEE = digestible organic matter intake x 4.4 kcal·kg DOMI<sup>-1</sup>

<sup>2</sup> DEE = Σ (energetic cost of activity x duration or distance)

<sup>3</sup> MIC = mobile indirect calorimetry

<sup>4</sup> CERT = carbon dioxide entry rate

<sup>5</sup> assumes maintenance DEE = 105 kcal·BW<sup>-.75</sup>

<sup>6</sup> moderate levels of activity

<sup>7</sup> RE = respiratory exchange method
This range of values and the values for maintenance in Table 1 can be attributed to differences in methodology, body size, food habits, breed, age, season, thermoregulatory demands, activity levels and thyroid activity (Berman 1968, Bouit et al. 1977, Dejen and Shkolnik 1978, McNab 1980, Silver et al. 1969, Toutain et al. 1977). Energy expenditure does appear to be independent of level of intake (Chappel and Hudson 1978, Webster 1972, Young 1975). However, a decrease in the quantity of forage available to the grazing animal may increase daily energy expenditure (due to an increase in grazing time) (Lambourne and Reardon 1963, Osuji 1974, Webster 1972) but this relationship has not been satisfactorily clarified (Farrell et al. 1972, Young and Corbett 1972b). The daily energy expenditure of the grazing ruminant is obviously a function of its unique set of physiological and environmental conditions, and this function is poorly quantified, at best.

**Calorimetry Techniques**

Many reviews of calorimetric techniques begin with reference to Lavoisier's late eighteenth century adiabatic system for measuring heat produced by the guinea pig. As one would hope, the passage of 200 years has brought substantial changes in the techniques and equipment of the bioenergeticist. The laborious, expensive and difficult-to-control methods of direct adiabatic calorimetry have been abandoned. Though still dealing with attempts to discover the amounts of the various chemical and physical processes that occur within the animal and their time course, the methodology has slowly evolved to new approaches
and assumptions. Lavoisier might have been hard pressed to associate his ice-packed calorimeter with techniques that employ heart rate telemetry, radioactive carbon or double-labeled water. Yet, the basic theories have remained unchanged.

Heat is that which produces a change in temperature. When involved in any chemical reaction heat is independent of the manner in which the reaction is achieved (the Law of Hess). Additionally, the sum of all energies in an isolated system is constant (the first law of thermodynamics) and all systems will approach a state of equilibrium (the second law of thermodynamics). As with any system the animal body labors under these laws and struggles to capture the free energy required for survival. It is the oxidation of this free energy, in the forms of carbohydrates, proteins and fats that liberates heat as well as carbon dioxide, water, methane and products of incomplete combustion.

Calorimetry is defined as the measurement of this heat, and it was the heat produced by guinea pigs, dogs, humans, livestock and other subjects that drove the calorimetry experiments of Lavoisier, Crawford, Boussignault, Atwater, Armsby, Rubner, Maynard and the other original workers in this field. Reviews of the early developments in calorimetry can be found in Lusk (1933) and McColleum (1957). Also, a discussion of the equipment and methodology of the first direct calorimeter used for large herbivores can be found in Graham (1933). Blaxter (1962) has also reviewed the development of the first calorimeters along with a review of more current methods. He has separated these methods into two general categories: direct and indirect methods. Direct approaches are of two types, (1) adi-
abatic, the type used by Lavoisier and Armsby, and (2) nonadiabatic or, more commonly, the gradient layer type which measures both sensible and evaporative heat directly. Adiabatic types have been abandoned because of excessive costs of labor and materials and the difficulty in controlling the heat exchange. Pullar (1969) has thoroughly reviewed the theory of gradient layer calorimetry. A diagram of this device can be found in Pullar (1963). The major advantage of gradient layer calorimetry over indirect approaches is the automatic production of continuous permanent records showing the minute-to-minute fluctuation in the heat loss of the subject (Pullar 1969).

Methods of indirect estimations of heat production are numerous. Flatt (1969) has categorized this type of approach into those which energy retention is measured directly and those where energy retention is measured indirectly by deducing the energy loss from the dietary intake. Indirect techniques have the advantage over direct types in being less expensive and indicators of changes in body substance and nutrient sources of energy. Comparisons of direct and indirect approaches can be found in Pullar et al. (1969) and Brockway et al. (1969). Traditional indirect techniques compare quite well with direct methods.

Indirect approaches are based primarily on the fact that heat production is closely correlated with oxygen consumption and carbon dioxide production (the respiratory quotient). Table 3 categorizes various types of indirect methods. The included citations are provided as an access route to the extensive literature on this general subject.
Table 3. A listing of various types of indirect calorimetry.

Indirect Calorimetry

A. Direct Estimate of Energy Expenditure
   1. Respiratory Exchange (Blaxter 1962)
      a. closed circuit (Kleiber 1961)
      b. open circuit (Kleiber 1961)
         (1) gas volume measurement (Blaxter et al. 1972)
         (2) gas analysis (Young et al. 1977)
         (3) heart rate and respiratory rate (Yamamoto et al. 1979)
         (4) carbon dioxide entry rate (Whitelaw et al. 1972)
   2. Carbon and Nitrogen Balance (Blaxter 1969)
   3. Comparative Slaughter Technique (Lofgreen and Otagaki 1961)

B. Indirect Estimate of Energy Expenditure
   1. Body Composition Estimation
      a. body weight gain (Blaxter 1962)
      b. body water content (Reid et al. 1963)
      c. carcass specific gravity (Lynch and Wellington 1963)
   2. Time Budget Analysis (Moen 1973)
   3. Food Intake Balance (Lambourne and Reardon 1963)
It is a tribute to the ingenuity of the animal scientist that many of the methods on this list are applicable to the free-roaming herbivore. Yet, many of these methods have serious drawbacks. Obviously, closed circuit techniques are not applicable. Several of the methods are imprecise because of their assumptive nature (Blaxter 1962, McDonald 1968, Reid et al. 1963). Energy balance models are still in their infancy (Gessaman 1973). The open circuit gas volume approach is limited for the same obvious reasons as the closed circuit method. Open circuit gas analysis is limited by the equipment required. For example, Holmes et al. (1978) used a gas analysis approach by enclosing the heads of steers grazing lugume grass pastures in a portable wooden box that sealed with the ground when the animals lowered their heads. The application of this methodology to western U.S. range-lands would be difficult. Typically, gas analysis methods with a grazing animal require fistulation of the trachea. Though improvements in this technique have been suggested (Cresswell and Harris 1958, Cresswell and Harris 1961, Young and Webster 1963), the equipment is awkward. Young and Corbett (1972a) have provided information on the construction of this equipment and estimated that this approach has an error of +12.3% of the mean. Heart rate (Webster 1967) and respiratory rate (Gessaman 1973) measurements have been frequently employed during recent years. Their value has been
marginal in some cases (Robbins et al. 1979). Yamamoto et al. (1979) encountered an error of +16 percent of the mean with heart rate measurements for estimation of energy expenditure of cattle. Individual calibration of heart rate with oxygen consumption is required and this relationship can be disrupted by changes in cardiac stock volume or responses to emotional factors (Brockway 1978). The carbon dioxide entry rate technique (CERT) was first proposed by Young et al. (1969), and has been touted as the possible savior for energy expenditure measurements with the grazing ruminant (Brockway 1978, Webster 1972). This method requires closer examination.

CERT is based on the theory and assumptions of isotope dilution, a familiar concept in the biological literature. The isotope dilution method has been applied to determinations of several different metabolic components of monogastric and ruminant metabolism. Baker et al. (1954) infused $^{14}$C-glucose into male human subjects in an effort to quantify glucose metabolism. Lifson et al. (1955) measured the volume and turnover rate of the glucose pool in dogs by intravenous injection of $^{14}$C-glucose. Acetate utilization in the ruminant was examined by Essig et al. (1961) through infusion of $^{14}$C-acetate.

Lifson and McClintock (1966) analyzed the theory behind isotope dilution. Though their review is specific to the use of body water turnover measurements for determination of energy and material balance, this treatise provides good insight into use of the isotope dilution method. The assumptions listed by these authors are basically four:
1. The study subject is in a steady state with an overall constant composition of body solids.

2. Input and output rates of the measured metabolic component are constant during the period of study.

3. The volume of the infused isotope is directly related to the total body volume of the measured metabolic component.

4. The specific activity of the extracted metabolic component is related to the output rate of that metabolic component from the body pool within the study subject.

Given these assumptions, Steele et al. (1956) described a mathematical treatment of isotope dilution. These authors were examining the size of the glucose pool in dogs and the inflow-outflow rate of carbon from this pool. Calculation of the glucose pool volume and its turnover rate is shown in equation 1,

\[ SA_t = \left( \frac{P}{C} - \frac{F}{G} \right) e^{-Gt/c} \]  

where: \( SA_t \) = specific activity of the extracted metabolic component (mCi/unit time) at time \( t \); \( t \) = time from initial injection of the isotope; \( F \) = constant infusion rate (mCi/unit time); \( G \) = turnover rate of the examined metabolic component (unit weight or volume/unit time); \( P \) = single injection rate (mCi); \( C \) = body pool volume of the metabolic component.

The presence of the \( F \) and \( P \) variables in the equation allows for calculation of \( G \) and \( C \) when a priming dose of isotope is injected and then followed by constant infusion of that isotope. A portion
of later work with CERT was devoted to testing the suitability of either \( F \) or \( P \) equalling zero (White and Leng 1968). These authors concluded that the condition \( P=0 \) was more favorable than \( F=0 \). Equation 2 is derived from equation 1 when \( P=0 \).

\[
SA_t = \frac{F}{G}(1-e^{-Gt/c})
\]

Solving for \( G \) (the turnover rate) provides the following equation:

\[
G = \frac{F}{SA_t(\delta t = \text{equilibrium})}
\]

Data by Steele et al. (1956), Annison and Lindsay (1961) and Whitelaw et al. (1972) support the relationship shown in equation 3. It should be noted that the calculation of \( CO_2 \) entry rate used by Young and Corbett (1968) was by the use of equation 3. It should also be noted that eight hours of infusion of \( NaH^{14}CO_3 \) into the ruminant \( CO_2 \) body pool are required for the SA to equilibrate (Whitelaw 1974).

Therefore, by constant infusion \( (F) \) of \( ^{14}CO_2 \) into the ruminant and subsequent determination of the specific activity of the \( ^{14}CO_2 \) body pool after equilibration of the \( ^{14}C/^{12}C \) ratio has been reached, the turnover \( (G) \) of \( CO_2 \) within the animal can be determined. CERT is based on the hypothesis that the turnover rate of \( CO_2 \) will provide an estimate of energy expenditure (Whitelaw et al. 1972), and changes in turnover, or entry, rate are principally due to variation in rate of endogenous production of \( CO_2 \) by the animal as determined by its physiological activities (Young et al. 1969).

Several problems with the basic assumptions of isotope dilution as they apply to CERT have been suggested. Firstly, experiments by
Annison et al. (1967) indicated that the body pool of CO₂ in the ruminant is a complex, multicompartmental system. This suggested that equation 2 (Steele et al.) was insufficient. However, Huber et al. (1965) have indicated that the basics of the technique lie in a measurement of the rate of respiratory CO₂ elimination, i.e., measurement of only one compartment within the overall CO₂ body pool. Thus, the single compartment mathematics seemed justified. Experiments by Young et al. (1969), White and Leng (1968) and Whitelaw et al. (1972) have supported this one compartment approach even when examining the SA of compartments other than the respiratory pool.

Secondly, it has been shown that values of G tend to overestimate actual CO₂ production. Whitelaw et al. (1972) reported a 3.7% overestimation. White and Leng (1968) reported a general overestimation, but also reported CERT was highly correlated with CO₂ production. This data has implied that either the SAₜₑ𝑞𝙪𝙞𝙡𝑖𝑏𝑟𝑖𝑢𝙢 has been diluted by unlabelled CO₂ or that some of the infused ¹⁴C-HCO₃⁻ has not completely equilibrated with the CO₂ body pool. Bone has a very slow carbon turnover rate (Whitelaw 1974), and Whitelaw et al. (1972) have attributed their overestimation to this uncontrollable factor.

Thirdly, the direct use of an energetic value for the estimated CO₂ production (kcal·1CO₂⁻¹) from an estimated respiratory quotient is hampered by the inability to determine the correct RQ value (Brockway and Whitelaw 1970). Though realistic estimates of RQ between 0.9 and 1.0 would create a possible error of less than 10%,
most investigators have established regression equations for relating CERT measures with actual energy expenditures measured by more traditional indirect calorimetry techniques. Application of these regressions established for animals held indoors to CERT measures with free-ranging animals would not bias energy expenditure estimates, nor would a change in RQ values over the measurement period create a large bias in the estimates (Engels et al. 1976).

These regressions have varied depending on site of infusion of $^{14}$C-HCO$_3$ and the CO$_2$ body compartment sampled for SA. For example, Young and McEwan (1975) intraperitoneally infused NaH$^{14}$CO$_3$ into caribou and collected both expired gas and jugular blood for SA determinations. The resulting regressions relating the CO$_2$ entry rate (mmoles·m$^{-1}$) from blood and gas to the rates of energy expenditure (J·m$^{-1}$) are shown in equations 4 and 5, respectively.

$$EE = 215 \text{ ER}_{\text{blood}} + 1707$$ (4)

$$EE = 195 \text{ ER}_{\text{gas}} + 2239$$ (5)

Though the problem of the selection of an appropriate RQ value is circumvented by using an available regression, all authors caution the use of a particular regression only when subject animal, infusion site and sampled CO$_2$ compartment are similar to the applied work.

Fourthly, Brockway (1978) has set four requirements for any method for estimating energy exchange in free-ranging animals. These are that: (1) the method works well independent of the nature of the physiological stimulus to alteration of metabolic rate, (2)
energy expenditure be measureable over periods of one hour or less, (3) the required equipment be portable, sturdy and automatically operable, and (4) the technique provide an estimate of energy expenditure within ±10 percent. CERT meets requirements 1 and 3, and requirement 2 can be ignored for measurements of daily energy expenditure. The persistent problem has been in satisfying requirement 4. Young et al. (1969) reported an error of ±20 percent. Values of ±7 percent (Whitelaw et al. 1972), ±11 percent (Young 1970) and ±12 percent (Young and McEwan 1975) have also been reported. The lowest variability of ±7 percent pertained to highly controlled studies while the ±11 percent and ±12 percent pertained to studies where animals were unrestrained. It becomes apparent that the variability of the CO₂ entry rate estimation of energy expenditure, even when the method was conducted by experienced researchers, has not met the requirements for acceptability set forth by Brockway (1978).
METHODOLOGY

Introduction

This experiment was designed to determine the energy expenditure of heifers grazing variable amounts of available forage. In addition, it was designed to determine the difference in energy expenditure between heifers grazing on a free-ranging condition and stall-fed heifers consuming a diet similar in quantity and quality.

Field Study, 1979

The field study was conducted at the Tintic Range Research Station located 13 kilometers south of Eureka, Juab County, Utah. This was an area designed for cooperative research involving the Bureau of Land Management, the Utah Agricultural Experiment Station and the Department of Range Science, Utah State University. This study was funded by Project 764 of the Utah Agricultural Experiment Station.

The field research was conducted on pasture 1, the southernmost pasture of this 24-pasture area. This 20-ha pasture, representative of a semidesert loam range site, was burned to remove its 100 percent sagebrush (*Artemisia tridentata*) cover and drilled with crested wheatgrass (*Agropyron cristatum*) in September, 1949. The grazing use of this pasture over the past 30 years has been variable, but the stand of crested wheatgrass has remained productive. Located at an elevation of approximately 1600 m, the study area is typical of the
foothill areas of the Great Basin. Average annual precipitation is approximately 330 mm (Rodgers 1979) with 30 percent as snow during the winter months and the remainder as rain spread erratically throughout the spring, summer and fall seasons. Average temperature range from 21.3°C during July to -3.2°C during January. Precipitation and temperature data recorded at the site during the study period are presented in Table 11 of the Appendix.

In March, 1979, ten yearling Angus heifers were purchased from a Juab County rancher. These animals were transported to holding facilities at Utah State University where they were halter-broken, tamed and trained to wear the necessary equipment. Four of the animals were selected for energy expenditure estimations, four were selected for total fecal output collections, and an esophageal fistula was established in each of the two remaining animals for collection of extrusa for chemical analysis.

During the first week of June, 1979, these animals were placed on pasture 1 of Tintic where they grazed for three weeks prior to the start of the study. On June 27 the 10 animals were weighed and the first of five trial periods began. The other four periods began on July 18, August 1, August 15 and August 29, respectively. Each trial period lasted 10 days. During the interim of trials 1 and 2 (an 11-day period) the animals remained alone on pasture 1. During the remaining three trial interims (each of four days, 30 additional yearlings were placed in pasture 1 to reduce the levels of available forage.
Energy expenditure

Field methodology. The apparatus used for estimation of energy expenditure from carbon dioxide entry rates follows that described by Young (1970).

A 500 ml plastic bottle was attached to the solenoid unit of a Harvard\(^1\) infusion pump, and the bottle and pump were fastened to the inside of a 225 mm x 325 mm x 100 mm aluminum box. One-hundred fifty ml of sterile saline (0.9 percent (w/v) NaCl and 0.1 percent (w/v) (NaHCO\(_3\)) was added to the container. Ten ml of this solution was removed and stored for later determination of specific activity. The saline solution contained approximately 600 nCi·m\(^{-1}\) of \(^{14}\text{C-HCO}_3^-\).

The infusion rate of \(^{14}\text{C-HCO}_3^-\) was approximately 50 nCi·min\(^{-1}\). This rate was less than the rate of 200 nCi·min\(^{-1}\) reported by Young (1970). The amount of \(^{14}\text{C-HCO}_3^-\) used during the field study was limited to 10 mCi by regulation by the Nuclear Regulatory Agency. This amount of radioisotope restricted the 40 attempted infusions to this lower rate. The coefficient of variation of the pump's delivery rates averaged 5 percent.

This unit was enclosed and placed in a canvas pouch fastened to a harness strapped around the animal's withers. A 305 mm x 9.5 mm surgical tube was attached to the pump outlet and connected to a 50 mm teflon intravenous catheter that had been placed subcutaneously in the animal's right shoulder. Surgical tape was wrapped around

\(^1\) Harvard Apparatus Company, Inc., 150 Dover Road, Mills, Massachusetts 02054.
the protruding head of this catheter and stitched to the skin to keep the catheter in place. In addition, a filter holder containing a 0.2 mm pore size, 13 mm diameter membrane filter was attached in line to filter bacteria from the infusate. Once connected and in place this assembly was not disturbed for 24 hours.

A canvas pouch on the left side of this harness held a custom designed extraction pump which automatically and mechanically withdrew a fluid sample of 0.5 to 1.0 ml every 10 minutes for the last 12 hours of the 24-hour period that NaH$_{14}$CO$_3$ was infused. This extraction process began automatically.

The fluid sample was originally to be saliva drawn through a catheter attached to a duct of the parotid salivary gland of the left cheek. Research has indicated that saliva is the most suitable of the CO$_2$ body compartments for CERT measurements (Whitelaw et al. 1972). Though information is available outlining this surgical procedure (Hecker 1974, Stewart and Stewart 1961), implantation of a french size (=1.6 mm ID) 560 mm polypropylene catheter provided unsuccessful and was abandoned. Of the remaining two potentially collectable fluids, blood and urine, the latter has proved to be a more reliable indicator of CO$_2$ entry rates (Whitelaw et al. 1972) and urine collections were made.

A 24 to 30 french size foley balloon catheter (30 cc or 75 cc balloon, either can be used) was inserted into the urethra and inflated with an injection of sterile saline. The catheter outlet was attached to 6 mm (outside diameter) surgical tubing fastened to a
crop strap attached to the wither harness. The tubing was connected
to a 3 cc syringe fastened below the extraction pump canvas pocket.
The syringe, equipped with an overflow outlet, served as a reservoir
for urine collection. All urine flowed through this assembly and
each micturition replaced the urine held within the reservoir.
Tubing (1.6 mm O.D.) attached to the extraction pump syringe was
positioned within the reservoir. This tube provided access to the
intermittent urine flow for collection of a sample for determination
of specific activity. It was important that the urine sampled be a
composite sample. Whitelaw et al. (1972) have shown that hourly
urine samples have four times the variability in specific activity
found in composite urine samples.

A few grains of CuSO₄ were placed in the extraction pump syringe
as a sterilant. This assembly was connected to the animal with the
start of infusion of ¹⁴C-HCO₃⁻. Following the 24-hour infusion period
all catheters and pumps were removed. The urine samples were stored
at 6°C for later laboratory analysis.

The use of the ¹⁴C-HCO₃⁻ was governed by application to the USU
Radiation Safety Committee. This application required an amendment
to the general USU radioisotope license allowing off-campus use of a
radioisotope. This amendment was approved following application to
the Nuclear Regulatory Agency, Washington, D.C. All applications re-
quested the use of 10 mCi of ¹⁴C (as NaH¹⁴CO₃), an amount deemed safe
for the facilities used in this experiment. Following the completion of
this experiment all animals infused with ¹⁴C-HCO₃⁻ were treated as
radioactive waste and destroyed and buried on the site of the experiment.
Laboratory analysis

The procedure described here followed methods outlined by Annison and Lindsay (1961) and Leng and Leonard (1965). All chemicals listed below were prepared with CO₂-free water (A.O.A.C. 1970).

Urine samples were thoroughly mixed and 2 ml were added to a custom designed warburg flask, i.e., a 125 erlenmeyer flask fitted with removable center well. Use of sample sizes > 2 ml prevented the appropriate pH changes required for wet oxidation. One ml of 1N NaOH was added to the center well and the flasks were covered with rubber caps. The use of argon gas to flush the vessel of atmospheric CO₂ prior to capping proved unnecessary. With a syringe 1 ml of 1N H₂SO₄ (with 1.0 percent w/v CuSO₄) was injected into the flask. Care was taken not to contaminate the NaOH with H₂SO₄. If this event occurred the reaction was terminated and restarted. The vessels were then left undisturbed for 24 hours. All samples were run in triplicate.

At the end of this period the flasks were uncapped and 0.5 ml of 20 percent (w/v) BaCl₂·2H₂O was added to the center well. This was followed by the addition of 1 ml of 5 percent (w/v) NH₄Cl and the white precipitate was washed from the well into 15 ml glass centrifuge tubes. The suspension (BaCO₃) was centrifuged for 5 minutes at 1000 g. The supernate was then poured off and the precipitate was washed with acetone onto 2" glass plates. This slurry was placed in an oven at 105°C for 45 minutes or until dry.
The dried precipitate was scraped into a fine powder and weighed in tared 20 ml plastic scintillation vials. Dry weights of 30 mg BaCO$_3$ were typically encountered but weights ranged from 15 mg-90 mg. Weights of BaCO$_3$ less than 15 mg proved inadequate for liquid scintillation procedures and were discarded.

The solid was suspended in 10 ml of a scintillation cocktail of 4.0 percent (w/v) (cab-o-sil) and 0.3 percent (w/v) PPO in toluene. Vials were shaken and then transferred to a liquid scintillation counter. Disintegrations per minute were determined following a 60-minute period where vials were kept in the dark. This precount period provided background radiation readings of 200-250 cpm, a necessary prerequisite for counting samples of low specific activity. Counting times were ten minutes and all samples were counted twice in a 24-hour period. A counting period longer than 24 hours resulted in settling of the precipitate. The counting device used an external standard and counting efficiencies of 90 percent or greater where expected (Packard 1978). One ml samples of the stored infusate solution were added directly to the scintillation cocktail and the specific activity was determined as described above.

Results were expressed as dpm·mg$^{-1}$BaCO$_3$ and converted to nCi·g$^{-1}$CO$_2$ carbon. The averages of each of the three subsamples were used to compute CO$_2$ entry rates with units of gCO$_2$ carbon·m$^{-1}$. Entry rate values were converted directly to estimates of energy expenditure (kcal·m$^{-1}$) using Young's (1970) regression:

$$EE = 1.018 + 5.178 \text{ER.}$$ (4)
This equation was chosen because, though Young (1970) infused $^{14}\text{C}-\text{HCO}_3$ introperitoneally, the collection fluid, the subject animal and the general methods of the research approximated Young's (1970) work to a greater degree than any other research encountered in the literature. The metabolic body weight of each animal was then used to express estimates of energy expenditure in units of kcal·BW$^{-0.75}$·d$^{-1}$.

**Intake**

The equation:

\[
\text{Organic Matter Intake} = \frac{\text{Total fecal organic matter output}}{1 - \text{organic matter digestion coefficient}}
\]

was used to estimate the forage intake of the experimental heifers.

Fecal production was determined from total fecal collections. Four animals were harnessed with fecal bags for a 96-hour period during each trial. This equipment was similar to that suggested by Kartchner and Rittenhouse (1979). Fecal bags were weighed, emptied into plastic tubs, cleaned, relined with plastic bags, and reattached to the animal every 12 hours during the collection period. Following each 12-hour collection the individual fecal samples were thoroughly mixed with a beater attached to an electric drill and sampled for dry matter and organic matter determinations. These 100 g aliquots were frozen immediately, dried at 105°C for 96 hours at a later date, and then ashed at 500°C for 3 hours according to A.O.A.C. (1970) procedures.

Tilley and Terry (1963) outlined procedures used in determining the organic matter digestion coefficient. Samples analyzed were extrusa collected from esophageal fistulated animals (see METHODOLOGY-
Diet quality for sampling procedures. Residual matter for each sample, analyzed in triplicate, was ashed to determine residual organic matter. In vitro organic matter digestibility coefficient (IVOMD) was calculated as in vitro dry matter digestibility with organic matter fractions replacing dry matter fractions.

Diet quality

Diet quality measurements (IVOMD and crude protein) were made on extrusa samples collected from esophageal fistulated heifers. The fistulation procedure and development of custom-designed cannulae for the two Angus heifers used in this study were described by Van Dyne and Torrel (1964). The heifers were fistulated in April, 1979, and remained with the other eight animals throughout the study.

For sampling the fistulated animals were penned overnight to minimize contamination of samples by regurgitation of previously grazed forage. Forty-five minutes were allowed for each sample collection and animals were allowed total freedom of movement during this period. Extrusa collections were made once during each trial on Day 1. Collection bags were canvas with a screen bottom that allowed for saliva drainage. Following these morning collections samples were immediately frozen. The extrusa samples were freeze-dried at a later date, ground through a Wiley Mill (equipped with a 1 mm screen) and stored for chemical analyses.

Crude protein was calculated as a function of nitrogen content (6.25 x N). Duplicate samples were analyzed for dry matter, ash and nitrogen constituents.

Forage availability

A circular plot 1.0 m$^2$ in area was used to sample the available forage during each trial. The ocular-weight estimate method described by Pechanec and Pickford (1937), refined by Wilm et al. (1944) and discussed by the Sub-committee on Range Research Methods (1967), was used to determine levels of available forage. Stein's two stage sample formula (Steel and Torrie 1960) was used to determine the sample size required for a 90 percent confidence interval of not more than 100 kg·ha$^{-1}$. A sample size of 40 plots was determined. Twenty of the 40 randomly located and ocularly estimated plots were clipped, weighed, dried at 60°C for 48 hours and reweighed. Twenty cages were randomly distributed throughout the pasture prior to initiation of grazing for determination of total forage production. A 1.0 m$^2$ area within these 20 cages was clipped, weighed, dried at 60°C for 48 hours and reweighed during the last two days of trial 5. An additional 20 cages were distributed and a 1.0 m$^2$ area was clipped from each cage at the beginning of each trial to provide a means for estimating forage regrowth occurring during each trial.

Following the reweighing, four samples were randomly selected from the 20 clipped samples of each vegetation sampling. These forage samples were ground, stored and later analyzed for dry matter, ash, IVOMD and nitrogen as previously described.
Laboratory Study, 1980

This study was conducted at the Utah State University Green Canyon Ecology Center located three miles north of the USU campus. Four yearling Angus heifers, similar to those used in 1979, were purchased in March, 1980, from the same source used the previous year. These animals were transported to handling facilities at the Ecology Center where they were halter-broken, tamed and trained to wear the necessary equipment. Four large-animal metabolism stalls were assembled following in general the design of Breen and Siebert (1974).

During early July crested wheatgrass was cut and baled from a 14 ha area on the Utah Agricultural Experiment Station Nephi Field Station facility located 5 kilometers south of Nephi and 75 kilometers east of the Tintic Experimental Research Station. Forty-five hundred kg of this baled hay was selected and transported to the Ecology Center facility. By late July all animals were consuming 50-60 g organic matter basis·BW\(^{-0.75}\)·d\(^{-1}\) of this hay as their sole feed source. In mid-August the animals were placed in the metabolism stalls housed in a basement of a building on the Green Canyon Compound. As suggested by Schneider and Flatt (1975), a ten day preliminary trial was conducted. The animals were fed the crested wheatgrass hay at a level of 55.4 g OM·BW\(^{-0.75}\)·d\(^{-1}\) in equally proportioned, twice daily feedings. This level of intake was similar to that determined during the 1979 field season. Orts and waste feed, which were usually less than 100 g, were collected before each
feeding, weighed and refed. Total fecal collections were made in galvanized oval tubs placed under the rear of each stall. Fecal flaps described by Kartchner and Rittenhouse (1979) were attached to the heifers to facilitate feces placement in the tubs. Feces were weighed in these tared tubs following each feeding, transferred to plastic tubs, and the cleaned oval tubs were replaced underneath the stalls. The collected fecal material was mixed, sampled, stored and analyzed with the same procedure as described for the 1979 field season.

Foley balloon catheters (24 french size (3.8 mm), 30 cc balloon) were inserted into the urethra, inflated with sterile saline and connected to 6 mm O.D. surgical tubing fastened to a crop strap. This tubing was connected to a 19 liter plastic container for total urine collection. The Foley catheters remained in place throughout the trial.

Energy expenditure

CERT methodology was followed as outlined previously (p. 29) with three alterations. First, the infusion rate was doubled to 100 nCi·m⁻¹·min⁻¹. Second, the use of extraction pumps for urine collection was omitted. Though urine was periodically sampled over the 24-hour infusion period in order to quantify the time-related increase in specific activity, pooled urine samples from the last twelve hours of infusion were used for calculation of CO₂ entry rates. Third, infusate tended to pool at the site of infusion, a problem discussed
by others (Whitelaw et al. 1972) but which had not been encountered during the 1979 field season. The use of a 16 ga 127 mm teflon catheter during these stall trials alleviated this problem.

CERT measurements were conducted five times with each animal. Three of these measurements were conducted during the 10-day digestion balance trial described below, and used as an estimation of maintenance energy expenditure. The other two were conducted after 48 hour fasting periods, one following the preliminary trial and the other following the digestion balance trial. This postabsorptive state, combined with the thermoneutral environment and restraining stanchion provided the necessary conditions for estimation of fasting energy expenditure (Blaxter 1962).

Energy, nitrogen and organic matter balances

The balance trial was begun four days after completion of the preliminary trial. Body weights used to determine the appropriate feeding level for each animal were an average of weighings taken 12 days apart, and each taken following a 16-hour fast. Feeding schedules and methods as well as fecal collection methods were the same as described above. In addition, a 5 percent aliquot of each fresh fecal sample was collected from each weighing and stored fresh in a plastic-lined container for nitrogen determinations (A.O.A.C. 1970). Feces were sprayed with ethyl alcohol as a preservative (Schneider and Flatt 1975). Subsamples of these composite samples were freeze-dried and analyzed for gross energy as determined by adiabatic bomb calorimetry (Parr 1968).
During the balance trial urine output was gravimetrically and volumetrically measured following the morning feeding period. A 10 percent aliquot from each weighing was composited over days and stored in glass bottles at 4°C. Urine was collected in 100 ml of 50 percent (v/v HCl) (Egan and Ulyatt 1980), except when collecting during for determination of specific activity. These accumulated aliquot samples were analyzed for nitrogen and gross energy as described above.

**Statistical Analysis**

The experimental design for the study was nonreplicated and completely randomized (Steel and Torrie 1960). One-way analyses of variance tests were conducted for level of intake (OMI and COMI), forage availability, diet quality indices, body weight and body weight change measurements. Analyses which resulted in significant F-statistics were tested for mean differences using least significant difference statistics (LSD) (Steel and Torrie 1960). The chosen alpha level for determination of significance was 0.10. Confidence intervals were computed for estimates of energy expenditure, using an alpha level of 0.10.
RESULTS

It was the purpose of this study to estimate the energy expended by heifers while grazing crested wheatgrass rangeland and compare that to an estimate of the maintenance energy expenditure of heifers consuming a diet of similar quantity and quality. The main finding was that grazing heifers expended 161 kcal·BW$^{-0.75}·d^{-1}$. This value was independent of the levels of available forage encountered during this study (from 880 kg DM·ha$^{-1}$ to 284 kg DM·ha$^{-1}$).

Field Study

Energy expenditure

CERT measurements were conducted ten times with each animal, twice during each of the five trials, for a total of 40 measurements. Seventy-five percent of these measurements failed to yield a urine sample for subsequent specific activity determination. Over one-half of the failures could be attributed to malfunction of the extraction pump. I was unable to rectify this problem. Other reasons for failure were catheter expulsion, broken fluid tube connections, infusion pump failure and broken harnesses.

Of the ten measurements which were successful, two occurred during each trial, and for two trials the results came from the same animal. These results are shown in Table 4. The resulting confidence interval ($P<0.10$) for the overall mean was 118-204 kcal·BW$^{-0.75}·d^{-1}$. 
Table 4. The estimated daily energy expenditure (kcal·BW\(^{-0.75}\)·d\(^{-1}\)) of heifers grazing crested wheatgrass in 1979.

<table>
<thead>
<tr>
<th>Trial #, Collection #</th>
<th>Animal #</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>(\bar{x})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1,1</td>
<td></td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>94</td>
<td>170</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>246</td>
<td></td>
</tr>
<tr>
<td>2,1</td>
<td></td>
<td>186</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>180</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>---</td>
<td>174</td>
<td>---</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td>3,1</td>
<td></td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>222</td>
<td>155</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>88</td>
<td></td>
</tr>
<tr>
<td>4,1</td>
<td></td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>132</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>---</td>
<td>---</td>
<td>177</td>
<td>86</td>
<td></td>
</tr>
<tr>
<td>5,1</td>
<td></td>
<td>---</td>
<td>64</td>
<td>---</td>
<td>---</td>
<td>170</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>275</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td>overall</td>
<td>(\bar{x})</td>
<td>SD</td>
<td>SE</td>
<td>(%CV)</td>
<td>CI (^2)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>161</td>
<td>74.2</td>
<td>23.5</td>
<td>46.0</td>
<td>43</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)CV = coefficient of variation

\(^2\)CI = confidence interval @ P < 0.10
Intake

The quantity of organic matter intake fluctuated over the grazing season. However, these differences were not consistent or significant. When intake was expressed as digestible organic matter, the level of intake declined significantly during the fifth trial. These results are shown in Table 5 along with fecal output data. Feces averaged 18 percent DM and 75 percent OM across the five trials with no significant difference between trials.

The overall mean of $54.5 \text{ gOM·BW}^{-0.75} \cdot \text{d}^{-1}$ equals $4.5 (±1.0)$ kg DM·head·d$^{-1}$ for 305 kg animals and when diets are 88 percent organic matter.

Intake is expressed as a function of body weight and both body weight and average daily change in body weight are presented in Table 6. Total body weights did not differ significantly across trials. However, the average daily change in body weight during trial 4 was significantly lower than in the previous trials. The animals were not weighed at the completion of trial 5 and an average daily weight change was not available for that period. I feel that weight loss during trial 5 was at least as high as during trial 4.

Diet quality

Indices of diet quality (crude protein and IVOMD) for each trial are presented in Table 7. In addition, crude protein and IVOMD of
Table 5. Organic matter intake (OMI), digestible organic matter intake (COMI), and fecal output (organic matter basis) (g·BW⁻⁰.⁷⁵·d⁻¹) during the five trials of 1979.

<table>
<thead>
<tr>
<th>Trial</th>
<th>OMI</th>
<th>DOMI</th>
<th>fecal output</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>51.8</td>
<td>22.5</td>
<td>29.4</td>
</tr>
<tr>
<td>2</td>
<td>57.6</td>
<td>23.8a</td>
<td>33.8</td>
</tr>
<tr>
<td>3</td>
<td>58.6</td>
<td>22.4a</td>
<td>36.2</td>
</tr>
<tr>
<td>4</td>
<td>55.1</td>
<td>21.2a</td>
<td>33.9</td>
</tr>
<tr>
<td>5</td>
<td>49.2</td>
<td>16.9b</td>
<td>32.3</td>
</tr>
<tr>
<td>x</td>
<td>54.5</td>
<td>21.3</td>
<td>33.1</td>
</tr>
</tbody>
</table>

LSD statistic

1 Means followed by a different lower case letter are significantly different at P<0.10

2 ANOVA F-statistic for treatment mean squares was nonsignificant
Table 6. Body weights (kg) and the change in body weight (kg·d⁻¹) for each trial and during each of the first four trials, respectively during 1979.

<table>
<thead>
<tr>
<th>Trial #</th>
<th>LSD statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>body weight</td>
<td>293 305 310 313 301 305 NS</td>
</tr>
<tr>
<td>body weight change</td>
<td>+.57ᵃ⁻¹ +.43ᵃ +.18ᵃ -.63ᵇ -- +.14 0.41</td>
</tr>
</tbody>
</table>

¹Means followed by a different lower case letter are significantly different at P<0.10.
Table 7. In vitro organic matter digestibility (%, IVOMD) and crude protein (CP as % of organic matter basis) of available forage and the IVOMD, crude protein and crude protein intake (gCP·d⁻¹) of cattle diets for five trial periods, 1979.

<table>
<thead>
<tr>
<th></th>
<th>Trial 1</th>
<th>Trial 2</th>
<th>Trial 3</th>
<th>Trial 4</th>
<th>Trial 5</th>
<th>LSD statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>forage IVOMD</td>
<td>45.7ᵃ¹</td>
<td>43.1ᵃᵇ</td>
<td>40.3ᵇ</td>
<td>40.0ᵇ</td>
<td>35.3ᶜ</td>
<td>41.6</td>
</tr>
<tr>
<td>diet IVOMD</td>
<td>43.3ᵃ</td>
<td>41.3ᵃᵇ</td>
<td>38.3ᵇᶜ</td>
<td>38.4ᵇᶜ</td>
<td>34.3ᶜ</td>
<td>39.1</td>
</tr>
<tr>
<td>forage CP</td>
<td>5.6ᵃ</td>
<td>4.3ᵇ</td>
<td>3.4ᶜ</td>
<td>3.5ᶜ</td>
<td>3.6ᶜ</td>
<td>4.1</td>
</tr>
<tr>
<td>diet CP</td>
<td>7.3</td>
<td>6.1</td>
<td>5.9</td>
<td>5.8</td>
<td>5.7</td>
<td>6.2</td>
</tr>
<tr>
<td>CP intake</td>
<td>275</td>
<td>256</td>
<td>259</td>
<td>241</td>
<td>212</td>
<td>249</td>
</tr>
</tbody>
</table>

¹Means followed by a different lower case letter are significantly different at P<0.10
the available forage are also presented in this table. Forage and dietary IVOMD and forage crude protein declined as forage matured, though crude protein content stabilized in August during trials 3, 4 and 5. Dietary crude protein content declined, though nonsignificantly, yet remained above the highest value of forage crude protein content during all five trials.

As IVOMD percentages were combined with intake data to calculate DOMI levels, intake levels (OMR) were combined with dietary crude protein content to provide data on crude protein intake (gCP·c⁻¹). This information is also shown in Table 7, though there were no significant differences between trial means. The NRC (1976) recommendations for daily crude protein intake by 300 kg heifers is 400 g.

Available forage

The levels of available forage declined as the study progressed as shown in Table 8. No measureable forage regrowth occurred during the 1979 field season. Total forage production yield was 870 kg·DM·ha⁻¹. The phenological stage of crested wheatgrass during each trial is listed below the respective value for quantity of available forage (Provenza 1980).

The decline in available forage was from forage removal by grazing. Assuming these heifers were equivalent to 0.75 animal unit
Table 8. Levels of available forage (kgDM·ha⁻¹) and the representative phenological stage occurring during the five trial periods, 1979.

<table>
<thead>
<tr>
<th>Trial #</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>x</th>
<th>LSD statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>available forage</td>
<td>880&lt;sup&gt;a&lt;/sup&gt;</td>
<td>762&lt;sup&gt;b&lt;/sup&gt;</td>
<td>481&lt;sup&gt;c&lt;/sup&gt;</td>
<td>389&lt;sup&gt;cd&lt;/sup&gt;</td>
<td>284&lt;sup&gt;d&lt;/sup&gt;</td>
<td>559</td>
<td>90.4</td>
</tr>
<tr>
<td>phenological stage</td>
<td>head</td>
<td>head</td>
<td>hard</td>
<td>hard</td>
<td>hard</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>seed</td>
<td>seed</td>
<td>seed</td>
<td>seed</td>
<td>seed</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>

<sup>1</sup>MMeans followed by a different lower case letter are significantly different at P<0.10.

<sup>2</sup>Provenza (1980)
months, the stocking rate for pasture 1 during this study was approximately 1.7 AUM·ha^{-1} (1.5 ac·AUM^{-1}).

Laboratory Study

Energy expenditure

The laboratory study provided estimations of maintenance and fasting energy expenditure. These estimates and associated statistics are shown in Table 9. These estimates were not significantly different and were combined to provide an overall estimate of maintenance energy expenditure of 110 kcal·BW^{-0.75}·d^{-1}. Accumulation of infusate at the site of infusion caused a reduction in sample size from 8 to 4 for the basal estimates and from 12 to 10 for the maintenance estimates.

Figure 1 shows the increase in urine specific activity with time after infusion initiation for two selected examples. The two infusion rates, 110.1 nCi·min^{-1} and 40.6 nCi·min^{-1}, were from measures of maintenance and fasting metabolism, respectively. The time sequence for the higher infusion rate shows the depression in urine specific activity following the feeding of the subject at 600 minutes and the variation between the non-pooled urine samples of 1300 minutes and 1400 minutes. The lower infusion rate was utilized only to provide information on the CO_{2} dynamics of the infusions conducted during 1979. Analysis of this time sequence for all fourteen \textsuperscript{14}C-HCO_{3} infusions indicated that the infused \textsuperscript{14}C-HCO_{3} reached equilibrium with the CO_{2} body pool between 700 and 970 minutes after infusion initiation. The coefficient of variation for specific activity among urine samples
Table 9. The estimates of fasting and maintenance energy expenditure (kcal·BW⁻⁰.⁷⁵·d⁻¹) of stall-fed heifers consuming 53.7 g OM of crested wheatgrass hay·BW⁻⁰.⁷⁵·d⁻¹.

<table>
<thead>
<tr>
<th></th>
<th>( \bar{x} )</th>
<th>SD¹</th>
<th>SE²</th>
<th>%CV³</th>
<th>CI⁴</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>fasting</td>
<td>105</td>
<td>21.7</td>
<td>10.9</td>
<td>20.6</td>
<td>25.7</td>
<td>4</td>
</tr>
<tr>
<td>maintenance</td>
<td>111</td>
<td>22.1</td>
<td>7.0</td>
<td>19.8</td>
<td>12.6</td>
<td>10</td>
</tr>
<tr>
<td>combined</td>
<td>110</td>
<td>21.3</td>
<td>5.7</td>
<td>19.5</td>
<td>10.1</td>
<td>14</td>
</tr>
</tbody>
</table>

¹standard deviation

²standard error

³coefficient of variation

⁴confidence interval at P<0.10
Figure 1. Specific activity of carbon in urine CO₂ following continuous infusion of NaH¹⁴CO₃.
collected at a single point in time (as contrasted to pooled samples) was 21 percent.

**Organic matter, nitrogen and energy balances**

Table 10 presents the data on organic matter, nitrogen and energy balances from this laboratory study. The *in vivo* organic matter (OM digestibility of 50.3 percent has a confidence interval ($P<0.10$) of 47.4 to 53.2 percent. The inclusion of the OM balance data from the 10 day preliminary trial reduced this interval to 49.1 to 54.3 percent for a mean *in vivo* digestibility of 51.2 percent. Estimates of *in vitro* organic matter digestibility were 51.0 percent and 47.2 percent when rumen inoculum sources were taken from cattle consuming diets of 100 percent alfalfa and 100 percent crested wheatgrass hay, respectively.

Feces averaged 25 percent dry matter (DM) and 89 percent OM for individually analyzed samples collected twice daily. Feces averaged 25 percent DM and 90 percent OM for fecal composite samples from daily 10 percent aliquots.

Nitrogen retention data indicated an apparent negative balance. The crude protein content of the hay was 5.1 percent (OMB) and of the 28.3 g N fed daily, nearly 50 percent was excreted in the urine. Fecal losses were 75 percent of the intake level, a value 7 percent higher than estimated metabolic fecal losses (MFN) of 19.2 gN·d$^{-1}$ assuming MFN losses of 0.48 gN·100 g$^{-1}$ DM intake (McDonald et al. 1973). The resulting confidence interval of nitrogen retention was -8.3 to -4.3 gN·d$^{-1}$. 
Table 10. Organic matter (g·BW^{-0.75}·d^{-1}), nitrogen (g·d^{-1}), and energy (kcal·d^{-1}) balances of stall-fed heifers consuming crested wheatgrass hay.

<table>
<thead>
<tr>
<th></th>
<th>Organic matter</th>
<th>Nitrogen</th>
<th>Energy</th>
</tr>
</thead>
<tbody>
<tr>
<td>intake</td>
<td>53.7</td>
<td>28.3</td>
<td>14582</td>
</tr>
<tr>
<td>fecal losses</td>
<td>26.7</td>
<td>21.1</td>
<td>8678 (-60%)</td>
</tr>
<tr>
<td>urine losses</td>
<td>--</td>
<td>13.5</td>
<td>524 (-3.5%)</td>
</tr>
<tr>
<td>methane losses</td>
<td>--</td>
<td>--</td>
<td>847{\textsuperscript{1}} (-5.8%)</td>
</tr>
<tr>
<td>heat increment</td>
<td>--</td>
<td>--</td>
<td>2990{\textsuperscript{2}} (-21%)</td>
</tr>
<tr>
<td>balance</td>
<td>+27.0</td>
<td>-6.3</td>
<td>+1633 (11.0% of GE)</td>
</tr>
<tr>
<td></td>
<td>(50.3% digestible)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>confidence interval</td>
<td>+1.2</td>
<td>+7.0</td>
<td>+708</td>
</tr>
<tr>
<td>(P&lt;0.10)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\textsuperscript{1} Estimated from the equation of Blaxter and Clapperton (1965):

\[ CH_4 (\text{kcal} \cdot \text{100 kcal}^{-1} \text{ fed}) = 1.30 + 0.112D - (2.37 - 0.05D) \]

where: D = % digestibility of dietary energy (=40%).

\textsuperscript{2} Based on Cook (1970) where HI = 450 kcal·1b^{-1} DM fed (=0.87 kcal·g^{-10MI}).
Calculation of energy balance required estimation of methane and heat increment losses as indicated in the footnotes in Table 10. The resulting energy balance of \(+1633 \text{ kcal} \cdot \text{d}^{-1}\) had a confidence interval of \(+925\) to \(+2341\). This would imply a deficiency in energy intake as this slightly positive balance (synonymous with NEm) would be insufficient to meet the basal energy demands of the restrained animal.
DISCUSSION

Energy Expenditure

The energy expended by heifers grazing crested wheatgrass range-land was estimated at 161 (±43) kcal·BW⁻⁰.⁷⁵·d⁻¹. Thus, the 305 kg heifers expended 11.75 Mcal·d⁻¹. This estimated level of energy expenditure was independent of levels of available forage which ranged from 294 to 880 kg DM·ha⁻¹, and the hypothesis of this study was rejected.

The estimated fasting metabolism as 105 kcal·BW⁻⁰.⁷⁵·d⁻¹, a value higher than that reported by Brody (1945) but the same as that reported by Webster et al. (1974). In fact, Webster et al. (1974) recommended that this value should be used for estimating fasting metabolism and that direct measurement of this parameter, for any body weight or previous level of feed intake was not necessary.

The maintenance level of energy expenditure was estimated as 111 kcal·BW⁻⁰.⁷⁵·d⁻¹ and was not significantly different from the estimated value for fasting metabolism. This was not unexpected since maintenance measurements were conducted with restrained animals and the only increase in heat production above fasting would be factors associated with energy losses attributable to feed ingestion.

Blaxter (1962) has indicated this additional loss would be approximately 5 kcal·BW⁻⁰.⁷⁵·d⁻¹. Additionally, the two hours of eating daily the the restrained heifers would represent an additional energetic cost of 6.5 kcal·BW⁻⁰.⁷⁵·d⁻¹. Fasting and maintenance estimates were combined to increase the number of observations and reduce the
associated standard error, and this combination produced a mean of 110 kcal·BW$^{-0.75}$·d$^{-1}$.

The estimated energy expenditure associated with free-roaming conditions was 45 percent higher than the estimated maintenance energy expenditure. This increase was less than the 60 percent suggested by Young (1970) or the 50 percent increase suggested by Wallace (1956) for cattle under free-ranging conditions. However, the 161 kcal·BW$^{-0.75}$·d$^{-1}$ estimate was nearly equal to Young's (1970) estimate of 160 kcal·BW$^{-0.75}$·d$^{-1}$ obtained using CERT measurements with three heifers grazing pastureland in Australia. The estimated 45 percent increase falls within the range of values for sheep reported by other workers as reviewed in Table 2.

The estimated increase in energy expenditure could be attributed to several factors. Graham (1964) determined the energetic cost of eating as 0.54 kcal·kgBW$^{-1}$·hr$^{-1}$. Osuji (1974) used 0.45 kcal·kgBW$^{-0.75}$·hr$^{-1}$ and estimated that increased time spent grazing by free-roaming sheep would increase energy expenditure by 25 percent above maintenance. Holmes et al. (1978) worked with calves and estimated a range of 0.52 kcal to 0.82 kcal·kgBW$^{-1}$·hr$^{-1}$ for heat production of eating. Also, these authors reaffirmed the conclusion that the heat production associated with grazing is related to BW$^{1.0}$. Osuji et al. (1975) reported that the energy cost of eating was more a function of time spent eating than the level of intake and their research reaffirmed Graham's (1964) earlier estimate. Webster (1972) has reported a range of values similar to
Holmes et al. (1978), and has attributed this energetic cost to physiological changes that are apparent fifteen minutes after initiation of eating. These changes included increases in systolic blood pressure, heart rate and plasma angiotensin due to release of renin and a decreased plasma volume. Additionally, Young (1966) reported an eating energy cost of 0.32 to 0.74 kcal·kgBW$^{-1}$·hr$^{-1}$ with no difference between normal feeding and sham feeding where 77 percent of the intake was removed through an esophageal opening. Osuji (1974) has reaffirmed Webster's (1972) earlier observations, but suggested that further research in this area is required.

Using 0.82 kcal·BW$^{-1}$·hr$^{-1}$, the upper limit reported by Holmes et al. (1978) and a value applicable to the grazing animal consuming a roughage diet, the energy expenditure associated with 9.2 hours of grazing would be 32 kcal·BW$^{-0.75}$·d$^{-1}$. The 9.2 hours of grazing time was derived from an average of 9.1 hours reported by Scarnecchia (1980), 8.4 hours reported by Nastis (1979), both from studies conducted under similar conditions to that reported here, and the 10.0 hours I determined from 24-hour observations conducted during trials 1, 2 and 4. The combined average of 9.2 hours was within the range of grazing times reported by other investigators as cited by Arnold and Dudzinski (1978).

This estimated energy expense would be 25 kcal·BW$^{-0.75}$·d$^{-1}$ more than for a stall-fed animal spending two hours eating a similar quantity of feed. This then represented a 23 percent increase in energy expenditure above maintenance, or 50 percent of the total in-
crease attributed to free-ranging conditions. This increase was for the act of eating exclusive of the activities of walking and standing associated with grazing.

Travel represents an energetic cost of free-roaming conditions and has been estimated by several researchers. Graham (1964) reported 0.60 kcal·kgBW⁻¹·km⁻¹ of travel. Malechek and Smith (1976) used the value reported by Brody (1945) of 0.45 kcal·kgBW⁻¹·km⁻¹. Osuji (1974) used 0.59, a compromise value that included consideration of vertical as well as horizontal travel. Cook (1970) used a range of 0.58 to 0.78 kcal·kgBW⁻¹·km⁻¹, a value suggested by Blaxter's (1962) comment that 0.1 kcal is required to move 100 lbs of live weight one vertical foot. Moen (1973) used 0.59 (horizontal) and 6.45 (vertical) kcal·kgBW⁻¹·km⁻¹, as reported by Clapperton (1961), to calculate the energetic cost of travel by white-tailed deer. Using the lower value suggested by Cook (1970) for travel on 2 percent slopes the energetic cost of travel for these heifers was estimated as 9.5 kcal·BW⁻¹·75·d⁻¹. This was calculated for an average daily distance traveled of 3.9 km. This value was an average of 5.4, 2.2 and 4.1 km recorded during the 24 hour observation periods for trial 1, 2 and 4, respectively. This distance value was similar to others cited by Arnold and Dudzinski (1978) for cattle grazing small paddocks, but usually less than those values cited for cattle grazing pastures of 260 to 2000 ha. The estimated value of 9.5 kcal represented a 9 percent increase above maintenance
and was 20 percent of the observed increase due to free-ranging conditions.

Vercoe (1973) indicated that standing expended 14 kcal·BW\(^{-0.75}\)·d\(^{-1}\) more than lying, a value 2.5 kcal greater than reported by Clark et al. (1972). The reported time cost values for these two studies were 0.14 kcal and 0.12 kcal·kgBW\(^{-1}\)·hr, respectively, approximately one-third of the value reported by Graham (1964). The 13.8 hours spent standing (a summation of observed times for grazing and standing idle) converts to an energetic cost of 7 to 20 kcal·BW\(^{-0.75}\)·d\(^{-1}\) using the low and high values reported above. This range was regarded as indicative of only a small additional free-roaming expense since stall-fed animals spent 6 to 12 hours standing daily. Also, the cost of position changes, at an energy expense of 0.6 kcal·kgBW\(^{-1}\) per double change (Clark et al. 1972) was ignored. Additionally, lying was treated as a non-energy demanding activity, though the 40 percent of the day the heifers spent lying was a relatively low value (Arnold and Dudzinski 1978) and indicated a relatively high daily energy expenditure due to an energy demanding 14.4 hours (60 percent) of activities each day.

Other activity factors deserving mention are thermoregulation and rumination. Though these two factors represented a portion of the daily energy expenditure, neither were expected to have had a quantifiable effect upon the free-roaming conditions of this study. As seen in Table 11 of the Appendix, the summer temperatures were within a range of 0°C to 35°C with most daily temperatures between
10°C to 30°C. McLean and Calvert (1977) reported no differences in mean rates of heat production for 15°C vs 35°C. Rogerson (1960) reported no differences in energy losses for cattle in respiration chambers at ambient temperatures of 20°C, 30°C and 40°C. Young (1975) did report that housed animals moved outside and exposed to temperatures of 17°C and 12°C exhibited increases in heat production of 18 percent and 37 percent, respectively. However, lower critical temperatures and lower increases in heat production result from temperature acclimation (Young 1972). Interestingly, Young and Christopherson (1974) indicated that the major effect of cold is not through the increase in heat production for the maintenance of homeothermy, but the reduction in feed digestibility caused by low temperatures and the resulting increase in the animal's maintenance requirements. Blaxter and Wainman (1961) indicated lower critical temperatures of -1°C and 6°C for cattle gaining weight and at maintenance, respectively. Malechek and Smith (1976) cited Young (1971) in identifying the animal's minimum critical temperature as -14°C, a value well below those reported for this study. Extrapolating from Young's (1972) work, the rangeland cattle used in this study could be considered as adapted to moderate temperatures encountered during the study.

No observations were made of the restrained cattle for time spent ruminating. From the three completed 24-hour observations conducted during the field study, the study heifers spent 390 minutes daily ruminating. Graham (1964) has estimated the energetic cost of rumin-
nating at $0.24 \text{kcal} \cdot \text{kgBW}^{-1} \cdot \text{hr}^{-1}$, a value considerably higher than that implied by Osuji et al. (1975). Despite this discrepancy the contribution of rumination time to total daily energy expenditure is small. Using Graham's (1964) value results in an estimated expenditure of $6 \text{kcal} \cdot \text{BW}^{-0.75} \cdot \text{d}^{-1}$. Though the third most time-consuming activity of these heifers, ruminating represents less than 4 percent of the daily energy expenditure, certainly a further indication of the energetic advantage of the ruminant digestive processes. The 6.5 hours these heifers spent ruminating falls within the average range of 5 to 9 hours reported by Arnold and Dudzinski (1978). Since rumination time is a function of quantity and quality of feed, little difference in energetic cost for stall-fed animals would be expected.

Though the energy balance data provided in Table 10 could not be regarded as a product of a conventional calorimetry measurement, the information does yield insight into energy losses associated with metabolism of this feed. The gross energy of the crested wheatgrass hay was 4232 cal·gOM, a value similar to the 4330 cal·gDM reported by Cook and Harris (1968), and within the general range for roughages outlined by Graham (1969). Apparent fecal energy losses were 60 percent of the gross intake, a value on the high end of the scale as indicated by Kromann (1973), but 15 percent higher than expected for this feed from the information provided by Cook and Harris (1968).

The discrepancy with this earlier work was attributed to differences in diet quality between diets selected by grazing animals.
and diets consumed by stall-fed animals. The fact that grazing animals are selective and that this selection process results in a more nutritious diet is well-documented (Kothmann 1980). The stall-fed animals in this laboratory study were fed whole plants and selection was not a component of intake. The 10 percent discrepancy between in vivo digestibility and DE is difficult to explain. Typically, digestibility and DE values differ by only a small percentage (Moir 1961), and the reasons for this 10 percent differences are unknown.

It should be noted that the data in Table 10 is for apparent digestible energy (DE) and differs from true DE due to presence of materials other than undigested food residues.

Estimated methane losses were within the range outlined by Kromann (1973) who indicated gaseous losses of digestion, of which CH₄ is a major component, would be between 5 percent and 9 percent of gross energy.

Street et al. (1963) have indicated urine energy losses are related to urinary nitrogen percentage. Using their formula:

\[ \text{Urinary Energy} = 0.022 + 0.118 \times (\% \text{urinary N}) \text{ (kcal·ml}^{-1} \text{)} \]

provided an estimate of urine energy losses of 659 kcal·d⁻¹, 26% greater than that observed. Additionally, using a similarly derived regression reported by Blaxter et al. (1966) provided an estimate 35 percent lower than that observed. Obviously, these regressions are approximations and not universal in their application.
Following subtraction of the above losses from gross energy, the calculated metabolizable energy (ME) content of the hay was 1336 cal·gDM⁻¹, considerably lower than the 2011 cal·gDM⁻¹ reported by Cook and Harris (1968). This difference was largely attributed to the larger fecal energy losses observed for this experiment since Cook and Harris (1968) reported an ME value which was 83 percent of DE and this experiment provided an ME value which was 78 percent of DE.

Blaxter (1962) indicated ME is generally 85 percent of DE. From this information it was estimated that 1 kg DOMI of this hay provided 2.7 kcal ME, a value much lower than the traditional conversion factor of 4.0 kcal ME·kg DOMI⁻¹ (Lambourne and Reardon 1963). Additionally, 2.7 kcal·kg DOMI⁻¹ was possibly higher than actual since gaseous losses other than methane were not estimated.

Assuming 2.7 Mcal ME·kg DOMI⁻¹ remains constant during the later phenological stages of crested wheatgrass growth, the ME intake of heifers during the first four trials of the 1979 field season averaged 4.4 Mcal·d⁻¹. This intake declined to 3.3 Mcal ME·d⁻¹ during the fifth trial. The NRC (1976) recommendation for maintenance of 300 kg heifers is 9.3 Mcal ME·d⁻¹.

Kromann (1973) indicated that heat increment losses would be 10 to 40 percent of gross energy. Included in this category were heat of fermentation losses and nutrient metabolism heat losses. The estimated losses of 21 percent due to the heat increment reduced the energy balance to near zero. It was apparent that as digestibility and DE decrease with advancing maturity the constant daily
energy expenditure of 11.6 Mcal by the free-roaming 300 kg heifer cannot be satisfied unless daily intake levels are increased.

**Intake**

Van Dyne et al. (1980) have compiled a comprehensive literature review of studies of daily intake levels for several animal species when grazing different plant communities and at different seasons of the year. For cattle, this review presented a range of daily intake levels from 1.1 to 2.6 percent of BW when grazing summer ranges. Raleigh and Lesperance (1972) have stated that intake varies between 1.5 and 2.5 percent of BW with 3 percent occurring under the best of conditions. Church and Pond (1974) indicated that intake was closely related to forage DE with dry matter intake of 1.0 to 1.5 percent of BW expected for forages with DE of 1.76 to 1.98 kcal·g⁻¹, a range which brackets the DE of the crested wheatgrass hay used in this study. Similar relationships have been reported by Blaxter et al. (1966) and Ammann et al. (1973). Nastis (1979) reported a daily intake of 1.2 percent (OMD) of BW for heifers grazing crested wheatgrass rangeland during summer and fall seasons. This was similar to the daily intake level of 1.3 percent (OMD) of BW determined during this study. In both of these latter studies the daily level of intake was independent of the amount of available forage.

Recently, Milchunas et al. (1978) have condensed and summarized the literature concerning factors which regulate feed intake. Under
bulk limiting conditions, when digestibility of forage is less than 52-66 percent (Conrad et al. 1964, Montgomery and Baumgardt 1965, Jones 1972) and meal size is not a function of energetic demands under physiological control (Balch and Campling 1962, Baile and Forbs 1974), these authors outline two categories of factors which regulate daily intake. These are fill and turnover time. Fill is controlled by gut capacity, seasonality, and palatability factors; factors which are a function of physiological characteristics of the animal species and environmental characteristics of the forage supply. Turnover time is a function of rate of digesta passage and the rate of digestion, rates which are mostly a function of rumen structure and feed qualities. It is this latter category of turnover time that is pertinent to a discussion of the short-term control of the daily intake of the grazing ruminant.

Ellis (1978) has discussed the controlling factors of this latter category and has explained that the voluntary intake of poorly digestible forage was limited by reticulo-rumen volume, the volume occupied by forage residues undergoing digestion, and the rates of chemical and physical processes which determine the turnover time of this volume. Further, he has formulated that:

$$VI = UDMF \times \frac{kp}{kp/(Kd+Kp)}$$

where: $VI = \text{daily voluntary intake (percent of BW)}$; $UDMF = \text{undigested dry matter fill}$; $kp = \text{rate of digesta passage}$; $kd = \text{rate of digestion}$, and where $UDMF = kp \times \text{undigested dry matter excretion.}$
This formulation of VI as a function of the rates of excretion, digesta passage and digestibility has significance when discussing the factors controlling the VI of heifers grazing crested wheatgrass rangelands during summer months when forage digestibility is well below 66 percent. Data from this study and Nastis (1979) indicated that UDME remained constant throughout the grazing periods. These rates were 0.77 and 0.79 kg OM·100 kg BW·d⁻¹ for Nastis (1979) and this study, respectively. Conrad et al. (1964) have also reported constant UDME rates for dairy cattle consuming roughage diets of varying digestibility. If UDMF is also a constant value, as indicated by Rice et al. (1974) (where UDMF = 0.145 kgBW⁻⁷⁵), then kp would also have had to remain constant throughout the grazing period of this study. Thus, the daily intake level of the free-roaming ruminant on summer ranges can be formulated as:

\[ VI = \frac{C}{1-kd} \]  

where:  
C = a constant rate of UDME, or the kp for a known UDMF.  
Either constant can be determined for a particular forage diet.

Data presented by Meissner et al. (1979) supported the work of Ellis (1978). UDME can be determined by total fecal collections while kp and UDMF can be estimated using dilution theory as outlined by Ellis et al. (1977). For crested wheatgrass rangelands grazed by heifers during summer months UDME equals 0.78 and VI can be predicted from estimates of dietary digestibility. However, the between
animal variability of C prevents VI from being directly proportional to kd values. That is, the average C of 0.78 has an experimental range of ±0.10 and this fluctuation will mask the effects of kd upon VI. For example, VI decreases from 1.4 percent to 1.2 percent of BW for an average C of 0.78 as kd declines from 0.45 to 0.35. For a 300 kg heifer, this example represents an intake decline of 58 to 50 g·BW\(^{-0.75}·d^{-1}\), with mean extremes which would not be significantly different because of the between animal variability of UDME. Therefore, it can be concluded that the daily intake of heifers grazing summer ranges will fluctuate between 1.0 percent and 1.6 percent of BW as a function of kd and the variability associated with estimation of daily rates of UDME, and that VI can be estimated by determining dietary kd and setting C = 0.78.

The findings of the study indicated that the free-ranging animal had a daily intake of both metabolizable energy and crude protein during all trial periods of the 1979 field study that were below the NRC (1976) recommended levels. Yet, under these conditions a weight loss was observed only during the latter half of the field study. I can suggest several reasons for this apparent contradiction:

1. The NRC recommendations are inflated. The guidelines set by the NRC are not exact standards for all animals. The NRC tables are constructed for use in intensive animal production systems, and are probably excessive both in their recommendations and
in their application to the extensive production systems of the rangeland animal.

2. The gravimetric determination of body weight did not accurately reflect the nutritional status of the animal. Total body weight is a measurement which does not delineate between changes in body fat content, weight of reticulo-rumen contents, or water retention. However, there were no observable circumstances during the study which would have suggested these types of changes occurring at different rates over the course of the field season.

3. The metabolizable energy content of the grazing animal's diet was higher than that determined for crested wheatgrass hay. The ability of the free-ranging animal to select a diet may reduce the losses associated with calculation of metabolizable energy observed with a stall-fed animal. This factor is plausible and may explain the discrepancy between the data reported in this study and that reported by Cook and Harris (1968). Utilizing the metabolizable energy content of crested wheatgrass presented by these latter authors would increase the ME intake I reported by 50%. The ME intake would be 7.8 Mcal·d⁻¹, only 18 percent less than the NRC (1976) recommendation.

4. In vitro organic matter digestibility underestimated the actual in vivo digestion of the grazing animal's diet. I found a 2.9 percent underestimation by the in vitro technique of in vivo digestibility as reported in results of the laboratory study. If
this discrepancy can be applied to the field study, the use of the in vitro technique underestimated daily intake by 6 percent.

5. The CERT field-conducted measurements overestimated the energy expenditure of the free-ranging animal. CERT does not provide a direct measure of daily energy expenditure, and the relative estimate may overestimate actual energy expenditure by at least 10 percent. This overestimation cannot be quantified without the concurrent use of a conventional calorimetric technique.

Given the possible limitations, two final points can be discussed:

1. The central hypothesis of this study was that the daily energy expenditure of the free-ranging animal would be a function of the quantity of available forage. As this quantity diminished the daily time spent grazing would increase and with it, the daily energy expenditure. However, if each additional hour spent grazing increases the daily energy expenditure 2 percent (Holmes et al. 1979), and grazing time increases from 6 to 12 hours with a decreasing forage supply, the increase in the daily energy expenditure would be ≤ 12 percent. CERT methodology, even with the suggested modifications, could not detect that change.

2. Assuming that the body weight changes I recorded were accurate reflections of the nutritional status of these heifers, several standards for their maintenance can be suggested. These are:
   a. a digestible organic matter intake of \( > 21 \text{ g} \cdot \text{BW}^{-0.75} \cdot \text{d}^{-1} \),
   b. a crude protein intake of \( > 241 \text{ g} \cdot \text{d}^{-1} \).
c. a dietary *in vitro* organic matter digestibility of $\geq 38$ percent, and

d. a forage supply of $\geq 390$ kg·ha$^{-1}$.

The energy standard cannot be defined because of the variability associated with the mean value I have reported.

**Summary and Conclusions**

This study was designed with three objectives. These were to (1) determine the energy expended by heifers grazing a variable supply of available forage during the summer grazing season, (2) determine the differences in energy expended by heifers grazing seeded rangelands and penned animals consuming a diet of similar quantity and quality, and (3) develop a table of energy requirements for a heifer grazing crested wheatgrass rangeland during the summer grazing season.

Energy expenditure was estimated twice for four heifers during each of five ten-day trials during June, July, August and early September, 1979. These estimates were obtained using the carbon dioxide entry rate technique. In addition, total fecal output, dietary crude protein, and dietary *in vitro* organic matter digestibility (IVOMD) were estimated while the animals grazed a 20 ha pasture. Four-day total fecal collections with four heifers were made during each period. Forage availability during each period was estimated using the ocular-weight estimate method and forty $1\,m^2$ circular plots.
The energy expended by free-roaming animals was estimated as 161 kcal·kgBE\(^{-0.75}\)·d\(^{-1}\). The associated confidence interval was ±27 percent of the mean. This large variation was due to the inability to collect in the field a urine sample pooled over 12 hours and the failure of 75 percent of the samplings to provide any urine sample for subsequent analysis for specific activity. The estimated mean showed no response to a forage supply which declined from 880 kgDM·ha\(^{-1}\) in late June to 284 kgDM·ha\(^{-1}\) in early September.

Daily intake, estimated from the ratio of total fecal output to the undigested fraction of the dietary extrusa samples, averaged 1.3 percent (OMB) of BW and was independent of the amount of available forage. Fecal excretion rates averaged 0.78 percent (OMB) of BW per day and demonstrated no significant changes across trials.

Body weights averaged 305 kg and did not differ significantly across trials. The change in body weight showed a significant decline during trial 4 when animals had an average daily weight loss of 0.63 kg.

Dietary crude protein content declined from 7.3 percent to 5.7 percent, but these apparent changes proved statistically nonsignificant. In addition, the low value of 5.7 percent was greater than the highest CP content of available forage (5.6 percent on a whole plant basis). The ability of the grazing animal to select a diet higher in CP content than that available on a whole plant basis is well documented (Kothmann 1980). Changes in crude protein intake across trials were also nonsignificant, and the total daily intake average of 249 g·d\(^{-1}\)
was 40 percent less than the NRC (1976) recommended level of 400 g·d⁻¹. Dietary IVOMD was continually less than the IVOMD of the available forage, but these within-trial percentages were nonsignificant. However, the 29 percent decline in dietary IVOMD from 43.3 percent in late June to 34.3 percent in early September was statistically significant (P<0.10).

During early July, 1980, crested wheatgrass was harvested as hay and fed to 260 kg yearling Angus heifers restrained in metabolism stalls in a thermoneutral and constantly illuminated laboratory. Daily feeding levels were 1.3 percent (O MB) of BW. Energy expenditure under these conditions was 111 (+12) kcal·kgBW⁻.⁷⁵·d⁻¹, 6 kcal greater than the mean estimate of the fasting metabolism. These two estimates of maintenance and fasting metabolism were combined to provide an estimate of 110 kcal·kgBW⁻.⁷⁵·d⁻¹ (n=14). The confidence interval of this estimate was +9 percent of the mean (P<0.10). This 67 percent reduction in the variability of this estimate compared to that obtained during the field study was attributed to the controlled collection of a urine sample over 12 hours and the doubling of ¹⁴C-HCO₃⁻ infusion rates to 100 nCi·m⁻¹.

Of the 45 percent increase in the estimated energy expenditure by heifers under free-roaming conditions, 50 percent was attributed to the energetic cost of the time spent grazing. The energetic cost of this activity was assumed as 0.82 kcal·kgBW⁻¹·hr⁻¹ of grazing time. Daily travel was estimated as 3.9 km and at an assumed ener-
getic cost of 0.58 kcal·kgBW⁻¹·km⁻¹ accounted for 20 percent of the estimated increase in energy expenditure. I could not account for the remaining 30 percent.

In vivo OM digestibility of the crested wheatgrass hay was 50.3 percent as compared to IVOMD percentages of 51.0 and 47.2 when using rumen inoculum from heifers consuming diets of alfalfa and crested wheatgrass hay, respectively.

The resulting nitrogen balance for the stall-fed animals was -6.3 gN·d⁻¹. The N intake was equivalent to 177 g CP·d⁻¹, a value below that determined for grazing heifers during the five trials of the field study. These data would indicate an apparent zero balance of N when CP intake equaled 216 g·d⁻¹, assuming N losses were similar during the 1979 field season. Thus, though CP intake levels were well below NRC (1976) recommendations, protein intake under summer grazing conditions could be assumed to be adequate for maintenance.

The energy balance data indicated that crested wheatgrass would not provide sufficient energy for maintenance at an intake of 1.3 percent of BW·d⁻¹. Given the estimated ME content of the crested wheatgrass hay, the daily intake of ME by the grazing animal would be 5.2 Mcal·d⁻¹, nearly 40 percent below the recommended (NRC 1976) daily level of 9.3 Mcal·d⁻¹. The estimated heat increment losses reduced NE intake to a level insufficient to meet basal energy demands.
Recommendations

Recommendations resulting from this research are divided into two categories. These categories are future research objectives and improvements in CERT methodology.

Future research objectives would include:

1. Comparative estimates of energy expenditure for seeded vs. native ranges, different grazing systems, and between grazing species.
2. Estimation of undigested dry matter fill and digesta passage rates for changing digestion rates of a particular forage or diet.
3. Clarify the minimum standards for maintenance proposed in this study.
4. Re-examine the daily energy expenditure of the free-ranging animal using the improvements in CERT methodology suggested below. Combine this with a field-obtained estimate of metabolizable energy intake.

Improvements in CERT methodology:

1. Infuse $^{14}$C-\(\text{HCO}_3^-\) intraperitoneally to provide a closer correlation with regressions by Young (1970) relating CO$_2$ entry rate to energy expenditure.
2. Make total collections of urine rather than utilizing an untested mechanical device.
3. Increase infusion rates to 200 nCi·min$^{-1}$. 
4. Analyze urine samples immediately upon collection for specific activity.

5. Reduce the bulk of the $^{14}$C-HCO$_3^-$ infusión pump system.
LITERATURE CITED


Appendix A. Table 11. Mean Monthly Precipitation (mm) and Maximum and Minimum Temperatures (°C) of the Field Study, 1979.

<table>
<thead>
<tr>
<th>Month</th>
<th>Precipitation</th>
<th>Temperature</th>
<th></th>
<th></th>
<th></th>
<th></th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>Maximum</td>
<td>Minimum</td>
<td>Maximum</td>
<td>Minimum</td>
</tr>
<tr>
<td>May</td>
<td>29</td>
<td>--</td>
<td>25.3</td>
<td>7.8</td>
<td>31.1</td>
<td>1.7</td>
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<tr>
<td>June</td>
<td>0</td>
<td>28.6</td>
<td>12.1</td>
<td></td>
<td>32.7</td>
<td>7.8</td>
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<td>July</td>
<td>6</td>
<td>29.4</td>
<td>12.8</td>
<td></td>
<td>33.3</td>
<td>11.1</td>
</tr>
<tr>
<td>August</td>
<td>29</td>
<td>29.3</td>
<td>10.0</td>
<td></td>
<td>30.5</td>
<td>10.0</td>
</tr>
<tr>
<td>September (1-5)</td>
<td>0</td>
<td></td>
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</tr>
</tbody>
</table>
VITA

Kris Mark Havstad

Candidate for the Degree of

Doctor of Philosophy

Dissertation: The Energy Expenditure of Heifers Grazing Crested Wheatgrass Rangeland in West-Central Utah

Major Field: Range Science

Biographical Information:

Personal Data: Born in Kansas City, Missouri, August 30, 1952; son of M. Peter and Alice L. Havstad; married Patti K. Meek August 17, 1976; two children—Jonathan J. and Jessica M.

Education: Graduated from Archbishop Mitty High School in San Jose, California, June, 1970; received Bachelor of Science with a major in range science from Oregon State University, June, 1975; received Master of Science with a major in range science and a minor in experimental statistics from New Mexico State University, June, 1977; completed requirements for Doctor of Philosophy with a major in range science at Utah State University, April, 1981.

Professional Experience: 1981—, Assistant Professor, Department of Range and Animal Science, Montana State University, Bozeman, Montana; 1977-1980, Graduate Research Assistant, Department of Range Science, Utah State University, Logan, Utah; 1975-1977, Graduate Research Assistant, Department of Range and Animal Science, New Mexico State University, Las Cruces, New Mexico; 1972-1975, Work/Study Student, Rangeland Resources Program, Oregon State University, Corvallis, Oregon.