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Maintenance Energy Requirements of Free Ranging Goats and Sheep

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MAINTENANCE ENERGY REQUIREMENTS OF
FREE RANGING GOATS AND SHEEP

by

Ederlon Ribeiro de Oliveira

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Range Science

UTAH STATE UNIVERSITY
Logan, Utah

1987

DEDICATION

This piece of work is dedicated to my parents Hélio Tavares de Oliveira and Maria José Ribeiro de Oliveira. The solid moral education they gave me and the lessons in love, patience and perseverance they taught me over all those years, were fundamental for my career. This small appreciation shows all the love I have for them.

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ABSTRACT

Maintenance Energy Requirements of Free-ranging Goats and Sheep

by

Ederlon Ribeiro de Oliveira, Doctor of Philosophy

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Major Professor: Dr. John C. Malechek
Department: Range Science

Measurements of energy expenditures for domestic animals are used as a basis to determine the total energy requirements for maintenance and for production. Most studies on energy metabolism have been conducted under controlled, confinement conditions, and the results extrapolated to free-ranging animals. Such approaches do not always represent the real energy costs of free existence in the range or pasture environment.

This study compared energy expenditures of sheep and goats under free-grazing conditions and assessed the accuracy of the carbon dioxide entry rate technique (CERT) as compared to the oxygen consumption method. In addition, 24-hour activity budgets were used to construct energy budgets for both animal species. These estimates were compared to CERT measurements. Dietary organic matter, crude protein, gross energy, digestible protein, and digestible energy intakes, as well as the apparent digestibility coefficients for crude protein and gross energy were compared for both species in one of the grazing trials.

The validation of CERT yielded the linear regression equation: $Y = 0.878 + 5.333\ ER$ where Y = energy expenditure in $\text{Kcal}\cdot\text{min}^{-1}$, and ER is the CO_2 entry rate in grams of CO_2 $\text{carbon}\cdot\text{min}^{-1}$. The coefficient of determination (r^2) was 0.979, and the residual standard deviation of ± 0.12 $\text{Kcal}\cdot\text{min}^{-1}$. Daily energy expenditure of goats was higher ($P<.05$) than that of sheep in all grazing experiments. The overall means were 127.1 and 88.4 $\text{Kcal}\cdot\text{BW}^{-.75}\cdot\text{d}^{-1}$ for goats and sheep, respectively.

High ambient temperatures during one of the grazing trials apparently caused heat stress to the grazing animals. Both species responded to this situation by using behavioral adaptations and avoidance mechanisms.

The energy budget method over-estimated energy expenditures of sheep by 9 percent, and grossly underestimated the energy expenditures of goats by 39 percent.

The nutritive value of the diets selected by both species was similar. However, goats had higher ($P<.05$) organic matter, crude protein, gross energy, digestible protein and digestible energy intakes. The apparent crude protein digestibility coefficient for goats was 20 percent higher ($P<.05$) than that for sheep. On the other hand, gross energy digestibility coefficients were similar for both species. Goats appeared to have an edge in meeting their dietary protein requirements under free-ranging conditions.

CERT can predict energy expenditures within ± 8 percent of the mean. It is a feasible technique for assessing energy expenditures of small ruminants under range conditions. The energy budget method was not reliable for estimating energy costs in small ruminants, especially goats.

(115 pages)

INTRODUCTION

The overwhelming growth of the human population has been worrying those working in the field of food production for some time. In some areas, the growth of large cities as well as the appearance of new villages and towns have been relegating farms and ranches to the less productive lands. Researchers feel that one of the best ways to cope with the increasing demand for food is through an increase in productivity and by better utilization of the so called "marginal lands".

The term "marginal lands" is in most cases synonymous with rangelands. According to Stoddart et al. (1975, p.2), rangelands "are those areas of the world, which by reason of physical limitations--low and erratic precipitation, rough topography, poor drainage, or cold temperatures -- are unsuited to cultivation and which are a source of forage for free-ranging native and domestic animals, as well as a source of wood products, water and wildlife".

The majority of the world's total ruminant population grazes on these rangelands, converting an otherwise unused natural resource into animal protein of high biological value. Among the domestic ruminants, cattle, sheep and goats are the animal species which provide the human population the major portion of its edible protein from animal origin. According to McDowell and Bove (1977), the increase in the demand of meat for human consumption will be around four percent per year up to the end of the twentieth century. McDowell (1979) states that the total protein supplied by animal sources to human consumption is nearly equivalent to that supplied by wheat and corn, and half of that supplied by all cereals together. Also according to the same author, meats and edible organs provide forty-five percent of the protein, and together with edible fats, supply fifty-three percent of the energy from animal products to the human diet.

According to Fitzhugh et al. (1978) and Tracey (1975), around eighty-five percent of the human population desires food of animal origin in their diets. However, as pointed out by Cunha (1982) the total protein level in the diet of people from developing countries remains at about one-half of those living in developed countries.

With this increasing pressure on land due to a growing human population, animal and range scientists around the world are becoming more aware of small ruminants, and in the last few years there has been an increasing interest in studying sheep and particularly goats as alternative animals to use on rangelands. Sheep and, especially, goats play an important role in developing countries and are responsible for providing high quality protein to rural populations, especially small farmers. Small ruminants also serve as a source of cash income for small holders.

The world population of sheep and goats is estimated at 1.028 billion and 410 million head, respectively (FAO 1978), concentrated principally in the tropics. In Africa the number of small ruminants is increasing in relation to cattle (Wilson 1984). Among the possible causes for this change is the supposedly better performance of goats under range conditions on harsh environments, a wider dietary range than cattle, an earlier physiological maturity, higher twinning rate and a shorter gestation period which, in turn, make them able to produce returns more rapidly than larger ruminants. However, much of the information available about goats is based on indirect observations and opinions, and not much is known about these small ruminants under free-grazing conditions, the predominant way they are raised. The development of studies on free-ranging animals will help to understand better the complexity of the soil-plant-animal inter-relationships, and will provide information to improve the management of rangelands.

Measures of energy expenditure for domestic animals have been used as a basis to determine energy requirements for maintenance, and for different phases of their productive cycle. Such studies on energy metabolism are important under practical conditions because the values found give animal nutritionists a guide on amounts of energy that must be supplied to the animals in order to meet their requirements.

This study investigated the energy expenditures of goats and sheep under grazing conditions, with the aim of better understanding the amount of energy needed by the free-grazing animals. The Carbon Dioxide Entry Rate Technique (CERT), which was used to estimate the energy expenditures of the free-ranging animals, was later compared with the oxygen consumption method for the same animals under confinement.

REVIEW OF LITERATURE

Among the nutrients required by living organisms, energy is, quantitatively, the most important item in the diet (Kearl 1982). Energy, in general, has been defined as the capacity to do work. However in nutritional terms, one must be concerned with the energy transformations and exchanges within the animal. This is the object of the study of bioenergetics.

The basic approach traditionally used in determining energy requirements for animals is to evaluate the animal's needs under controlled conditions and set up guidelines which serve as a basis for evaluating the ability of feedstuffs to supply those needs. The total energy present in a feedstuff is determined by measuring the amount of dry matter present, and from a determination of its energy density by bomb calorimetry, a value commonly termed gross energy is derived. This value, multiplied by the dry matter intake of the animal, will result in gross energy intake. However, this food energy is only partially available to the animal. Classically, the energy is partitioned in the schematic way shown in Figure 1. This net energy system for partitioning of dietary energy has been widely used for evaluating feedstuffs and to express the energy requirements of domestic and wildlife animals.

In measuring the energy requirements of living animals, researchers have used several methods with basically two approaches. In direct calorimetry, heat emission is measured directly in the

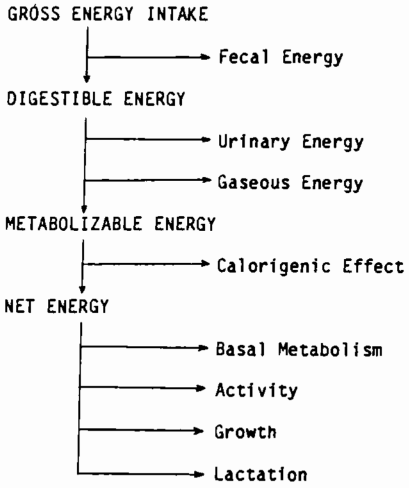

Figure 1. Biological partitioning of dietary energy.

different forms it assumes, namely, radiation, conduction, convection and latent heat of water evaporation. On the other hand, in indirect calorimetry, the methods used are dependent upon measurements which are based on chemical changes that occur when different nutrients are catabolized or stored in the organism.

Pullar (1969) stated that the history of direct calorimetry began with the experiments of Lavoisier and Laplace who used the adiabatic principle to measure the quantity of heat given off by a guinea pig surrounded by a pack of ice. After this, several other calorimeters were built using this direct approach. Those built according to the gradient layer calorimetry principle were the basis for the classical direct calorimetric studies conducted at the Rowett Institute in Scotland (Pullar 1969).

The indirect approach has received considerable use in this century, principally because this technique is less time consuming, cheaper, and gives similar results as those obtained through direct calorimetry methods. The theoretical basis and experimental evidence for indirect calorimetry rest on the fact that heat production can be calculated if one knows the amount of oxygen consumed and/or carbon dioxide produced (respiratory quotient method). Alternatively, if the total dietary intake, energy retention and energy losses in excreta are known (carbon and nitrogen balance and slaughter methods), heat production can be calculated by difference. Several reports dealing with this subject can be found in the literature (Brody 1945; Swift and French 1954; Kleiber 1961; Blaxter 1962; Flatt 1969; Blaxter et al. 1972; Young and Webster 1963; Corbett et al. 1969; Young et al. 1969; Datta and Ramanathan 1969).

The several methods of indirect calorimetry available have been used with success to estimate energy requirements of penned animals. However, few of the indirect methods work satisfactorily with free-ranging animals. Complications of data collection and restrictions of equipment may impose limitations on the animals such that biased values are likely to result.

Among the few methods of indirect calorimetry suitable for measuring energy expenditure of free grazing animals, the Carbon Dioxide Entry Rate Technique (CERT) developed by Young et al. (1969) seems to be an approach which can be used in grazing animals without excessively restraining them. Results are more closely related to those for free-roaming animals than those derived using indoor measurements and extrapolated to range animals. Osuji (1974) maintained that the values obtained using CERT are closer to the estimates of maintenance energy requirement at pasture based on digestible organic matter intake than those obtained from measurements made in calorimeters and adjusted to account for the increased activities of grazing.

CERT is based in the principle of isotope dilution, a classical approach used in radiological studies in animal research. Some of these studies are described by IAEA 1966, Havstad 1981, and Davis 1969. The basic assumption is that after an equilibrium is reached between the continuously infused isotope ^{14}C and the total CO_2 body pool, the rate of entry of metabolic CO_2 can be calculated from the following relationship:

$$CO_2 \text{ entry rate (g/min)} = \frac{\text{Rate of infusion of labelled } CO_2 \text{ (nCi/min)}}{\text{Specific Activity of } CO_2 \text{ (nCi/g).}}$$

According to Havstad (1981), CERT is based on the hypothesis that the turnover rate of CO_2 will provide an estimate of energy expenditure, 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.

Corbett (1981b) indicates that the result of this calculation will not necessarily equal CO_2 production as determined in a respiration chamber. However, there is a close relationship between CO_2 entry rate and energy expenditure, as demonstrated by Young (1968, 1970); Whitelaw et al. (1972); Engells et al. (1976); Young and Corbett (1972a); and Corbett et al. (1971) who concurrently used CERT and respiratory gaseous exchanges to determine energy expenditure.

According to Engells et al. (1976), the regression equations derived from those studies and applied to CERT measurements with free-ranging animals would not bias energy expenditure estimates, nor would a change in RQ over the measurement period create a large bias in the estimates, providing that the subject animal, infusion site and samples CO_2 compartment are similar to the applied work.

Those results, together with the relatively simple technique, have made CERT an important tool to be used by range animal nutrition researchers to determine energy expenditures of free-ranging animals. The possible difference between the energy requirements of confined and free-ranging animals have been recognized and discussed for some time as can be seen in the papers by Blaxter (1962); Clapperton (1964); Knox (1979); Corbett (1981a); Young and Corbett (1972a); Yamamoto et al. (1979); Coop (1962); Coop and Hill (1962); Graham (1964), and Webster (1967).

Researchers in the field of range animal nutrition recognize that the results for energy expenditures obtained from confined, hand-fed animals maintained in a controlled environment may differ widely from those kept under free-grazing conditions. Young and Corbett (1972a) state that energy requirements of free-ranging animals have been reported to range from approximately equal to three times higher than those for confined animals.

Graham (1964) working with sheep, indicated that the energy cost of grazing accounted for an increase of forty percent when compared with hand-fed animals. However, the results he reported were obtained by simulating grazing in a respiration chamber. This probably does not reflect the real situation under range conditions.

Coop and Hill (1962) found estimates of maintenance for 45 kg grazing sheep varying from 0.62 to 0.74 kg of digestible organic matter per day, values which were 48 to 76% higher than the estimate of 0.42 kg of digestible organic matter per day for pen-fed sheep. On the other hand, Langlands et al. (1963a, b), found a value of 0.46 kg of digestible organic matter per day for a 45 kg grazing sheep. This was 24 percent higher than the estimate of 0.37 kg of digestible organic matter per day obtained by the same authors for a 45 kg sheep kept indoors. Young and Corbett (1972a), using calorimetric estimates obtained from a mobile indirect calorimeter (Corbett et al. 1969) and CERT found that the energy requirements of grazing animals were in general 60-70 percent greater than those for housed sheep of similar weight. However, these authors did not find statistical differences between the estimates obtained by the two methods used.

The increase in energy expenditures of grazing animals when compared to housed ones may be due to several causes. Blaxter (1962) suggested that these might include increased costs of body movement during grazing, environmental factors or errors due to the measurement of organic matter intake. On the other hand, Osuji (1974) stressed that the increased energy expenditure at pasture might be due to increased overall costs associated with grazing, especially the costs of walking and harvesting herbage, which in turn depend on the availability of herbage and on environmental stresses. Benjamin et al. (1977) reported metabolizable energy requirements of 153 and 88 Kcal $ME \cdot BW^{-.75} \cdot d^{-1}$ for grazing sheep and sheep individually caged within the confines of the pastures. This shows the association of increased energy expenditure with the act of harvesting forage.

Graham (1964) reported that sheep grazing low availability pastures have maintenance requirements 40% higher than those of pen-fed animals. On the other hand, Lambourne (1961) stated that sheep grazing good quality pasture have a requirement varying from 10-30 percent higher than housed sheep. Those grazing a poor quality pasture had energy requirement up to 100 percent higher than those pen-fed animals. In a later study, Lambourne and Reardon (1963) reported values up to three times greater when comparing pen-fed animals to those grazing pastures with very low availability forage.

These very large increases reported by Lambourne and Reardon (1963) have been disputed by Young and Corbett (1972a, b), who said that the excessively high values they found for sheep grazing poor pasture and also those reported by Lambourne and Reardon (1963) may be due to bias introduced by the use of the fecal nitrogen concentration technique to estimate the digestibility of the herbage grazed. According to these authors, the in vitro digestibility values obtained through the use of extrusa collected from esophageally fistulated animals gives a less biased estimate of digestibility than those obtained using the fecal nitrogen approach, even though neither technique can be considered completely without bias.

A considerable number of reports dealing with energy requirements of sheep can be found in the literature. However, the majority of these estimates were obtained under confinement conditions or by using data obtained in this way and adjusted to account for activities. These limitations have resulted from the lack of a practical method to measure energy expenditures under free-ranging conditions.

On the other hand, data on energy requirements of goats are almost entirely lacking in the literature. The few that were found were all obtained under confinement conditions. According to Graham (1982), the goat is thought to resemble the sheep in requirements for maintenance, growth, and fattening as well as in size. However, there is evidence that goats travel more extensively in search of feed so that their energy expenditures may be higher than those of sheep under the same conditions, as suggested by McDowell and Woodward (1982), Robertshaw (1982), Huston (1978), and Graham (1982).

Goats are described in the literature as very active animals, highly selective, and primarily a browsing species that makes use of the bipedal stance to browse above head height (Devendra and Coop 1982; Morand-Fehr 1981; Merrill and Taylor 1981; Arnold and Dudzinski 1978). Sheep, on the other hand, are characterized as a less active species, less selective, and basically grazers. The less selective behavior is supposed to confer a smaller need to walk during the feed selection process.

The values for energy requirements for maintenance of goats and sheep found in the literature vary widely as can be seen in Table 1. Values for sheep ranged from 72 Kcal $ME \cdot BW^{-.75} \cdot d^{-1}$ (Mohammed and Owen 1980) to 147 Kcal $ME \cdot BW^{-.75} \cdot d^{-1}$ (Coop and Hill 1962), while the values for goats ranged from 87 Kcal $ME \cdot BW^{-.75} \cdot d^{-1}$ (Itoh et al. 1979) to 165 Kcal $ME \cdot BW^{-.75} \cdot d^{-1}$ (Huston 1978).

Although in the last ten years there has been an increasing research effort to study small ruminants, the literature is obviously still scarce in data on nutrient requirements of sheep and goats, particularly under free-ranging conditions. The question of energy expenditures of free-ranging animals have not yet been fully clarified, and more research is needed. An especially large need is for work that relates variations in energy expenditures to particular functional causes, e.g. feeding activities, environmental conditions, and physiological demands.

Objectives

The major objective of this study was to determine the energy expenditures of goats and sheep grazing a paddock composed mainly of grass species. Later, potted shrub plants were artificially placed in feeding stations, and by manipulating the height the shrubs were placed on the feeding stations, attempts to obtain estimates of energy costs associated with browsing and the bipedal stance were performed.

Table 1. Energy requirements for maintenance of goats and sheep.

Species	Energy Requirements Kcal ME$\cdot$BW$^{-.75}\cdot$d^{-1}	Source
Goats	165	Huston 1978.
	140	French 1944.
	111	Haenlein 1950.
	115	Majumdar 1960.
	92	Webster and Wilson 1980.
	104	Mohammed and Owen 1980.
	95	Mackenzie 1967.
	90	Devendra 1967.
	110	Singh and Sengar 1970.
	96	Lindahl 1972.
	93	Akinsoyinu 1974.
	92	Winter and Gorsh 1974.
	128	Rindsig 1977.
	102	Rajpoot et al. 1981.
	89	Morand-Fehr and Sauvant 1978.
	113	Sengar 1980.
	87	Itoh et al. 1979.
	100	Skjevdal 1982
	101	NRC 1981b.
Sheep	98	ARC 1965
	96	Olantunji 1974.
	92	Adu 1975.
	98	NRC 1975.
	97	Steyn 1974.
	79	Hofmeyr 1972.
	98	Ranjhan 1981.
	88	Benjamin et al. 1977.
	110	Olatunji et al. 1976.
	73	Wilke and van der Merwe 1976.
	72	Mohammed and Owen 1980.
	92	Toutain et al. 1977
	81	Langlands et al. 1963a.
	105	Huston 1978.
	115[a]	Young and Corbett 1972a.
	90	Graham 1964.
	90	Coop 1962.
	147	Coop and Hill 1962.
	94[a]	Corbett et al. 1980.
	100[a]	Corbett et al. 1982.
	101	Langlands et al. 1963a.

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[a] Determined under grazing conditions using CERT.

The specific objectives were:

1) To compare the daily energy expenditure of goats and sheep under free grazing conditions.
2) To determine the energy cost associated with browsing on the total energy expenditures of goats and sheep.
3) To determine the energy cost associated with bipedal stance for goats and sheep.
4) To construct an energy budget for goats and sheep under uniform pasture conditions.
5) To estimate the amount of energy harvested by free grazing animals under pasture conditions.
6) To construct an activity budget for goats and sheep under pasture conditions.
7) To measure differences in the quality of the diet harvested by the two animal species under study.

Working Hypotheses

1) The energy expenditure of goats under free ranging conditions is higher than that of sheep under the same environmental conditions.
2) In the absence of browse plants in the available forage, the distance travelled by goats is higher than the distance travelled by sheep.
3) The energy expenditures associated with browsing and bipedal stance are more related to goats than to sheep.

4) The higher energy expenditure for activity of goats is more associated with browsing and use of bipedal stance, than with the costs associated with walking.

5) The quality of the diet selected by goats is higher than that selected by sheep under the same experimental conditions.

MATERIALS AND METHODS

This study was conducted at the Green Canyon Experimental area, in Logan, Utah, during August and September, 1985, and August and November, 1986. The whole study comprised four separate experiments. The first one (a validation trial) compared energy metabolism estimated by the carbon dioxide entry rate technique (used during the grazing trials) and by the oxygen consumption technique under respiration chamber conditions. The three remaining experiments focused on estimation of energy expenditures of free-ranging goats and sheep using CERT.

The free-ranging experiments were conducted in a uniform paddock measuring 2.5 hectares in area. The forage sward was composed basically of orchard grass (*Dactylis glomerata*), brome grass (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*). The respiration chamber experiment was carried out in a building next to the grazing paddock.

Validation Trial

Experiment 1

The carbon dioxide entry rate technique used in the three grazing experiments was validated against a standard indirect calorimetry technique (oxygen consumption) for animals under confinement. A metabolism chamber large enough to accommodate a large sheep or goat and allow some free movement inside was built. This chamber was constructed of plywood sides and a plexiglass cover. A small electric fan was attached to the underside of the cover to help homogenization of the air mixture inside the cage. The external dimensions of this cage were: 150 cm length, 75 cm width and 125 cm height. A raised floor was constructed of expanded metal having large enough openings to allow fecal droppings and urine to pass through and be collected in a galvanized metal pan placed underneath. The cage also had removable food and water containers, so that feed and water could be provided for the animal.

The chamber had to be as airtight as possible, since air leaks would affect the measurement of the oxygen consumed by the animal. To check against any large air leakage, an alcohol combustion technique was used prior to any animal experimentation. In this technique, the amount of oxygen required to combust a measured amount of ethanol under steady state conditions was calculated. The result was then compared against the result obtained by measuring with an electrochemical oxygen analyzer (Applied Electrochemistry, model S-3A). Only after the efficiency of the system, measured as the value obtained through the use of the oxygen analyzer divided by the value calculated to burn a known amount of ethanol, was over 0.95 in three successive trials was it declared ready. This required several trials and modifications, until the chamber was properly sealed and suitable for experimentation with animals.

For this experiment, three goats and three sheep were randomly selected from the same group of individuals used in the field experiments.

Two days prior to the beginning of a respiration measurement trial, an animal was randomly selected for implantation of a cannula in the parotid salivary duct. The selected animal was deprived of food and water for at least 18 hours. Then, before surgery it was lightly sedated with Rompum^{TM} (goats) or sodium pentothal (sheep). A Teflon^{TM} catheter (1.1 mm ID and 1.7 mm OD) was inserted into the parotid salivary duct opening, to a depth of approximately 5 to 10 cm. The animal's cheek was then pierced with a 18 gauge needle at a location lateral to the salivary duct opening. The catheter was then passed through the needle to the exterior of the animal's cheek. The tube was first oriented toward the muzzle, where it was fixed and protected with glued tape, and then looped over the animal's face up to the top of the head. After surgery, the animal was checked several times daily to make sure that the cannula remained in place and that saliva was flowing through the tubing.

On the following day, the animal was harnessed with a back pack carrying a four-channel, battery driven, peristaltic infusion/extraction pump (Siropump^{TM}) in one side of the pack and two 500 ml plastic bottles in the other side. One bottle contained a solution of $NaH^{14}CO_3$ diluted in sterile saline (0.9 percent w/v solution), and the other was an empty bottle to collect the saliva. At this time, another catheter was inserted into the animal's peritoneal cavity, fixed in place with a suture and glued tape, and then connected to the infusion tubing coming from the pump. This tubing was connected to the infusion solution bottle. The catheter coming from the salivary duct was connected to the withdrawal channel of the pump, which in turn was connected to the saliva collecting bottle.

Once the animal was fitted with the equipment, the peristaltic pump was turned on and the animal released in a holding pen where water and alfalfa pellets were available. The peristaltic pump was continuously infusing intraperitoneally the $NaH^{14}CO_3$ at an approximate rate of 20 $nCi \cdot min^{-1}$ according to the infusion procedures described by Engells et al. (1976). The infusion commenced approximately four to six hours prior to the initiation of the sampling of parotid saliva, to allow for equilibrium of the $NaH^{14}CO_3$ solution being infused and the CO_2 body pool.

Four to six hours after the infusion started, the bottle collecting saliva was replaced by another empty bottle and the contents of the original bottle were discarded. The animal was then put inside the respiration chamber, where it remained for a 24-hour period. Saliva was withdrawn continuously into the new bottle during the 24-hour period at an approximate rate of 5 $ml \cdot h^{-1}$. The plastic bottle collecting saliva contained a few crystals of $CuSO_4$ as sterilant to prevent bacterial growth. The saliva collected was stored under refrigeration for subsequent specific activity determination in a liquid scintillation counter.

Air was pulled from the cage by a vacuum pump at a rate of 30-32 $liters \cdot m^{-1}$, and passed through a series of six 3.8 liter polyethylene bottles, alternately containing drierite (for humidity absorption) and soda lime (for carbon dioxide absorption).

The temperature inside and outside the chamber, the barometric pressure in the lab room, the rate of air flowing through the system, the animal body weight and the oxygen concentration of both ambient air and that leaving the chamber were recorded to be utilized in the calculations of oxygen consumption by the animal.

Data were gathered and stored on floppy disks by a micro-computer directly coupled to the oxygen analyzer. Later on, the data were retrieved and analyzed using a computer program package written by John Lighton and distributed by Acorn Computers Corporation.

The first four hours the animal was in the chamber were allowed for air equilibration inside the chamber. Therefore, the measurements made during that period were not used for the calculations of oxygen consumption. The amount of oxygen consumed was determined on an hourly basis as the mean of 640 samples per hour taken by the oxygen analyzer, for the remaining 20-hour period. Due to the failure to absorb CO_2 using soda lime, energy expenditures were calculated using a RQ of 0.84, as suggested by Engells et al. (1976), for each one of the 20 hourly estimates. Those values were then averaged to give the estimate of energy expenditures in $Kcal \cdot BW^{-.75} \cdot d^{-1}$. The failure to completely absorb CO_2 was probably due to the large size of the calcium oxide particles used in the soda lime mixture. This probably allowed the carbon dioxide to pass thru without being completely absorbed. Regression analysis was performed using the CO_2 entry rate as the independent variable and the actual energy expenditure measured by the oxygen consumption method as the dependent variable. The predictive equation was then used to estimate the energy expenditure during the grazing trials.

Grazing Experiments

Experiment 2

This experiment was initially attempted during August 13-14, 1985. However, due to technical problems which were discovered during laboratory analysis phase in November, 1985, it was necessary to repeat this experiment. This was done during August 1-2, 1986. The procedures outlined below apply generally to all field experiments, including both the initial and repeat attempts of Experiment 2.

Two days prior to the beginning of an experiment, five goats and five sheep approximately 3-4 years old, dry females in excellent body condition, were selected for cannulation of the parotid salivary duct. The same surgical, cannulation, infusion and collection procedures described for the respiration chamber validation experiment were used to execute the carbon entry rate technique during all tne three grazing experiments.

Digi-pedometers (Edge Mark^{TM}) were fitted to each animal's left hind leg at the carpel joint to estimate the distance walked during a 24-hour period. Previously, these pedometers had been calibrated by driving the animals a known distance, and calculating an adjustment factor relating the pedometer readings to the actual distance walked.

Once all animals were fitted with the equipment, the peristaltic pumps were turned on and the animals released into the 2.5 ha pasture.

The ten animals in this experiment were systematically observed at 5-minute intervals during the whole 24-hour experimental period. This allowed the construction of an activity budget based on the following major activities: grazing, walking, standing, lying, ruminating, browsing and using bipedal stance. The last two activities were expected to occur more frequently in the third and fourth experiments, which were purposely designed to stimulate these behaviors. The definitions of the activities are as follows:

1) Grazing: Feeding activity in which the animal holds its head down actually taking mouthfuls of herbage, or with its head down in activities related to small moves from one plant to another.
2) Walking: Movement activity in which the animal holds its head up in the process of travelling from one place to another. This did not include the short walks when the animal was moving from one plant to another with head down (see above). This activity comprised time which animals actually spent searching for food or going to drink water.
3) Standing: Activity in which the animal stayed in an upright posture without being engaged in any other locomotor activity. It was subdivided in two major subclasses:
    3.1) Standing Idle: The animal was simply standing, and looking around, without being involved in any other apparent physical activity.
    3.2) Standing Ruminating: The animal was standing, but involved in rumination activities, as characterized below.
4) Lying: This measured the total time the animal was resting in a recumbent position, without being involved in any other apparent physical activity. This class was also subdivided in two major subclasses:

4.1) Lying Idle: The animal was simply resting in a recumbent position, without being involved in any other apparent physical activity.

4.2) Lying Ruminating: The animal was lying down, but involved in rumination activities.

5) Ruminating: This measured the total time the animal was involved in the postprandial regurgitation, remastication and reswallowing of ingesta. This activity was measured as the sum of the subclasses 3.2 and 4.2 described above.

6) Browsing: Feeding activity in which the animal was in an upright position, with its head up, and actually taking mouthfuls of browse located at its shoulder height or higher, but without standing on its hind legs. This activity also measured activities related to small moves from one plant to another at a particular browse feeding station.

7) Using Bipedal Stance: Feeding activity in which the animal was standing on its hind legs actually biting browse from above the plane of its head, or making efforts to do so. This activity also measured activities related to small moves from one plant to another.

8) Other Activities: This category included activities not described above, such as drinking water, licking salt, defecating, urinating, social interactions, etc.

After the completion of the 24-hour period, the pedometers were read and the distance walked by the experimental animals recorded.

During a pre-experimental period, five additional animals (two goats and three sheep, all esophageally fistulated) were run together with the experimental animals. One day before the energy expenditures were measured, those animals were penned overnight. In the following morning, the esophageal plugs were removed, and animals were allowed to graze for a period of 30-45 minutes and the material ingested (extrusa) was collected in screen-bottom bags. The extrusa was immediately frozen and stored for later laboratory analysis. These samples were subsequently freeze dried, ground through a 1 mm screen and analyzed for dry matter, organic matter, crude protein, gross energy and *in vitro* organic matter digestibility, according to the procedures outlined by the A.O.A.C (1970) and Goto and Minson (1977).

These animals were also dosed twice daily with 1 gram of chromic oxide over a 10-day period. During the last three days, fecal grab samples were collected for estimation of total fecal output. The fecal samples were frozen for subsequent dry matter, chromium, organic matter, gross energy and crude protein determinations, according to the procedures described by the A.O.A.C. (1970) and Stevenson and De Langen (1960).

The organic matter digestibility of the esophageally collected extrusa, together with the estimated total fecal organic matter output were used to estimate the total organic matter intake using the following equation:

$$\text{Organic Matter Intake} = \frac{\text{Total Fecal Organic Matter Output}}{\text{1-Digestible Organic Matter Coefficient}}$$

The value for the organic matter intake was then used to estimate the gross energy and dietary crude protein intakes. Those values together with the fecal output estimates and the gross energy and crude protein in the feces were used to estimate digestible energy intake, and digestible crude protein intake.

Experiment 3

The same animals used in Experiment 2 were used in Experiment 3. A period of four weeks was allowed between the two experiments for the animals to rest and for preparatory steps and checking of equipment, instruments and radioisotope solution. The animals were handled in the same way as described for Experiment 2, and all the other pre-experimental and experimental procedures outlined for Experiments 1 and 2 were also followed for Experiment 3.

In Experiment 3, the animals grazed the same experimental paddock used in Experiment 2, carried the same equipment and were observed in the same way as described for Experiment 2. Additionally, twelve browse feeding stations, each containing six serviceberry (*Amelanchier alnifolia*) plants 30-35 cm height and in 7.6-liter pots, were distributed across the grazing paddock. The plant pots of serviceberry were located at a height corresponding to the animals head height so that the animals could browse them while standing in the quadrapedal posture. This procedure and arrangement of the feeding stations across the grazing paddock was expected to stimulate browsing by both animal species.

The data of this experiment were analyzed separately for differences between animal species, and were also pooled with the data from Experiment 2 to allow an estimate of the possible additional energy cost associated with browsing. However, as mentioned earlier, it was necessary to repeat Experiment 2 during the grazing season of

1986; thus the comparison of results between Experiments 2 and 3 are potentially confounded with the years effect.

Experiment 4

This experiment was carried out during September 26-27, 1985, and the same methodology utilized for the previous experiments was followed. The only difference was related to the height which the serviceberry shrub plants were made available for the animals. In Experiment 4, in order to browse the plants, the animals were forced to make use of the bipedal stance to reach them. The plants were placed at a height of 1.5-1.6 m above the ground to simulate tree height.

The data collected were analyzed separately for differences between animal species. As outlined for Experiment 3, the pooling of the data from Experiments 2 and 4 was supposed to give estimates of the energy costs associated with the bipedal stance.

Possible differences in terms of energy costs associated with grazing, browsing and use of bipedal stance were checked by pooling data from Experiments 2, 3 and 4.

The data for individual grazing experiments were analyzed using the statistical package Minitab (Ryan, Jr. et al. 1976) for a completely randomized design. The pooled data were analyzed using Rummage (Bryce 1980), for completely randomized design with repeated measurements.

Laboratory Analysis

CERT Energy Expenditures Determinations

The saliva samples collected from the experimental animals were taken to the laboratory where they were prepared for counting in a Packard liquid scintillation counter. The procedure utilized followed that outlined by Annison and Lindsay (1961) and Leng and Leonard (1965), as described by Havstad (1981). Some minor modifications were introduced, and the whole procedure can be described as follows:

The saliva sample was taken from refrigeration and shaken and thoroughly mixed. A 2.0 ml sub-sample was removed and placed in a 250 ml Erlenmeyer flask fitted with a removable glass center well designed to hold at least 3 ml. The flask was then closed with a number 6 rubber stopped after the sub-sample had been placed inside. This was done to minimize the entrapment of atmospheric CO_2 inside the flasks.

Following this, the flask was uncapped and 1 ml of 1N NaOH was added to the center well, and the flask immediately covered with a layer of Parafilm^{TM}. With the help of a syringe and a 22 gauge x 3.8cm needle, 1.0 ml of 1N H_2SO_4 (with 1.0 percent w/v $CuSO_4$) was carefully injected through the Parafilm^{TM} cover into the saliva solution in the bottom of the Erlenmeyer flask. Great care was taken not to contaminate the NaOH in the center well with the H_2SO_4 being injected. If this occurred, the sample was discarded and the procedure was restarted. The flask was then tightly recapped with a rubber cap over the Parafilm^{TM} and left undisturbed for a 24-hour period.

All samples were run in triplicate, and all reagent solutions used in this procedure were made with CO_2-free distilled water, prepared as described by A.O.A.C. (1970).

At the end of the 24-hour period, the flasks were uncapped, and 0.5 ml of a 20 percent (w/v) $BaCl_2 \cdot 2H_2O$ solution was added to the center well. This was followed by the addition of 1.0 ml of a 5 percent (w/v) NH_4Cl solution also to the center well. This produced a yellowish-white $BaCO_3$ precipitate.

The removable center well with the $BaCO_3$ precipitate was then carefully removed from the Erlenmeyer flask, and the precipitate was washed from the well into a 15 ml glass centrifuge tube. This suspension was then centrifuged for 10 minutes at 1500 rpm. The supernatant was discarded and the precipitate was carefully washed with acetone onto a 5 cm watchglass. The watchglass was then placed in an oven at 105^{o}C until all the acetone evaporated and the precipitate was totally dry.

The dried precipitate was carefully broken up into a fine powder, transferred to a previously tared 20 ml glass scintillation vial and weighed. Normally, dry weights of 40-50 mg of $BaCO_3$ were recovered, but quantities as large as 108 mg and as little as 8 mg were encountered. Values less than 15 mg were not used for liquid scintillation counting.

The $BaCO_3$ precipitate was re-suspended in the vial in 10 ml of a commercial liquid scintillation cocktail (Ready Solv^{TM}). The vials were capped, labelled, shaken, and then transferred to a Packard liquid scintillation counter. Counting times were 10 minutes, and counting efficiencies were always above 95 percent. The counts in disintegrations per minute (dpm), were automatically adjusted for 100 percent counting efficiency. There was very little quenching in all the samples counted. The mean value for quenching was 70, with a range of 63 to 85, indicating a very small amount of contamination in all the samples.

The infusion solution samples were prepared for analysis by adding 1 ml of the solution used in a particular trial to the 10 ml liquid scintillation cocktail, shaking the mixture, and transferring it directly to the scintillation counter.

Carbon dioxide entry rates (ER) in grams of CO_2 carbon$\cdot$min^{-1} were calculated by converting dpm in the infusion solution to nCi$\cdot$min^{-1}. By knowing that $BaCO_3$ contains 6.086 percent carbon, the specific activity of the saliva was transformed from dpm$\cdot$mg^{-1} of $BaCO_3$ to nCi$\cdot$g^{-1}CO_2 carbon. The CO_2 entry rates (ER) were then used to estimate energy expenditures in Kcal$\cdot$min^{-1} through the use of the equation validated during Experiment 1.

The values obtained were then used to calculate the energy expenditures in Kcal$\cdot$d^{-1} and through the use of the animals' metabolic body weights, to express the estimates of energy expenditures in Kcal$\cdot$BW$^{-.75}\cdot$d^{-1}.

RESULTS

Validation Trial

Experiment 1

The carbon dioxide entry rate values obtained from CERT procedures were regressed against the 24-hour mean energy expenditures measured by the oxygen consumption technique. The results obtained can be seen in Figure 2.

The regression equation obtained was

$$EE = 0.878 + 5.333\ ER$$

where EE is the rate of energy expenditure in $Kcal \cdot min^{-1}$, and ER is the CO_2 entry rate in grams of CO_2 $carbon \cdot min^{-1}$. The coefficient of determination (r^2) for this equation was 0.979 ($P<.0002$) and the standard error of the estimate was 0.12 $Kcal.min^{-1}$. The latter value represented approximately 7.8 % of the mean rate of energy expenditure. The regression line for the data seems to indicate that the predictive equation based on CO_2 entry rate might be used interchangeably between the two animal species.

Even though I did not have a large number of data points, our actual measurements of energy expenditure from both animal species covered a range of 73 to 138 $Kcal \cdot BW^{-.75} \cdot d^{-1}$. The observed energy expenditures values by animals, as well as the estimated CERT values derived from the regression equation are presented in Table 2.

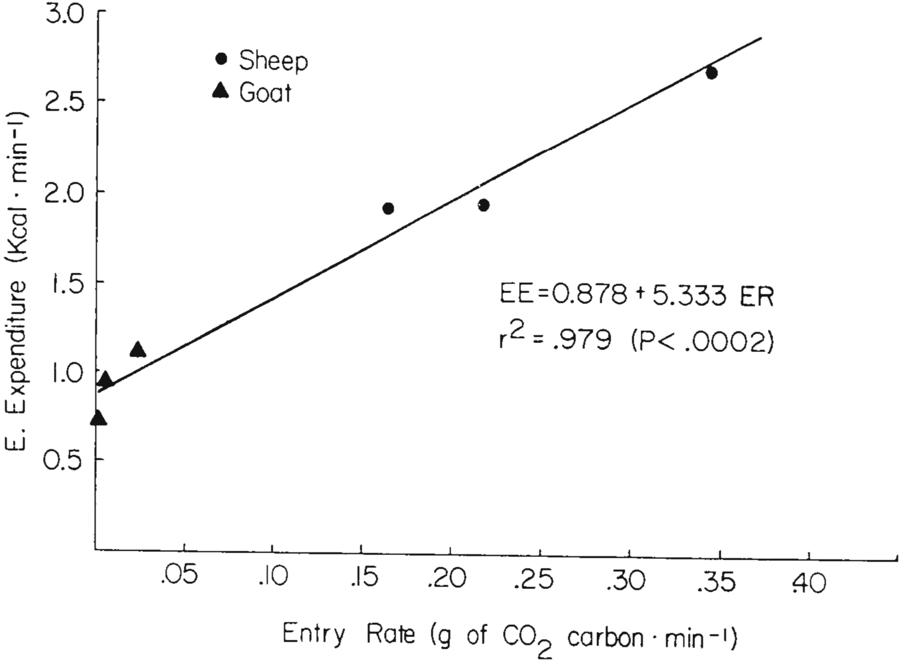

Figure 2. Regression of energy expenditure on carbon dioxide entry rate for sheep and goats in respiration chamber.

Table 2. Observed and estimated values of energy expenditures of goats and sheep during the validation trial.

Animal Number	O_2 Consumption ($Kcal \cdot BW^{-.75} \cdot d^{-1}$)	Carbon Entry Rate Technique ($Kcal \cdot BW^{-.75} \cdot d^{-1}$)	% Error[1]
SHEEP			
01	116.11	109.43	-5.8
04	138.32	141.52	+2.3
05	119.13	124.35	+4.4
GOATS			
06	72.67	89.24	+22.9
07	114.85	103.10	-10.2
09	86.66	82.97	-4.3
Mean ± SE	107.96±9.8	108.44±8.9	1.6±4.8
Paired t value			-0.12
Significance			N. Sig.

[1] Calculated as 100 (CERT - O_2 consumption) / O_2 consumption.

Goats seemed to adapt to the respiration chamber environment better than did sheep. Goats tended to stay calm and stand in a single position, while sheep tended to turn around more. Even though the temperature inside the chamber was within 16-18°C for all trials, there was a distinct build-up of humidity inside the chamber in those trials involving sheep. This did not happen when a goat was in the chamber. This suggests that the flow rate might have not been adequate for larger animals. Therefore, it is possible that sheep might have suffered a high humidity stress while in the chamber. This may account for the slightly higher ($P>.05$) energy expenditure for sheep during this trial.

Grazing Experiments

Energy Expenditure Estimates

Of the thirty attempted saliva collections during the three grazing trials, I failed to collect saliva on only three occasions. Those were from goats numbered 10 and 6 during Experiments 2 and 4, respectively, and from sheep number 4 during Experiment 3. All other attempts yielded quantities of saliva ranging from 50 to 150 ml, amounts more than sufficient for laboratory analysis.

In all experiments, no problems were encountered with the intraperitoneal infusion procedure or the backpack harnesses and pumps. The peristaltic pumps delivered an average of 5.1 ± 0.3 $ml \cdot h^{-1}$ of the intended 5.0 $ml \cdot h^{-1}$ delivery rate.

A major problem with Experiment 2 was discovered at the time of laboratory analysis for specific activity. For an unknown reason, perhaps an error in the dilution of the isotope, the specific activity of the infusion solution was much lower than intended and very inconsistent findings resulted. Therefore, the whole experiment was repeated in the following year. This rendered the results from Experiment 2 not comparable with the results from Experiments 3 and 4, as originally planned. Even though I conducted the experiment on approximately the same calendar dates in the following year, different climatic conditions with higher temperatures prevailed, as can be seen in Table 3.

Carbon dioxide entry rate technique estimates of energy expenditures for the three grazing trials were obtained through the use of the predictive equation presented on page 30.

Overall goats had a higher ($P<.05$) energy expenditure than sheep, with means of 127.1±3.5 and 88.4±4.3 $\mathrm{Kcal \cdot BW^{-.75} \cdot d^{-1}}$ for goats and sheep, respectively, a 44 percent difference (Table 4). This difference between species was consistent across all three field experiments. The small standard error within samples (see Appendix Tables 1 through 3) indicates that specific activity analyses were very consistent and that sampling procedures and laboratory analyses introduced little error. Individual results (Appendix Tables 1 through 3) also indicate relatively small variation among animals within species. The only exception for this was sheep number 4. This animal consistently presented lower energy expenditures on two grazing experiments when saliva was collected from it.

There was a species-by-experiment interaction ($P<.05$), indicating experiment differences between goats and sheep. Further tests indicated that those differences occurred in sheep between Experiments

Table 3. Air temperatures (°C) recorded at the experimental site during the three field experiments.

Time of Day	Experiment 2 Aug. 01-02, 1986	Experiment 3 Sept. 13-14, 1985	Experiment 4 Sept. 26-27, 1985
6:00 PM	29.6	14.8	12.9
7:00 PM	20.1	14.9	9.1
8:00 PM	19.4	--	--
9:00 PM	18.1	9.5	10.5
10:00 PM	17.9	--	--
11:00 PM	16.5	11.5	10.9
12:00 AM	13.2	--	--
1:00 AM	11.9	6.9	9.0
2:00 AM	11.7	--	--
3:00 AM	11.0	6.8	6.3
4:00 AM	10.8	--	--
5:00 AM	9.6	6.7	7.3
6:00 AM	11.6	--	--
7:00 AM	15.4	11.7	5.1
8:00 AM	22.9	--	--
9:00 AM	23.5	18.6	19.1
10:00 AM	29.9	--	--
11:00 AM	28.9	22.9	22.1
12:00 PM	36.7	--	--
1:00 PM	34.3	23.3	21.3
2:00 PM	30.3	--	--
3:00 PM	34.3	24.7	19.3
4:00 PM	33.9	--	--
5:00 PM	28.7	21.8	14.9
Min.	9.6	6.7	5.1
Max.	36.7	24.7	22.1
Mean	21.7	14.9	12.9

Table 4. Estimated daily energy expenditures in Kcal·BW$^{-.75}$·d^{-1} of free-ranging goats and sheep (means ± SE).

Species	Experiment Number			Species Means
	2	3	4	
Sheep	81.17±6.2^{b,1}	80.08±4.4^{b,1}	102.21±6.4^{b,2}	88.37±4.3^{b}
Goats	134.68±5.9^{a,1}	118.05±4.2^{a,1}	130.87±6.2^{a,1}	127.11±3.5^{a}
Experiment Means	107.51±10.2^{2}	96.54±7.3^{3}	115.99±6.6^{1}	

[a] Means in the same column with different letter superscripts are statistically (P<.05) different.

[1] Means in the same row with different number superscripts are statistically (P<.05) different.

2 and 4 and between Experiments 3 and 4. Given the experimental design, this was anticipated for goats, but not for sheep.

When the data were analyzed for each animal species separately, no differences were detected (P>.05) for goats among the three grazing trials. Sheep, on the other hand, had a higher (P<.05) energy expenditure in Experiment 4 than in either Experiment 2 or 3.

Activity Budget

Overall mean durations of the various activities for each species in Experiments 2-4 are shown in Table 5. Individual results by animals are presented in the Appendix Tables 5 through 7. The analyses of variance tables are shown in the Appendix Tables 8-17.

Grazing

A significant species-by-experiment interaction was detected for this variable. Overall, animals grazed more in Experiments 3 and 4 than they did in Experiment 2. This was probably related to the unseasonably higher ambient air temperatures (Table 3) recorded during Experiment 2. Feeding and feeding related activities are known to be depressed by elevated temperatures (NRC 1981a). Sheep grazed more (P<.05) than goats over the three experiments combined (Table 5). Within species, sheep grazed longer (P<.05) during Experiments 3 and 4 than they did in Experiment 2. Goats, on the other hand, grazed more during Experiment 4 than during Experiment 2. However, there was no difference (P>.05) for goats either between Experiments 2 and 3 or 3 and 4, even though there was a 100-min difference (240 vs. 340 minutes) between Experiments 2 and 3.

Table 5. Activity budgets in minutes·d^{-1} for goats and sheep under free-ranging conditions (mean ± SE).

Activity/Species	EXPERIMENTS Experiment 2	 Experiment 3	 Experiment 4	Overall Mean
SHEEP:				
Grazing	$334 \pm 33^{a,2}$	$526 \pm 26^{a,1}$	$607 \pm 64^{a,1}$	489 ± 39^{a}
Walking	$31 \pm 7^{a,1}$	$27 \pm 5^{b,1}$	$22 \pm 7^{a,1}$	27 ± 4^{a}
Standing Idle	$162 \pm 23^{b,1}$	$57 \pm 17^{b,1}$	$114 \pm 48^{a,1}$	111 ± 21^{b}
Standing Ruminating	$6 \pm 2^{a,1}$	$26 \pm 14^{b,1}$	$32 \pm 6^{b,1}$	21 ± 6^{b}
Lying Idle	$675 \pm 68^{a,1}$	$501 \pm 29^{a,2}$	$424 \pm 43^{a,2}$	553 ± 38^{a}
Lying Ruminating	$224 \pm 45^{a,1}$	$283 \pm 26^{a,1}$	$222 \pm 40^{a,1}$	243 ± 22^{a}
Ruminating**	$230 \pm 45^{a,1}$	$309 \pm 17^{b,1}$	$254 \pm 35^{a,1}$	264 ± 20^{a}
Browsing	$0^{a,1}$	$2 \pm 1^{b,1}$	$0^{a,1}$	$1 \pm .5^{b}$
Bipedal Stance	$0^{a,1}$	$0^{a,1}$	$0^{a,1}$	0^{a}
Others	$8 \pm 3^{a,1}$	$18 \pm 6^{a,1}$	$19 \pm 4^{a,1}$	15 ± 3^{a}
GOATS:				
Grazing	$240 \pm 41^{a,2}$	$340 \pm 26^{b,1,2}$	$413 \pm 37^{b,1}$	331 ± 27^{b}
Walking	$41 \pm 11^{a,1}$	$46 \pm 5^{a,1}$	$30 \pm 4^{a,1}$	39 ± 4^{a}
Standing Idle	$332 \pm 56^{a,1}$	$337 \pm 49^{a,1}$	$256 \pm 50^{a,1}$	308 ± 29^{a}
Standing Ruminating	$24 \pm 9^{a,3}$	$193 \pm 36^{a,1}$	$112 \pm 26^{a,2}$	110 ± 23^{a}
Lying Idle	$749 \pm 32^{a,1}$	$301 \pm 54^{b,2}$	$396 \pm 22^{a,2}$	482 ± 55^{a}
Lying Ruminating	$37 \pm 13^{b,2}$	$194 \pm 29^{a,1}$	$207 \pm 24^{a,1}$	146 ± 24^{b}
Ruminating	$61 \pm 9^{b,2}$	$387 \pm 27^{a,1}$	$319 \pm 30^{a,1}$	256 ± 40^{a}
Browsing	$0^{a,2}$	$19 \pm 2^{a,1}$	$0^{a,2}$	6 ± 3^{a}
Bipedal Stance	$0^{a,1}$	$0^{a,1}$	$10 \pm 5^{a,1}$	3 ± 2^{a}
Others	$17 \pm 5^{a,1}$	$10 \pm 2^{a,1}$	$16 \pm 3^{a,1}$	14 ± 2^{a}

**Ruminating = Standing Ruminating and Lying Ruminating

[a] Means for the same activity in the same column with different letter superscripts are statistically ($P<.05$) different.

[1] Means for the same activity in the same row with different number superscripts are statistically ($P<.05$) different.

Walking

Overall, there was no difference ($P>.05$) either among experiments or between species when data for this variable were pooled. Within species neither sheep nor goats showed differences ($P>.05$) for this behavior among the three experiments.

Standing Idle

There was not a statistically detectable ($P>.05$) difference among experiments for this variable. However, goats spent more time ($P<.05$) engaged in this activity than did sheep over the three grazing trials combined. This might be related to the degree of alertness observed in goats. Throughout all observation periods, they appeared particularly alert to movements and activities in the surrounding areas and were ready to react by running away. Within species there was no difference ($P>.05$) either for sheep or goats among the three experiments.

Standing Ruminating

A significant ($P>.05$) species-by-experiment interaction was detected for this behavior, also. Overall, both species stood ruminating more in Experiments 3 and 4 ($P<.05$) than in Experiment 2. Experiments 3 and 4 did not differ ($P>.05$) between them.

Between species, goats spent more time ($P<.05$) standing ruminating than did sheep over the three grazing trials combined. This difference might also be related to the higher degree of alertness observed in the goats when compared to sheep. For sheep alone, the amount of time utilized in this activity was similar ($P>.05$) among the three experiments. Goats on the other hand, stayed standing ruminating during the most time in Experiment 3 ($P<.05$), followed by Experiment 4.

Goats spent the least time standing ruminating during Experiment 2 (P<.05).

Lying Idle

There was again a significant (P<.05) species-by-experiment interaction when the combined data for the three grazing trials were analyzed. This indicates different responses by sheep and goats to the different treatment (experiments) effects. Overall, animals used more (P<.05) of their daily time in this activity during Experiment 2 than during either Experiment 3 or 4. Animals might have suffered from heat stress during Experiment 2 and used this behavior as a mechanism to decrease heat load.

Results from Table 5 indicate that there was no statistical difference (P>.05) for this behavior between sheep and goats over the three experiments. Within species, goats used more lying idle time during Experiment 2 (P<.05) than during either Experiment 3 or 4. The latter two did not differ. Sheep also showed a similar pattern by spending more time (P<.05) in this behavior during Experiment 2 than during either Experiment 3 or 4. Again, the latter two did not differ.

Lying Ruminating

As with lying idle, there was a significant (P<.05) species-by-experiment interaction for this behavior when the pooled data set was analyzed. Among experiments, the animals spent more time lying ruminating in Experiments 3 and 4 than they did in Experiment 2 (P<.05). There was not, however, a difference (P>.05) between Experiments 3 and 4. On the other hand, both species spent more time engaged in lying activities (lying idle plus lying ruminating) in

Experiment 2 than they did in the other two experiments. This is another indication of heat stress during Experiment 2. Overall, sheep spent 15 and 39 percent more time lying in Experiment 2 than they did for Experiments 3 and 4, respectively. Goats on the other hand, spent 59 and 30 percent more time, respectively. There was a significant difference (P<.05) between species, with sheep devoting more time to lying ruminating than did goats. This relates to the degree of alertness of the two animal species. While goats spent more time (P<.05) standing ruminating, sheep spent more time (P<.05) lying ruminating. However, there was no difference between the two species for total rumination time.

Within species, there was no difference (P>.05) among trials for lying ruminating in sheep. Goats on the other hand, spent less time (P<.05) on this behavior during Experiment 2, while there was no statistical difference (P>.05) between Experiments 3 and 4.

Total Rumination Time

This activity comprised the sum of standing ruminating and lying ruminating. A significant (P<.05) species-by-experiment interaction was identified for this behavior. Also, there was an overall significant experiment effect; the animals ruminated less (P<.05) in Experiment 2 than in either Experiment 3 or 4. There was no difference (P<.05) between the last two experiments.

The lower rumination time recorded during Experiment 2 might be a result of a lower voluntary feed intake by the animals, which in turn might have been a consequence of the also lower (P<.05) grazing time observed. Ultimately, it seems probable that all those animal responses might have been related to a possible heat stress due to the higher air temperatures recorded during Experiment 2 (Table 3).

There was not a statistically significant difference detected in total rumination time between sheep and goats in this study. Within species sheep spent a similar (P>.05) amount of time in rumination activities among the three grazing trials. Goats on the other hand, spent the least time (P<.05) ruminating during Experiment 2, while there was no difference (P>.05) for this behavior between Experiments 3 and 4. The total rumination time for goats during Experiment 2, represented only 16 and 19 percent of the values observed in Experiments 3 and 4, respectively. Those results strongly suggest that goats might have suffered more from heat stress during Experiment 2, than did sheep.

Browsing

There was a significant (P<.05) species-by-experiment interaction for browsing. This was expected because the experiment was designed to stimulate this behavior during Experiment 3. Animals spent more time (P<.05) browsing in Experiment 3 than they did in either Experiment 2 or 4. Between species, goats spent more time (P<.05) browsing than sheep. Within species, goats exhibited the most (P<.05) browsing behavior in Experiment 3; there was no browsing during either Experiment 2 or 4. Sheep browsed briefly during Experiment 3, but not enough to cause a statistically significant difference (P>.05) among any of the three grazing trials.

The shrub plants introduced in the pasture during Experiment 3 quickly stimulated the goats to browse. However, the animals rapidly defoliated all 72 plants available. Even though there were no more shrubs left to browse, goats kept checking back in the feeding stations searching for more plants. Apparently, goats would have used more time browsing if more shrubs had been available to them. Sheep on the other hand, just noticed the plants, and only two animals nibbled the shrubs when they discovered them, but then continued grazing.

Bipedal Stance

There was no difference ($P>.05$) either among experiments or between sheep and goats for this behavior. Within species, there was no statistical test for sheep, because they did not exercise this behavior at all. For goats, there was not a statistically significant ($P>.05$) difference detected among the three grazing experiments. This was due to the small amount of time (Appendix Table 7) the goats exercised this activity. The small amount of shrubs available, combined with plenty of good quality herbage for grazing, might be an explanation for this finding. The optimal foraging decision by goats might have been that it was not worth investing time and energy on bipedal stance for a small amount of shrubs available, when there was plenty of forage to graze. However, the goats kept visiting the feeding stations even without attempting to use bipedal stance.

The small amount of time goats used for this behavior was also responsible for no detectable ($P>.05$) species by experiment interaction and experiment effect. This would be expected, had the animals used this behavior further, since this activity did not happen during Experiments 2 and 3.

Others

This category comprised several behaviors, and represented a very small amount of time in the overall daily activity budgets of the animals. This indicates that we were successful in identifying the major daily behaviors of the animals. Overall, there was no species by experiment interaction, nor did experiment effect nor species differences (P>.05). Within species, neither goats nor sheep showed statistical differences among experiments.

Distance Walked Daily

The distances walked by sheep and goats during Experiments 2, 3, and 4 are presented in Table 6. The corresponding individual animal data and the analysis of variance table are shown in the Appendix Tables 18-21.

Overall, there was no species by experiment interaction. However, there was a significant (P<.05) treatment (experiment) effect. The animals walked further (P<.05) during Experiment 4 than during either Experiment 2 or 3. On the other hand, there was no difference (P>.05) between goats and sheep for distance walked daily.

Within species, sheep walked further (P<.05) during Experiment 4 than during either Experiment 2 or 3. This probably also relates to the also higher (P<.05) grazing time sheep had in Experiment 4 as compared to Experiment 2. However, no statistically significant difference (P>.05) was detected between Experiments 2 and 3, even though sheep grazed 3.2 hours longer in the latter experiment Table 5). Goats on the other hand, walked further during both Experiments 3 or 4 (P<.05), than during Experiment 2. This also might be related to the

Table 6. Distance walked ($km \cdot d^{-1}$) by goats and sheep under free-ranging conditions (mean ± SE).

Species	Experiment Number 2	 3	 4	Species Means
Sheep	$3.92 \pm 0.3^{a,2}$	$3.87 \pm 0.4^{a,2}$	$5.44 \pm 0.5^{a,1}$	4.41 ± 0.3^{a}
Goats	$3.42 \pm 0.4^{a,2}$	$4.54 \pm 0.4^{a,1}$	$4.89 \pm 0.2^{a,1}$	4.28 ± 0.3^{a}
Experiment Means	3.67 ± 0.3^{2}	4.20 ± 0.3^{2}	5.16 ± 0.3^{1}	

[1] Means in the same row with different number superscripts are statistically (P<.05) different.

[a] Means in the same column with different letter superscripts are statistically (P<.05) different.

higher (P<.05) grazing time observed during Experiment 4 as compared to Experiment 2. However, as with sheep, there was no grazing time difference (P>.05) between Experiments 2 and 3, even though goats grazed 1.7 hours longer during Experiment 3. Another possible explanation for the differences for distance walked daily in goats, is the fact that during Experiments 3 and 4, goats kept checking back at the feeding stations where the shrubs were placed. This together with the grazing time might well account for the differences observed.

Energy Budget

The activity values, together with the distance walked daily were used to construct separate energy budgets for goats and sheep. Unit-cost values for various activities were taken from Osuji (1974). In order to construct the energy budgets, the following steps and assumptions were necessary because of the scarcity of data in the literature, principally for goats.

In that calculations involved interspecies comparisons, I decided to use the interspecies mean for basal metabolic rate (BMR) of 70 $W^{.75}$. To calculate the resting metabolic rate (RMR), a factor of 1.1 BMR was used (Osuji et al., 1975). This factor was used to compensate for the heat of nutrient metabolism and some thermo-regulatory activity by the animals, as well as animal interaction and their degree of alertness under free-ranging conditions, among other factors. Rumination time was the sum of standing ruminating plus lying ruminating. The time the animals spent in other activities was included in the total standing time, since almost all activities in this category (e.g. drinking water, urinating, social interaction, defecating and licking salt), the animals were standing. Therefore, the total standing time was computed as the sum of the following activities: grazing, walking, standing idle, standing ruminating and other activities. Lying time was included in the calculation of the RMR, and the cost of rumination was calculated separately from the other costs as implied in Osuji (1974) paper. The same values were used for both sheep and goats.

I assumed a 25% higher energetic cost for browsing over grazing. This value was a compromise between the 33% higher value for wapiti and 28% higher value for moose suggested by Fancy and White (1985). Due to the lack of data in the literature regarding energetic values for activities in goats, I arbitrarily assumed that the energetic costs for the use of bipedal stance was two times greater than the costs for grazing.

The comparison of results for the CERT and energy budget techniques are presented in Table 7. Individual animal values and the analysis of variance table are shown in the Appendix Tables 22-25.

Overall, the energy budget technique underestimated ($P<.05$) CERT results by 14 percent (94.05 vs. 107.02 $\mathrm{Kcal \cdot BW^{-.75} \cdot d^{-1}}$). The disparity between the two techniques can be better demonstrated when data are analyzed on a species-by-species basis. For sheep, energy budget calculations overestimated CERT values by 9 percent (96.7 vs. 88.4 $\mathrm{Kcal \cdot BW^{-.75} \cdot d^{-1}}$). This difference was not statistically ($P>.05$) significant. For goats, the energy budget grossly underestimated the CERT result by 39 percent (91.4 vs. 127.1 $\mathrm{Kcal \cdot BW^{-.75} \cdot d^{-1}}$). This difference was statistically ($P<.05$) significant.

The results in Table 7 also indicate that when the energy budget calculations were used, sheep had a higher ($P<.05$) energy expenditure

Table 7. Comparison of energy expenditures of free-ranging goats and sheep using CERT and energy budget estimates (Means ± SE).

	EXPERIMENTS							
	Experiment 2		Experiment 3		Experiment 4		Species Means	
SPECIES	CERT	E. Budget	CERT	E. Budget	CERT	E. Budget	CERT	E. Budget
Sheep	$81.17 \pm 6.2^{a,2}$	$92.80 \pm 1.2^{a,1}$	$80.08 \pm 4.4^{b,2}$	$96.30 \pm 1.0^{a,1}$	$102.21 \pm 6.4^{a,2}$	$101.00 \pm 2.2^{a,1}$	$88.37 \pm 4.3^{a,2}$	$96.69 \pm 1.2^{a,1}$
Goats	$134.68 \pm 5.9^{a,1}$	$87.90 \pm 1.2^{b,2}$	$118.05 \pm 4.2^{a,1}$	$92.50 \pm 1.1^{b,2}$	$130.87 \pm 6.2^{a,1}$	$93.0 \pm 0.9^{b,2}$	$127.11 \pm 3.5^{a,1}$	$91.42 \pm 0.9^{b,2}$
Techniques Means	104.95 ± 10.2^{a}	90.36 ± 1.1^{a}	101.18 ± 7.3^{a}	94.38 ± 0.9^{a}	115.99 ± 6.6^{a}	97.42 ± 1.6^{a}	107.02 ± 4.7^{a}	94.05 ± 0.9^{b}

[a] Means in the same row within the same heading having different letter superscripts are statistically ($P<.05$) different.

[1] Means in the same column having different number superscripts are statistically ($P<.05$) different.

than goats (96.7 vs. 91.4 $\mathrm{Kcal \cdot BW^{-.75} \cdot d^{-1}}$). This is exactly the opposite of results obtained using CERT. CERT results clearly indicate that goats have a higher ($P<.05$) energy expenditure per unit of metabolic body size than do sheep. This suggests that inter-species comparisons based on values calculated from activity budgets are invalid. These results also clearly show the inappropriateness of using energetic values obtained from one species to construct an energy budget for a different species.

Nitrogen and Energy Consumption and Dietary Quality

Nutritional variables were measured only during Experiment 2. The reason for that was that the amount of shrubs available during both Experiments 3 and 4 was too small to contribute measurably to the animal's overall intake.

Organic Matter Intake (OMI)

Organic matter intake, dietary crude protein intake, crude protein apparent digestibility and digestible crude protein intake, all expressed on a organic matter basis, are shown in Table 8. In general, organic matter intake was low, ranging from 21.7 to 40.9 $\mathrm{g \cdot BW^{-.75} \cdot d^{-1}}$ across animal species. Goats had a higher ($P<.05$) OMI than sheep, with mean values of 33.3 $\mathrm{g \cdot BW^{-.75} \cdot d^{-1}}$ and 24.9 $\mathrm{g \cdot BW^{-.75} \cdot d^{-1}}$ for goats and sheep, respectively. The *in vitro* organic matter digestibility was similar ($P>.05$) for both species, and averaged 58.32 and 58.21% for sheep and goats, respectively. The analysis of variance tables for organic matter intake, crude protein intake, crude protein apparent

Table 8. Organic matter intake (OMI), crude protein intake (CPI), crude protein apparent digestibility coefficients (CPD) and digestible crude protein intake (DPI) by free-grazing goats and sheep (Experiment 2).

Animal Number	OMI ($g \cdot BW^{-.75} \cdot d^{-1}$)	CPI ($g \cdot BW^{-.75} \cdot d^{-1}$)	CPD (%)	DPI ($g \cdot BW^{-.75} \cdot d^{-1}$)
SHEEP:				
01	29.2	3.9	52.02	2.0
02	22.7	3.0	49.84	1.5
03	23.8	3.1	57.08	1.8
04	27.1	3.6	57.44	2.1
05	21.7	2.9	43.43	1.2
Mean±SE[a]	24.9±1.4[b]	3.3±0.2[b]	51.96±2.6[b]	1.7±0.2[b]
GOATS:				
06	40.9	5.2	61.46	3.2
07	36.7	4.7	62.50	2.9
08	32.3	4.1	62.78	2.6
09	28.5	3.6	60.75	2.2
10	28.2	3.6	64.52	2.3
Mean±SE	33.3±2.4[a]	4.2±0.3[a]	62.40±0.6[a]	2.6±0.2[a]

[a] Means in the same column with different letter superscript are statistically (P<.05) different.

digestibility and digestible crude protein intake are shown in Appendix Tables 26-29, respectively.

Crude Protein Intake (CPI)

The crude protein content of the diet was 13.3 percent for sheep, and 12.8 percent for goats (organic matter basis). Even though dietary content of both species was similar, goats had a higher ($P<.05$) crude protein intake than did sheep. This was due to the higher OMI by the goats reported above. This, in turn, brought about a higher CPI in a similar order of magnitude ($P<.05$).

Crude Protein Digestibility (CPD)

The apparent crude protein digestibility coefficients for goats were significantly higher ($P<.05$) than were sheep's. As can be seen from Table 8, the CPD for the goats was 62.40 ± 0.6 percent, while for sheep it was 51.96 ± 2.6 percent. This amounted to a 20 percent difference in favor of goats.

Digestible Protein Intake (DPI)

As a consequence of the higher ($P<.05$) crude protein intake as well as the higher ($P<.05$) crude protein digestibility coefficient, goats also had a significantly higher ($P<.05$) digestible crude protein intake. The results from Table 8 indicate that goats had a DPI of 2.6 ± 0.2 $g \cdot BW^{-.75} \cdot d^{-1}$ while sheep had 1.7 ± 0.2 $g \cdot BW^{-.75} \cdot d^{-1}$.

Gross Energy Intake (GEI)

The gross energy intake, gross energy apparent digestibility coefficient and digestible energy intake, all expressed on organic matter basis, are presented in Table 9. The analysis of variance

Table 9. Gross energy intake (GEI), gross energy apparent digestibility coefficient (GED), and digestible energy intake (DEI) by free-grazing goats and sheep (Experiment 2).

Animal Number	GEI (Kcal·BW$^{-.75}$·d^{-1})	GED (%)	DEI (Kcal·BW$^{-.75}$·d^{-1})
SHEEP:			
01	140.84	51.08	71.93
02	109.34	51.49	56.30
03	114.59	51.88	59.45
04	130.87	51.62	67.56
05	104.41	49.75	51.94
Mean±SE[a]	120.01 ± 6.8^{b}	51.15 ± 0.4^{a}	63.81 ± 3.2^{b}
GOATS:			
06	195.29	52.73	102.99
07	175.40	54.86	96.22
08	154.23	53.83	83.02
09	136.23	51.32	69.91
10	134.73	51.00	68.71
Mean±SE	159.18 ± 11.7^{a}	52.75 ± 0.7^{a}	84.17 ± 6.9^{a}

[a] Means in the same column with different letter superscript are statistically ($P<.05$) different.

tables for the same variables in the same order, are shown in the Appendix Tables 30-32, respectively.

The gross energy content of the extrusa samples from both species was similar, with 4776±29 and 4823±22 $\mathrm{Kcal \cdot kg \cdot d^{-1}}$, for goats and sheep, respectively. This result indicates, as was also the case with the crude protein content of the diets, that both species selected a very similar type of diet. This was not surprising, since the paddock in which the animals were grazing was quite uniform and composed basically of three grass species. This might have prevented either animal species from exercising an edge in selecting a more nutritious diet.

However, as a consequence of the higher ($P<.05$) organic matter intake, goats also had a higher ($P<.05$) gross energy intake than did sheep. As can be seen from Table 9. Goats had an average gross energy intake of 159 $\mathrm{Kcal \cdot BW^{-.75} \cdot d^{-1}}$ while sheep had an intake of 120 $\mathrm{Kcal \cdot BW^{-.75} \cdot d^{-1}}$.

Gross Energy Digestibility (GED)

Contrary to what happened with the crude protein digestibility, there was no statistically significant difference ($P>.05$) between the two species for the apparent gross energy digestibility coefficient. Goats had a GED of 52.75±0.7 percent, while sheep had a GED of 51.15±0.4 percent.

Digestible Energy Intake (DEI)

Goats had a digestible energy intake of 84.2±6.9 $\mathrm{Kcal \cdot BW^{-.75} \cdot d^{-1}}$, while sheep had a DEI of 63.8±3.2 $\mathrm{Kcal \cdot BW^{-.75} \cdot d^{-1}}$. This difference is statistically significant ($P<.05$) and may be regarded as a direct consequence of the higher ($P<.05$) organic matter intake by the goats, since that there was no statistical difference neither in the gross energy content of the diet from both species, nor in the apparent digestibility coefficients for gross energy.

DISCUSSION

Validation Trial

Experiment 1

The majority of validation studies involving the carbon dioxide entry rate technique were made using blood and/or urine as the medium where the specific activity of $^{14}CO_2$ was measured. Also, those validation tests were carried out when this technique was first developed to be used as an alternative method for measuring energy expenditures of free-ranging animals.

Young (1968) tested several infusion pumps before selecting one which was suitable for infusion of the isotope solution. Also, the collection of blood and urine for radioassay was troublesome and could have stressed animals considerably. Young (1968) described that in order to collect urine samples for specific activity assays in some of his animals, he had to restrict their breathing.

Young (1968) indicated that sampling of blood or urine from animals at frequent intervals to obtain estimates of their daily rates of energy expenditure was undesirable principally because of the disturbance to the animals. Corbett et al. (1971) indicated that predictive equations based on specific activity of urine CO_2 were more precise than those based upon blood CO_2. They speculated that this was because samples of blood were taken at regular intervals, whereas the urine samples were pooled samples accumulated in the bladder over the period of measurement of heat production.

Since then, the CERT procedure has been refined. Engells et al. (1976), reported that saliva was a better medium to measure $^{14}CO_2$ than were either blood or urine. Corbett et al. (1980) suggested that intraperitoneal infusion was better than either intravenous or subcutaneous infusions.

The infusion/withdrawn devices have also improved and are lighter and more reliable today than they used to be in the past. Considerable progress has also been made in the counting devices. Whitelaw et al. (1972) reported counting efficiencies of 80 percent in their study. The counting efficiency in this study was over 95 percent, and quenching effects were negligible.

The overall standard error of estimation for this study represented 7.8 percent of the mean rate of energy expenditure. Those results compare favorably with the values of 16 and 13 percent of the mean energy expenditure by sheep, for blood and urine respectively, reported by Young (1968).

Young (1970) indicated that the standard error of the estimate for his predictive equation for cattle, using urine as the body fluid medium, represented approximately 11 percent of the mean rate of energy expenditure.

The lower values for the standard error of the estimate found in this study are slightly better than the overall value of 8.0 percent of the mean energy expenditure estimation reported by Engells et al. (1976), who also used saliva as the source of body CO_2.

Whitelaw et al. (1972), using urine as the source of body CO_2 to measure specific activity, derived a regression equation in which the residual standard deviation was equivalent to 7.5 percent of the mean value of energy expenditure. Their value is very similar to the result of 7.8 percent that was obtained in this study.

The regression equation derived in this study seems similar to the equations reported by Young (1970) for cattle ($Y = 1.018 + 5.178$ ER) and for pooled data from cattle and sheep measurements ($Y = 0.485 + 5.618$ ER). This supports the contention made by Young (1970), that the carbon dioxide entry rate technique is a useful tool to estimate the energy requirements of free-ranging animals, and that maybe there is a common relationship between the rate of energy expenditure and CO_2 entry rate when the entry rate values are derived by similar procedures. However, additional validation studies are required for other animal species over a wide range of weights, ages, physiological status and environmental constraints in order to generate equations with broader applications.

Grazing Experiments

A. Comparative Energy Expenditure (EE) of Goats and Sheep.

1. Inherent Species Differences. A major objective of this study was to compare the energy expenditures of goats and sheep under uniform free-grazing conditions. Overall results indicated that goats had a higher ($P<.05$) energy expenditure per unit of metabolic body size than sheep. Therefore, I failed to reject the central hypothesis that the

energy expenditure of goats under free-grazing conditions is higher than that for sheep.

Goats and sheep are frequently grouped together and thought to resemble each other in several ways. However, there are several differences which clearly indicate that knowledge accumulated using one species is not necessarily directly transferred to the other. Devendra and Coop (1982) list a series of differential characteristics for the two animal species. Even though the majority of the comparisons regarding goats and sheep are based principally on morphological and behavioral characteristics, it is expected that physiological differences are important features between those two animal species.

Graham (1982), indicates that there is a large volume of literature available on physiology and nutrition of sheep, while the knowledge about goats is rudimentary and derives principally from anecdotal information and extrapolation from other species. Based on these sources, the goat is believed to resemble the sheep in several aspects, including nutrient requirements.

Devendra (1967) indicated that 45 kg pen-fed indigenous Malayan goats had a maintenance energy requirement of 95.6 Kcal $ME \cdot BW^{-.75} \cdot d^{-1}$. His value is similar to the mean value of 92.0 Kcal $ME \cdot BW^{-.75} \cdot d^{-1}$ reported by Coop (1962) for pen-fed sheep of similar body weight. On the other hand, Graham (1982) suggests that wool growth requires more energy than hair growth and therefore under a fleece-free and hair growth-free basis, goats should have a higher maintenance energy requirement than sheep. NRC (1981b) suggests that goats are more active and travel greater distances than sheep which contributes to their higher energy expenditures.

Energy expenditures ultimately reflect physiological as well as morphological and behavioral adaptations by animals to situations they face within a given ecosystem. This is turn triggers other adaptations the animals must display in order to meet or minimize their nutrient requirements.

Except for a smaller body size and noticeably higher degree of alertness in the goats, both animal species were in the same physiological state, had similar body condition, faced the same environmental constraints, and walked similar distances during our three grazing experiments. However, the energy expenditures of goats were consistently higher than those of sheep. This suggests that the higher energy expenditures by goats should not be related to distance walked. Therefore, this should be linked to the lower metabolic body size and the higher degree of alertness observed in the goats.

Besides age, body size, degree of fatness and physiological state, other factors are also linked to higher energy expenditures. Baldwin and Bywater (1984) indicated that service function organs such as heart, lungs and liver, as well as tissue and cellular level functions such as ion transport and macromolecule re-synthesis, account for 30-50% of basal energy metabolism. The same authors also pointed out that relative (to body mass) higher weights of service organs are highly correlated to higher energy expenditures due to their major contributions to the basal metabolic rate.

Other authors have indicated that a higher level of feed intake is also associated with a rise in the basal component of the total heat production (Graham et al. 1974; Blaxter et al. 1966, 1982; and Hudson and Christopherson 1985). It is possible that differences, in terms of relative weight of internal organs as well as at the tissue and cellular level, do occur between sheep and goats, and that those might be responsible for observed differences in energy expenditures. However, a clear explanation of this difference can only be ascertained by simultaneous quantification of the physiological and metabolic processes which contribute to the overall heat production.

The overall mean value of 88.4 $Kcal \cdot BW^{-.75} \cdot d^{-1}$ I found for sheep is 14 percent lower than the 101 $Kcal \cdot BW^{-.75} . d^{-1}$ recommended by the NRC (1985). On the other hand, the recommended level suggested by the ARC (1980) for maintenance of 40 kg ewe lambs kept outdoors and having a metabolizability of the diet of 0.5 is 93.2 $Kcal \cdot BW^{-.75} \cdot d^{-1}$. The value reported in this study, is therefore about five percent lower than the value suggested by the ARC (1980). However, our ewes were bigger animals. Other values found in the literature ranged from 71.9 (Mohammed and Owen, 1980) to 153 $Kcal \cdot BW^{-.75} \cdot d^{-1}$ (Benjamin et al., 1977). Therefore, the values encountered in this study are within the range reported in the literature.

For goats, my overall results indicated a mean of 127.1 $Kcal \cdot BW^{-.75} \cdot d^{-1}$. This is similar to the 126.4 $Kcal \cdot BW^{-.75} \cdot d^{-1}$ recommended by the NRC (1981b) for 30 kg goats for maintenance plus low activity. The NRC (1981b) recommendation was derived by using a 1.25 correction factor times a mean value of 101.4 $Kcal \cdot BW^{-.75} \cdot d^{-1}$ for maintenance, as derived from pooled literature values.

The values for energy expenditure for goats in the literature range from 87 $Kcal \cdot BW^{-.75} \cdot d^{-1}$ (Itoh et al., 1979) to 165 $Kcal \cdot BW^{-.75} \cdot d^{-1}$ reported by Huston (1978). However, all those values were either estimated or measured under indoor conditions and extrapolated to free-grazing conditions. To the best of my knowledge, data on goats in this experiment are the first original values measured under free-grazing conditions.

2. Behavioral Differences. Even though the activity budgets were not the major objective of this work, these values together with the data on distance travelled daily were used to construct energy budgets for the two species under study. Additionally they were used as a valuable tool to better interpret estimates of energy expenditures.

The overall mean time used by both species for grazing was similar to the average reported in the literature. Sheep grazed an average of 8.2 hours, while goats grazed 5.5 hours daily. It was noticed that while goats rarely grazed during nighttime, sheep made use of this behavior principally during Experiment 2.

The amount of time goats spent standing idle was greater ($P<.05$) than the time sheep spent on this activity. Overall, goats used 21.4 percent of their daily time or 308 minutes, while sheep utilized 7.7 percent or 111 minutes. This might be related to the higher degree of alertness observed in the goats during our observations. This pattern was somewhat reversed for lying idle, but the difference was not significant.

Both species spent more time ($P<.05$) lying idle in Experiment 2 than during either Experiment 3 or 4. This higher time could have been due to the higher temperatures which were registered during the execution of that trial. The lying posture adopted might have been a way to decrease the body surface exposed to solar radiation, as an avoiding behavior mechanism to a higher heat load, and to use the cooler soil surface for heat transfer by conduction. NRC (1981a) indicates that for animals in sunlight a net gain of heat by thermal radiation usually takes place, resulting in an increased effective ambient temperature of 3 to 5°C. Naturally, this increased effective ambient temperature is beneficial during colder weather, but it becomes very detrimental under hotter environments since it increases the heat load and, therefore, the heat stress.

The distance walked by both species was similar ($P>.05$), and sheep walked 4.4 while goats walked 4.3 $km \cdot d^{-1}$. In the absence of browse, the distances walked by both species were 3.9 and 3.4 $km \cdot d^{-1}$ for sheep and goats, respectively. Therefore, I rejected hypothesis number 2.

The distance walked by free-grazing animals is highly variable and is influenced by several factors such as: species, breeds, technique used for measurement, physiological status of the animal, body condition, environmental factors, pasture size and herbage availability, among others.

Sheep walked practically the same distances in Experiments 2 and 3 (3.92 and 3.87 $km \cdot d^{-1}$), respectively. This might be an indication that sheep were able to deal with the heat stress they faced during Experiment 2 in a better way than goats did. The further distance sheep walked ($P<.05$) during Experiment 4 may have been related to the higher grazing time they have in that experiment.

Goats, on the other hand, walked more during Experiments 3 and 4, than they did during Experiment 2. This indicates that goats preferred to stay more inactive to face heat stress during Experiment 2. It may also be indicating the fact that goats grazed more during Experiments 3 and 4, and that they kept checking back at the feeding stations looking for more shrubs during the later two trials.

B. Environmental and Seasonal Effects on Energy Expenditure.

In addition to those factors discussed before, environmental factors, principally temperature, have a strong effect on voluntary feed intake, behavior, and ultimately on the overall metabolism of animals. NRC (1981a) points out that lactating dairy cows under continuous heat stress begin to show a decline in intake at 25-27°C, with sharp decline occurring above 30°C. When maximum daily temperature exceeds 25°C, voluntary dry matter intake by grazing animals may decline rapidly, due in part to the direct effects of heat stress on animals causing suppression of activities. These general principles seem to apply in a higher or lower degree to all animal species, depending on their inherent lower or upper critical temperatures, and their behavioral and physiological adjustments.

Until recently it was assumed that domestic sheep do not show a noticeable seasonality in metabolic rate. This does not now seem to be true. Recent work by Blaxter and Boyne (1982) demonstrated a sinusoidal cycle of metabolic rate in sheep, with an amplitude of about 14 percent around the mean. Minimum values were observed during the winter and maximum values in summer. This oscillating pattern was not related to an increase in the level of feed intake, since intake was maintained constant at the maintenance level. Therefore, it can be assumed that this cyclic pattern is independent of the level of food intake. Several other studies have demonstrated that sheep also exhibit a periodicity in voluntary feed intake, with consumption being greater in the summer than in the winter, providing the animals are not under heat stress (Milne et al. 1978; Blaxter et al. 1982; Kay, 1979).

Corbett et al. (1980) used CERT procedures for measuring energy expenditures of non-pregnant Merino ewes averaging 38 kg body weight under free-grazing conditions in Australia. They conducted measurements over three different periods of five days in May, July and August on five animals. They reported an average value of 94 $Kcal \cdot BW^{-.75} \cdot d^{-1}$ over the three different periods. However, there was a variation from period to period with the values averaging 90, 72 and 119 $Kcal \cdot BW^{-.75} \cdot d^{-1}$ for the measurements made in May, July and August, respectively. The authors attributed those differences to distinct ambient conditions during the three periods, and indicated that the higher value observed in August and the lower value measured in July might indicate seasonal variations in the metabolic rate of the animals. In a later study, Corbett et al. (1982), reported a variation between periods from 76.6 $Kcal.BW^{-.75} \cdot d^{-1}$ for two periods in July to 123.2 $Kcal \cdot BW^{-.75} \cdot d^{-1}$ for a mid-September period. They attributed this difference to an apparent seasonal variation in maintenance requirements, together with an increase level of feeding, which is associated with a rise in the basal component of the total heat production by the animals.

When analyzing data regarding energy expenditures of free-grazing animals, one must be aware of at least the major variables involved with the metabolic rate, and the results should be interpreted on the light of these interacting factors. While declining day length may have been a small factor, the effects of ambient temperatures were probably the major force responsible for differences between Experiment 2 versus 3 and 4.

In Experiment 2, temperatures were above 25°C from 10 AM to 6 PM. According to NRC (1981a), this is the point where a noticeable decline in feed intake starts to show up. From 12 PM to 4 PM temperatures were above 30°C, with a maximum of 36.7°C being recorded at 12 PM. For the other two grazing trials, temperatures were milder and were probably within the thermal neutral zones of the two animal species under study.

As a possible consequence of the relatively high temperatures during Experiment 2, animals tended to decrease the amount of time spent in grazing activities and to increase the time spent in less energetically costly activities such as lying idle and ruminating, or standing either idle and ruminating. During Experiment 2 sheep, in particular, spent almost 15 hours engaged in lying activities, while goats spent a little over 13 hours in those activities. Sheep also tended to seek shaded places where they could lie down during the hottest parts of the day. Goats did not seem to be as concerned about heat stress as sheep did. Sheep did most of their grazing very early in the morning, late in the evening, and even during the night. On the other hand, goats practically did not graze at night and did most of their grazing in short periods of one hour or less during the day. Goats spent almost 6 hours either standing idle or standing ruminating while sheep allocated 2.8 hours for these two activities.

The energy expenditure for sheep during Experiment 3 was 80.1 $Kcal.BW^{-.75}.d^{-1}$, a value very similar to the result of 81.2 $Kcal.BW^{-.75}.d^{-1}$ found in Experiment 2. Goats, on the other hand, tended to have a slightly higher energy expenditure during Experiment 2 than in Experiment 3 (Table 4).

Temperatures registered during Experiments 3 and 4 were somewhat milder than those in Experiment 2 (Table 3), and the animals seem to have responded accordingly by changing their behavioral strategies.

Hafez (1968a) indicates that behavior is one of the more effective adaptive mechanisms animals use to face thermal stress. This points out that activity budgets should provide a valuable tool to those interested in interpreting data on energy expenditures of free-ranging animals. Even though sheep had basically the same energy expenditures in Experiments 2 and 3, they grazed more in Experiment 3 than during Experiment 2. However, they spent more time ($P<.05$) lying idle in Experiment 2 than they did in Experiment 3.

According to Hafez (1968b) higher temperatures decrease animals' voluntary feed intake and increase energy expenditures, due to an increase on thermoregulation mechanisms. My results indicate that, probably as a response to the milder temperatures observed during Experiments 3 and 4, all animals increased their grazing time as compared to Experiment 2. At the same time, there was an inverse pattern for lying idle, with the animals spending more time ($P<.05$) on this behavior during Experiment 2 than during either Experiments 3 or 4.

According to Arnold (1981), the diurnal pattern of grazing in free-ranging animals is altered to adjust for climatic conditions and to maintain grazing time and thus feed intake. However, there are limits beyond which grazing time is no longer reduced.

Sheep made use of basically three behavior strategies to face the apparent heat stress they experienced during Experiment 2. First, they decreased grazing activities. Second, they increased lying idle time. The third, and seemingly most effective behavior, was an avoidance one; they selected the cooler parts of the day and even nighttime to graze. These three strategies combined seemed to have enabled them to maintain their energy expenditures in Experiment 2 at about the same level as was measured in Experiment 3. The higher energy expenditures measured during Experiment 4 might have been related to a slightly higher grazing and standing time, with correspondingly less time devoted to lying as seen in Experiment 3.

Goats on the other hand, had a tendency for a higher energy expenditure in Experiment 2 than in Experiment 3. Even though there was a 100 minute difference in grazing time, goats did not show a statistically significant difference (P>.05) between Experiments 2 and 3 (Table 6). However, they used more time lying idle in Experiment 2 than in either Experiment 3 or 4. Therefore, goats basically used the same two behavioral strategies sheep used (decrease grazing time and increase lying activities) to minimize their heat load in the first grazing experiment. However, they did not use, at least in the same intensity, the third strategy (to graze during cooler parts of the day) sheep used. This was probably one of the major reasons why goats were not able to keep their energy expenditures within a closer range, as sheep indeed were able to, between Experiments 2 and 3.

It seems clear from the previous discussion, that the higher temperatures observed in Experiment 2 brought a cascade of physiological reactions, behavioral responses and adaptations by the two animal species under study. Based on the results of energy expenditures, it seems apparent that goats may have paid a higher energetic cost for not using, at least in the same intensity, the behavioral adaptations sheep used to face an unusual heat stress, under temperate conditions, they faced during Experiment 2.

Taking into consideration all the variables that ultimately influence the energy requirements of free-grazing animals, it seems evident that more energy expenditure studies are needed. For areas with four distinct annual seasons, measurements should be made at least once a month, in order to cover possible differences in energy requirements from season to season. For areas with basically two seasons (e.g. northeastern Brazil characterized by a wet and a dry season), monthly estimates might not be as crucial. However, under the latter conditions one might also be concerned with the faster change in the nutritive value of available forage, which in turn might also influence energy requirements of free-ranging animals. Concomitant documentation of activity budgets together with measurements of environmental variables are vital components of such studies.

C. Energy Costs Associated with Grazing, Browsing and Bipedal Stance.

I was unable to test hypothesis number 4 because the amount of shrubs available for the animals to browse was too small, and the animals defoliated all of them in approximately 30 minutes. Besides that, the experimental design used assumed that, except for the treatment (experiment) effects, all the environmental variables were held constant or at least did not vary much from one experiment to another. This assumption held in terms of ambient temperatures for

Experiments 3 and 4 (Table 3); however, it was not the case during the repetition of Experiment 2. This made the baseline treatment (grazing) not comparable to Experiment 3 (browsing) or 4 (bipedal stance). Even so, the goats spent more time ($P<.05$) involved in browsing activities than did sheep. Additionally goats repeatedly checked the feeding stations to see if there were more shrubs available, clearly indicating that they would have spent more time browsing, had more shrubs been available.

Harrington (1982) indicated that browse contributed from 25 up to 100 percent to the diet of goats in Australia. Askins and Turner (1972) reported that browsing occupied approximately two-thirds of the total grazing time of goats in Texas. This makes the result of 1.3 percent obtained during Experiment 3 a very low value to try to estimate its contribution to the total daily energy expenditure of goats in that study.

The small amount of time that goats used the bipedal stance in Experiment 4 (10 minutes or 0.6 percent of their daily activity budget), does not seem sufficient to explain the slightly (10%) higher energy expenditure measured in Experiment 4 as compared to Experiment 3. This small increase was more likely associated with the slightly higher (21%) grazing time during Experiment 4 than with bipedal feeding posture alone. Again the small amount of shrubs available together with plenty of herbaceous forage available to graze might have influenced the goat's decisions to use a less energetically costly activity for feeding. However, both browsing and bipedal stance appear to be more related to goats than to sheep, and might be some of the factors contributing to a higher energy expenditure of goats as compared to sheep under free-ranging conditions.

D. Comparison of Energy Budget and CERT for Measuring Energy Expenditures.

The average daily energy expenditure of free ranging-animals is the sum of their basal metabolic rate plus the energy costs of activity and costs associated with thermoregulation. For researchers working with range animal nutrition, the lack of a reliable, non-stressful and cheaper method to estimate the energy expenditure, makes the factorial approach the only approach other than CERT to obtain broad estimates of energy requirements for free-ranging animals.

In order to calculate the energy expenditures of free grazing animals, it is necessary to have precise estimates of unit energy costs of several distinct and specified behavioral activities of the species under study. Naturally, this is not an easy task, and estimates of energy costs specific for some behavioral activities are still lacking for some species while there is no data available at all for others.

Another problem with this approach is that unit costs of behavioral activities are determined under laboratory conditions. Therefore such measurements do not really reflect the energy expenditure of that particular activity when the animal is interacting with other variables and their interrelationships in the natural environment. Since this approach assumes that various activity costs are additive, it is easy to see that over a wide range of measured activities, large differences can be obtained.

Weathers et al., (1984) point out that the cost of activity is frequently only a small fraction of the total daily energy expenditures of free living animals. They also indicate that combined basal metabolic and thermoregulatory requirements typically represent 40 to 80 percent of the total daily energy expenditures of free-living animals.

Traditionally, and by definition, the basal metabolic rate is measured with the animals at rest and within their thermal neutral zone while the energy costs associated with thermoregulatory processes are measured under conditions where changes in temperature are considered. Under free-ranging conditions, the animal is faced with changes in feed supply, temperature, wind speed, humidity, and insulation, among several other factors.

According to Weathers et al., (1984), differences in the cost assignments for basal metabolic rate and thermoregulatory requirements contribute more to errors in the energy budget method than do costs associated with activity. In order to assess the accuracy of the energy budget method, the total daily energy expenditure of free living animals must be measured simultaneously by an independent technique of known accuracy. Fancy and White (1985), maintain that the Carbon Entry Rate Technique is one of the techniques which can be used under field conditions to check the accuracy of the energy budget calculations.

In our study, the overall mean for both species as determined by CERT was 107.02 while the energy budget technique estimates indicated a value of 94.05 $Kcal.BW^{-.75}.d^{-1}$. Therefore, the value estimated by the energy budget was 13.8 percent lower than the value obtained using CERT.

When analyzed by species, it can be seen from Table 7, that comparative values for goats were quite different. The value estimated by the energy budget approach was 39.0 percent lower than the value obtained using CERT. This result clearly indicates the inappropriateness of using values obtained from one species (sheep) to construct an energy budget for a different species (goats) as was done in this experiment.

This exercise points out that for goats, we still do not have enough values to construct even an approximate energy budget for animals under free-ranging conditions. It also indicates that indirect calorimetry studies should be carried on to provide unit values which can be used with more confidence to build energy budgets for free-ranging goats.

For sheep, the energy budget estimate was 9.4 percent higher than the value obtained using CERT. These values were not statistically different.

Brockway (1978) indicates that any method of estimating energy expenditure in free-ranging animals must meet certain requirements before it can be adopted for general use. Among the requirements, he indicates that the accuracy of the technique should be such that energy expenditure can be estimated to within ± 10 percent of the overall mean. This criterion was not met for goats in this study, where the values estimated for goats using the energy budget technique were vastly different from results using CERT. For sheep, the energy budget value would, at first glance, seem acceptable. It falls within the limit of ±10 percent suggested by Brockway (1978). However, a closer look at the data in Table 7 is not reassuring. The only time the energy budget technique gave a close estimate of the CERT result was in Experiment 4 when the energy budget value was only 1.2 percent higher than the CERT value. However, during experiments 2 and 3, the energy budget values overestimated the results obtained using CERT by 14.3 and 20.3 percent respectively. Therefore, even though the overall difference fell within the ±10 percent suggested by Brockway (1978), two out of three tests gave values far outside the ±10 percent limit.

Weathers and Nagy (1980) using the double-label water technique (DLW) simultaneously with the time-energy budget method, reported that the energy budget technique underestimated the energy expenditure of Phainopeplas (Phainopepla nitens) kept in an outdoor aviary by 40 percent. In a later study Williams and Nagy (1984) again used the DLW technique to measure the energy expenditure of Savannah Sparrows (Passerculus sandwichensis), and compared the results with several energy budget models for birds from the literature. Of the seven energy budget models tested, three gave mean results outside the accepted ±10 percent range. However, for all the remaining four models which gave estimates within the ±10 percent range in relation to DLW, the variance around the mean was unacceptably high. This indicates that the estimates of energy expenditure of individuals using the energy budget technique may vary widely from those obtained using the DLW technique. They concluded that the total daily energy budget technique is still inadequate to measure the daily energy expenditure of any given individual with reliability.

Based on the results from our study, it can be concluded that the energy expenditures estimates obtained using the energy budget technique were totally unacceptable for goats. For sheep, even though the overall estimate fell within the ±10 percent margin, the results obtained by the energy budget technique were still not totally reliable. Therefore, any one using the energy budget method as a tool to estimate the energy expenditure of free-ranging animals, must be aware that it only provides a broad approximation of the real requirements.

E. Comparative Nitrogen and Energy Interrelationships.

Nutritional features were measured only during Experiment 2. This was initially decided upon the premise that there would be no major differences in the environmental conditions among the three grazing experiments, and the amount of shrubs consumed would not greatly affect overall forage intake. However, the necessity to repeat Experiment 2, and the higher temperatures recorded during the repeated experiment, might have affected the values found.

The higher organic matter intake (OMI) by goats (33.3 $\text{g}\cdot\text{BW}^{-.75}\cdot\text{d}^{-1}$) as compared to sheep (24.9 $\text{g}\cdot\text{BW}^{-.75}\cdot\text{d}^{-1}$) is consistent with the hypothesis raised by Van Soest (1982) that goats are a more selective species and have a higher voluntary intake than sheep. Cordova et al. (1978), reported values ranging from 36.7 to 151.1 g of $\text{OMI}\cdot\text{BW}-{}^{.75}\cdot\text{d}^{-1}$ for sheep, a range of values considerably higher than I found. For goats, Masson and Simiane (1981) indicated a value of 50 g $\text{DMI}\cdot\text{BW}^{-.75}\cdot\text{d}^{-1}$ for lactating animals under grassland conditions in France, while Schacht (1987) working in rangelands of northeast Brazil, reported values ranging from 33 to 71.5 g $\text{OMI}\cdot\text{BW}^{-.75}\cdot\text{d}^{-1}$. These literature values for goats are also higher than the results I found for goats. However, organic matter intake by free-ranging animals is subject to several influences, including those related to the animal itself, environmental influences, plant factors, and plant-animal interactions.

Factors such as age, body condition and forage availability have been shown to be important in some studies (Arnold, 1985; Arnold and Birrell, 1977); however, high temperatures recorded during Experiment 2 might have been the single most important variable affecting feed intake in this study. Arnold (1985) indicated that grazing time may decrease linearly with temperatures above 21°C. During Experiment 2, the only hours when the temperatures were below 21°C were from 7:00 PM to 7:00 AM, a total of twelve hours. These relatively high temperatures apparently depressed grazing time (Table 5) and probably contributed to the low voluntary OMI observed.

Independent of temperature effects, goats had a higher intake, relative to metabolic body size, than sheep. This was also reflected in a higher crude protein intake, even through the crude protein content of the diets was similar. This similarity was expected, since the animals were grazing a small and very uniform grass pasture, and this would have limited any advantage in dietary selectivity for either species.

On the other hand, the apparent digestibility of dietary crude protein was higher for the goats than sheep. The 20 percent advantage in favor of goats is similar to a 23.5 percent higher advantage of goats over sheep reported by Jones et al., (1972). However, the Jones et al., (1972) study was a conventional digestion trial where only two goats and two sheep were fed three different types of silage over three periods. Gihad (1976) used twelve small East African goats and twelve Dorper sheep in a conventional digestion trial with Hyparrahenia spp. He did not find a statistical difference for crude protein apparent digestibility.

Louca et al., (1982) reported that the majority of studies involving sheep and goats digestibility comparisons have been conducted in tropical environments and with a small number of animals and a wide intra-species variation in weight, age and body condition.

Feldmann et al., (1981) indicated that the possibility of real differences in digestive efficiency in ruminants exists through differences in retention time, metabolic organic matter excretion, rumen absorption capacity and/or the maintenance of unique rumen environments.

Louca et al., (1982) concluded that goats are able to digest crude protein better than sheep, principally of poor quality roughage. Data from this grazing trial seem to support this contention. However the mechanism responsible for this is not clearly elucidated yet.

The higher crude protein intake associated with the higher crude protein digestibility coefficient by the goats were responsible for a higher digestible protein intake. The literature (Feldmann et al., 1981; Harrington, 1982; Van Soest, 1982; McDowell, 1984; Oliveira et al., 1986) documents that goats are highly selective in their dietary habits. This behavioral ability is one of the mechanisms they use to exist under harsh environmental conditions.

Feldmann et al., (1981) concluded that a relatively high dry matter intake aids the goat in maintaining itself under conditions of poor quality feed. However, according to the same authors, the intake advantage attributed to goats is not enough to explain their ability to survive in areas where sheep and cattle suffer nutritional stress. My findings of a higher digestibility of crude protein may provide an additionally important advantage in terms of protein nutrition of free-grazing goats.

The greater dietary selectivity by goats described in the literature, associated with a higher voluntary organic matter intake and a higher crude protein digestibility would suggest that protein may not be the most limiting nutrient for goats under free-ranging conditions.

Even though the mechanisms involved in this higher utilization of nitrogen by goats are not understood, they possibly are related to differences in nitrogen recycling as well as the interrelationship between water intake and the rate of passage. It is possible that the reported higher water economy by goats (Louw, 1984; Ghosh, 1987) favors a higher protein degradation in the rumen and a higher urea recycling. Those factors associated with a quantitatively small protein requirement for maintenance (35 g of digestible protein for a 30 kg goat) may enable goats to meet their requirements under conditions too meager to adequately support sheep.

The dietary gross energy content of both species, as expected, was not different, and the higher gross energy intake by the goats was a direct consequence of their higher voluntary organic matter intake. Contrary to findings on crude protein digestibility, gross energy digestibility coefficients were similar for both species (52.7 for sheep vs. 51.2 percent for goats). This is in line with literature reviewed in which there were no reports on any significant edge favoring either species. Therefore, it can be concluded that both species are able to utilize energy with the same efficiency under free-grazing conditions.

SUMMARY AND CONCLUSIONS

The main purpose of this study was to compare the energy expenditures of free-ranging goats and sheep using the Carbon Dioxide Entry Rate Technique (CERT). Attempts were also made to estimate the energy costs associated with browsing activities and the use of bipedal stance. Energy budgets based on 24-hour activity budgets were constructed, and the results from those estimates were compared with the concurrent CERT measurements. Validation of CERT was performed by simultaneous measurements of carbon dioxide entry rate and the energy expenditure of the animals using the oxygen consumption technique in an open flow respiration chamber.

The energy expenditures of free-ranging goats and sheep were measured in three separate grazing trials using five goats and five sheep in each trial. Two of these trials were designed to stimulate the animals to browse and make use of bipedal stance.

During one of the three grazing trials, nutrient intake by animals was determined. Fecal organic matter output was estimated by the use of a chromic oxide marker. Dietary organic matter digestibility was estimated by _in vitro_ fermentation of esophageal extrusa samples obtained from esophageally fistulated goats and sheep grazing the experimental area, and estimates of total organic matter intake were derived as the ratio of fecal output to diet indigestibility. The nutritional content of diets from both species was examined and comparisons were made of organic matter, crude protein, gross energy, digestible protein and digestible energy intakes, and crude protein and gross energy apparent digestibility coefficients.

The validation of CERT yielded a predictive linear regression equation ($Y = 0.878 + 5.333$ ER) having a coefficient of determination (r^2) of 0.979 and a standard error of the estimate of 0.12 $\text{Kcal}\cdot\text{min}^{-1}$. This error represented approximately 8 percent of the mean rate of energy expenditure, indicating that CERT is accurate enough to estimate energy expenditures of free-grazing animals if properly calibrated indoors with the same animal species to be used in the field.

The overall energy expended by the animals for the three grazing experiments were 127.1 and 88.4 $\text{Kcal}\cdot\text{BW}^{-.75}\cdot\text{d}^{-1}$ for goats and sheep, respectively. This difference was statistically ($P<.05$) significant, and consistent for all three grazing trials.

Unseasonably higher air temperatures recorded during one of the field experiments apparently contributed to heat stress in the grazing animals. While both animal species responded to this situation by adjusting their daily activity budget, sheep appeared more successful than goats in using behavioral adaptations and avoidance strategies to face a higher heat load. The most used tactic was to decrease the amount of time devoted to grazing and grazing-related activities, and to increase less-costly activities such as lying. Lying may have helped the animals to decrease heat load by transferring heat through conduction to the cooler soil surface. Sheep, but not goats, chose to graze during the cooler parts of the day and even during the night.

We were unable to relate either browsing or bipedal stance to higher energy expenditures by either animal species but this may well have been a function of the flawed experimental design used rather than a real absence of differences. Higher energy costs incurred by either animal species during any particular trial was more related to time spent grazing or inability to withstand environmental constraints. The relatively minor use of browsing and bipedal stance behaviors that were observed seemed to be more related to goats than to sheep.

Activity budgets and meteorological data, especially air temperature, provided a valuable aid for interpreting energy expenditure measurements of free-ranging animals. These data should be taken concurrently in any attempt to determine the energy costs of free existence.

Activity budget derivations of energy expenditures did not provide a reliable estimate of daily energetic costs for either species. This technique underestimated CERT results for sheep by 1 percent in one case and overestimated 14 and 20 percent in two other cases. For goats the error was even larger; the activity budget method gave an estimate that was 39 percent lower than the value obtained using CERT. This suggests that energy budgets calculated from activity budgets are not reliable, and should be avoided when precise estimates of energy expenditures are desired. Results also show that unless unit energetic cost values for specific activities such as browsing and bipedal stance by goats are obtained, the energy budget technique is totally unacceptable to derive energy expenditure estimates for those animals.

The nutritive value of the diet selected by both animal species was similar. However, the highly uniform forage sward conditions of the pasture used in this study probably prevented either animal species from achieving a nutritional advantage through selective grazing. On a metabolic body size basis, goats had a higher voluntary organic matter intake, which in turn was responsible for higher digestible protein and digestible energy intakes. The apparent crude protein digestibility coefficient for goats was 20 percent higher than for sheep, but the apparent digestibility of gross energy was similar for both species. These results suggest that goats have an edge in meeting their dietary protein requirements through a higher organic matter intake and a higher crude protein digestibility coefficient. These findings are consistent with their measured higher rate of energy consumption. However, the mechanisms of these differences are not well known and more studies in species dynamics of utilization of protein and energy under range conditions are badly needed.

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APPENDIX

Appendix Table A.1. Daily energy expenditures in $Kcal \cdot BW^{-.75} \cdot d^{-1}$ of individual free-ranging goats and sheep. (Experiment 2).

Sheep Animal Number	$\bar{X}$ ± SE	Goats Animal Number	$\bar{X}$ ± SE
01	99.22 ± 0.1	06	131.53 ± 0.7
02	75.04 ± 1.1	07	143.47 ± 1.3
03	76.99 ± 1.2	08	119.42 ± 0.6
04	63.87 ± 0.3	09	144.28 ± 0.2
05	90.74 ± 0.5	10	-----
Mean ± SE	81.17 ± 6.2[b]		134.68 ± 5.9[a]

[a,b] Means in the same row with different superscripts are statistically (P<.05) different.

Appendix Table A.2. Daily energy expenditures in $Kcal \cdot BW^{-.75} \cdot d^{-1}$ of individual free-ranging goats and sheep (Experiment 3).

	Sheep		Goats
Animal Number	$\bar{X} \pm$ SE	Animal Number	$\bar{X} \pm$ SE
01	88.46 ± 0.7	06	111.61 ± 0.2
02	70.06 ± 0.2	07	130.66 ± 0.2
03	86.52 ± 0.4	08	109.89 ± 0.2
04	---	09	125.71 ± 0.1
05	75.29 ± 0.2	10	112.39 ± 0.1
Mean ± SE	80.08 ± 4.4[b]		118.05 ± 4.2[a]

[a,b] Means in the same row with different superscripts are statistically (P<.05) different.

Appendix Table A.3. Daily energy expenditures in $\mathrm{Kcal \cdot BW^{-.75} \cdot d^{-1}}$ of individual free-ranging goats and sheep (Experiment 4).

Sheep		Goats	
Animal Number	$\bar{X} \pm SE$	Animal Number	$\bar{X} \pm SE$
01	117.75 ± 1.4	06	----
02	100.69 ± 0.9	07	148.95 ± 1.2
03	105.52 ± 1.6	08	122.04 ± 0.2
04	79.10 ± 0.7	09	123.67 ± 0.2
05	107.99 ± 1.3	10	128.80 ± 0.4
Mean ± SE	102.21 ± 6.4[b]		130.87 ± 6.2[a]

[a,b] Means in the same row with different superscripts are statistically ($P<.05$) different.

Appendix Table A.4. Analysis of variance table for energy expenditure of goats and sheep, using the Carbon Entry Rate Technique.

Source	df	MS	F
Species (S)	1	10113	34.48**
Animal/Species	8	293	
Treatments (T)	2	891	25.59**
S x T	2	330	9.38**
Error	13	35	

Appendix Table A.5. Activity budget in minutes·d^{-1} for goats and sheep under free-ranging conditions (Experiment 2).

Animal			Standing		Lying			
No.	Grazing	Walking	Idle	Ruminating	Idle	Ruminating	Ruminating[1]	Others
SHEEP:								
01	400	30	125	15	640	225	240	5
02	345	40	115	0	635	305	305	0
03	245	10	240	5	840	90	95	10
04	410	25	190	5	460	335	340	15
05	270	50	140	5	800	165	170	10
$\bar{X}$ ± SE[2]	334 ± 33^a	31 ± 7^a	162 ± 23^b	6 ± 2^a	675 ± 68^a	224 ± 45^a	230 ± 45^a	8 ± 3^a
GOATS:								
06	295	45	270	10	740	65	75	15
07	325	35	310	60	690	5	65	15
08	195	20	295	15	875	25	40	15
09	285	80	235	15	720	70	85	35
10	100	25	550	20	720	20	40	5
$\bar{X}$ ± SE	240 ± 41^a	41 ± 11^a	332 ± 56^a	24 ± 9^a	749 ± 32^a	37 ± 13^b	61 ± 9^b	17 ± 5^a

[1] Ruminating = standing ruminating + lying ruminating.

[2] Means in the same column with different letter superscripts are statistically (P<.05) different.

Appendix Table A.6. Activity budget in minutes.d^{-1} for goats and sheep under free-ranging conditions (Experiment 3).

Animal No.	Grazing	Walking	Standing		Lying		Ruminating[1]	Browsing	Others
			Idle	Ruminating	Idle	Ruminating			
SHEEP:									
01	590	15	30	25	475	285	310	0	20
02	460	20	60	80	600	210	290	5	5
03	570	40	20	5	445	335	340	0	25
04	470	25	55	5	530	345	350	5	5
05	540	35	120	15	455	240	255	0	35
$\bar{x}$ ± SE[2]	526 ± 26^{a}	27 ± 5^{b}	57 ± 17^{b}	26 ± 14^{b}	501 ± 29^{a}	283 ± 26^{a}	309 ± 17^{b}	2 ± 1^{b}	18 ± 6^{b}
GOATS:									
06	360	65	310	145	355	180	325	15	10
07	335	40	235	175	360	255	430	25	15
08	275	40	295	105	440	265	370	15	5
09	305	40	525	230	195	110	340	25	10
10	425	45	320	310	155	160	470	15	10
$\bar{x}$ ± SE	340 ± 26^{b}	46 ± 5^{a}	337 ± 49^{a}	193 ± 36^{a}	301 ± 54^{b}	194 ± 29^{a}	387 ± 27^{a}	19 ± 2^{a}	10 ± 2^{a}

[1] Ruminating = Standing ruminating + lying ruminating.

[2] Means in the same column with different letter superscripts are statistically ($P<.05$) different.

Appendix Table A.7. Activity budget in minutes.d^{-1} for goats and sheep under free-ranging conditions (Experiment 4).

Animal No.	Grazing	Walking	Standing		Lying		Ruminating[1]	Bipedal Stance	Others
			Idle	Ruminating	Idle	Ruminating			
SHEEP:									
01	725	15	60	30	390	200	230	0	20
02	620	10	90	45	525	145	190	0	5
03	675	20	55	30	315	325	355	0	20
04	655	15	60	10	365	305	315	0	30
05	360	50	305	45	525	135	180	0	20
$\bar{X}$ + SE[2]	607 ± 64^{a}	22 ± 7^{a}	114 ± 48^{a}	32 ± 6^{b}	424 ± 43^{a}	222 ± 40^{a}	254 ± 35^{a}	0^{a}	19 ± 4^{a}
GOATS:									
06	540	25	160	105	380	200	305	10	20
07	445	35	150	155	370	260	415	10	15
08	380	30	220	65	445	260	325	30	10
09	375	40	355	185	335	140	325	0	10
10	325	20	395	50	450	175	225	0	25
$\bar{X}$ ± SE	413 ± 37^{b}	30 ± 4^{a}	256 ± 50^{a}	112 ± 26^{a}	396 ± 22^{a}	207 ± 24^{a}	319 ± 30^{a}	10 ± 5^{a}	16 ± 3^{a}

[1] Ruminating = Standing ruminating + lying ruminating.

[2] Means in the same column having different letter superscripts are statistically ($P<.05$) different.

Appendix Table A.8. Analysis of variance table for daily grazing time by sheep and goats.

Source	df	MS	F
Species (S)	1	187230	17.86**
Animal/Species	8	10486	
Treatments (T)	2	128290	18.91**
S x T	2	7720	1.14
Error	16	6785	

Appendix Table A.9. Analysis of variance table for daily walking time by sheep and goats.

Source	df	MS	F
Species (S)	1	1141	3.64
Animal/Species	8	314	
Treatments (T)	2	351	1.96
S x T	2	86	0.48
Error	16	179	

Appendix Table A.10. Analysis of variance table for time spent standing idle by sheep and goats.

Source	df	MS	F
Species (S)	1	292053	21.53**
Animal/Species	8	13564	
Treatments (T)	2	10813	1.48
S x T	2	13303	1.82
Error	16	7306	

Appendix Table A.11. Analysis of variance table for time spent standing ruminating by sheep and goats.

Source	df	MS	F
Species (S)	1	58521	29.08**
Animal/Species	8	2012	
Treatments (T)	2	22643	12.43**
S x T	2	14006	7.69**
Error	16	1822	

Appendix Table A.12. Analysis of variance table for time spent lying idle by sheep and goats.

Source	df	MS	F
Species (S)	1	19763	1.69
Animal/Species	8	11676	
Treatments (T)	2	313343	35.47**
S x T	2	47943	5.43**
Error	16	8834	

Appendix Table A.13. Analysis of variance table for time spent lying ruminating by sheep and goats.

Source	df	MS	F
Species (S)	1	70568	11.53**
Animal/Species	8	6123	
Treatments (T)	2	32160	7.54**
S x T	2	18610	4.36*
Error	16	4264	

Appendix Table A.14. Analysis of variance table for total rumination time by sheep and goats.

Source	df	MS	F
Species (S)	1	563	0.73
Animal/Species	8	4465	
Treatments (T)	2	107783	25.00**
S x T	2	48306	11.20**
Error	16	4312	

Appendix Table A.15. Analysis of variance table for time spent browsing by sheep and goats.

Source	df	MS	F
Species (S)	1	241	38.53**
Animal/Species	8	6	
Treatments (T)	2	368	58.80**
S x T	2	241	38.53**
Error	16	6	

Appendix Table A.16. Analysis of variance table for time spent in bipedal stance by goats and sheep.

Source	df	MS	F
Species (S)	1	83	3.33
Animal/Species	8	25	
Treatments (T)	2	83	3.33
S x T	2	83	3.33
Error	16	25	

Appendix Table A.17. Analysis of variance table for time spent in other activities by goats and sheep.

Source	df	MS	F
Species (S)	1	3.33	0.04
Animal/Species	8	87	
Treatments (T)	2	66	0.93
S x T	2	191	2.69
Error	16	71	

Appendix Table A.18. Daily distance walked by goats and sheep under free-grazing conditions (Experiment 2).

Sheep		Goats	
Animal Number	Distance Walked (km)	Animal Number	Distance Walked (km)
01	3.33	06	3.54
02	4.36	07	3.90
03	3.72	08	2.25
04	4.86	09	4.65
05	3.33	10	2.75
$\bar{X}$ ± SE	3.92 ± 0.3[a]	$\bar{X}$ ± SE	3.42 ± 0.4[a]

[a] Means are not statistically (P>.05) different.

Appendix Table A.19. Daily distance walked by goats and sheep under free-grazing conditions (Experiment 3).

Sheep		Goats	
Animal Number	Distance Walked (km)	Animal Number	Distance Walked (km)
01	5.04	06	4.90
02	3.90	07	3.86
03	4.08	08	3.58
04	2.54	09	4.65
05	3.79	10	5.69
$\bar{X}$ ± SE	3.87 ± 0.4[a]	$\bar{X}$ ± SE	4.54 ± 0.4[a]

[a] Means are not statistically (P>.05) different.

Appendix Table A.20. Daily distance walked by goats and sheep under free-grazing conditions (Experiment 4).

Sheep		Goats	
Animal Number	Distance Walked (km)	Animal Number	Distance Walked (km)
01	5.69	06	5.15
02	5.94	07	4.79
03	6.54	08	4.94
04	5.29	09	5.47
05	3.72	10	4.11
$\bar{X}$ ± SE	5.44 ± 0.5[a]	$\bar{X}$ ± SE	4.89 ± 0.2[a]

[a] Means are not statistically (P>.05) different.

Appendix Table A.21. Analysis of variance table for daily distance walked by goats and sheep.

Source	df	MS	F
Species (S)	1	0.12	0.70
Animal/Species	8	0.73	
Treatments (T)	2	5.74	8.28**
T x S	2	[illegible].18	1.70
Error	16	0.69	

Appendix Table A-22. Calculated daily energy budgets for free-grazing goats and sheep for Experiment 2.

Animal Number	Weight (kg)	RMR	Grazing	Walking	Standing	Ruminating	Total	
		Kcal·d^{-1}						Kcal·BW$^{-.75}$·d^{-1}
SHEEP:								
01	58.1	1620.4	174.3	114.1	33.0	7.0	1948.8	92.6
02	85.4	2163.1	221.0	219.7	42.7	13.0	2659.5	94.7
03	74.9	1960.4	137.6	164.4	38.2	3.6	2304.2	90.5
04	79.0	2040.4	242.9	226.5	25.5	13.4	2548.7	96.2
05	64.9	1760.7	131.4	127.5	30.8	5.5	2055.9	89.9
Overall mean±SE	72.5±4.9	1909.0±97.4	181.4±22.2	170.4±23.0	34.0±3.0	8.5±2.0	2303.4±136.7	92.8±1.2^{a}
GOATS:								
06	31.8	1031.1	70.4	66.4	20.2	1.2	1189.3	88.8
07	31.8	1031.1	77.5	73.2	23.7	1.0	1206.5	90.1
08	38.6	1192.4	56.5	51.2	20.8	0.8	1321.7	85.3
09	37.5	1166.8	80.2	102.9	24.4	1.6	1375.9	90.8
10	37.7	1171.5	28.3	61.2	26.4	0.8	1288.2	84.7
Overall mean±SE	35.5±1.5	1118.6±36.0	62.6±9.5	71.0±8.8	23.1±1.2	1.1±0.1	1276.3±35.0	87.9±1.2^{b}

[a,b] Species means in Kcal·BW$^{-.75}$·d^{-1} with different letter superscripts are statistically ($P<.05$) different.

Appendix Table A-23. Calculated daily energy budgets for free-grazing goats and sheep for Experiment 3.

Animal Number	Weight (kg)	RMR	Grazing	Walking	Standing	Ruminating	Browsing	Total	
		Kcal·d^{-1}							Kcal·BW$^{-.75}$·d^{-1}
SHEEP:									
01	55.4	1563.6	245.1	164.7	37.7	8.6	---	2019.7	99.5
02	68.1	1825.4	234.9	156.7	42.9	9.9	3.2	2272.1	95.8
03	56.8	1593.1	242.8	124.7	37.5	9.7	---	2007.8	97.0
04	61.7	1695.1	217.5	92.5	34.6	10.8	2.9	2053.3	93.3
05	47.2	1386.6	191.2	105.5	35.2	6.0	---	1724.5	95.8
Overall mean±SE	57.8±3.5	1612.8±72.8	226.3±10.0	128.8±14.0	37.6±1.5	9.0±0.8	1.2±0.7	2015.5±87.2	96.3±1.0[a]
GOATS:									
06	33.1	1062.6	89.4	95.7	30.0	5.4	4.7	1287.8	93.3
07	27.7	929.7	69.6	63.1	22.9	6.0	6.5	1097.8	90.9
08	34.1	1086.6	70.3	72.0	25.1	6.3	4.8	1265.1	89.7
09	29.5	974.7	67.5	80.9	33.5	5.0	6.9	1168.5	92.3
10	32.7	1052.9	104.2	109.7	36.8	7.7	4.6	1315.9	96.2
Overall mean±SE	31.4±1.2	1021.3±29.6	80.2±7.2	84.3±8.3	29.7±2.6	6.1±0.5	5.5±0.5	1227±40.7	92.5±1.1[b]

[a,b] Species means in Kcal·BW$^{-.75}$·d^{-1} with different letter superscripts are statistically ($P<.05$) different.

Appendix Table A-24. Calculated daily energy budgets for free-grazing goats and sheep for Experiment 4.

Animal Number	Weight (kg)	RMR	Grazing	Walking	Standing	Ruminating	Bipedal	Total	
		Kcal·d^{-1}							Kcal.BW$^{-.75}$.d^{-1}
SHEEP:									
01	54.5	1544.5	296.3	183.0	46.3	6.3	---	2076.4	103.5
02	67.2	1807.2	312.5	235.5	51.7	6.4	---	2413.3	102.8
03	55.8	1572.1	282.5	215.3	44.6	9.9	---	2124.4	104.1
04	63.6	1734.1	312.4	198.5	49.0	11.3	---	2305.3	102.4
05	48.1	1406.4	129.9	105.6	37.5	4.3	---	1683.7	92.2
Overall mean±SE	57.8±3.4	1612.9±71.2	266.7±34.7	187.6±22.3	45.8±2.4	7.6±1.3	---	2120.6±125.0	101.0±2.2^{a}
GOATS:									
06	31.8	1031.0	128.8	96.6	27.3	4.8	4.8	1293.4	96.6
07	27.7	929.7	92.4	78.3	22.4	5.7	4.2	1132.7	93.8
08	35.0	1108.0	99.8	102.0	25.7	5.7	15.8	1357.0	94.3
09	29.7	979.6	83.5	95.9	28.7	4.8	---	1192.5	93.7
10	32.2	1040.8	78.5	78.1	26.2	3.6	---	1227.2	90.8
Overall mean±SE	31.3±1.2	1017.8±30.1	96.6±8.8	90.2±5.0	26.1±1.1	4.9±0.4	5.0±2.0	1240.6±39.0	93.8±1.0.9^{b}

^{a,b}Species in Kcal·BW$^{-.75}$·d^{-1} with different letter superscripts are statistically ($P<.05$) different.

Appendix Table A.25. Analysis of variance table for CERT vs. energy budget comparisons in goats and sheep.

Source	df	MS	F
Species (S)	1	3352	19.28**
Animal/Species	8	174	
Techniques (T)	1	2332	15.13**
S x T	1	6844	44.41**
Animal/Technique	8	154	
Experiments (R)	2	630	30.79**
S x R	2	198	
T x R	2	385	
S x T x R	2	145	
Error	29	20	

Appendix Table A.26. Analysis of variance table for organic matter intake by goats and sheep in Experiment 2.

Source	df	MS	F
Species	1	178.4	8.95*
Error	8	19.9	

Appendix Table A.27. Analysis of variance table for crude protein intake by goats and sheep in Experiment 2.

Source	df	MS	F
Species	1	2.209	6.52*
Error	8	0.339	

Appendix Table A.28. Analysis of variance table for crude protein apparent digestibility coefficient by goats and sheep in Experiment 2.

Source	df	MS	F
Species	1	272.5	15.38**
Error	8	17.7	

Appendix Table A.29. Analysis of variance table for digestible crude protein intake by goats and sheep in Experiment 2.

Source	df	MS	F
Species	1	2.116	13.65**
Error	8	0.155	

Appendix Table A.30. Analysis of variance table for gross energy intake by goats and sheep in Experiment 2.

Source	df	MS	F
Species	1	3835	8.40*
Error	8	457	

Appendix Table A.31. Analysis of variance table for gross energy apparent digestibility coefficient by goats and sheep in Experiment 2.

Source	df	MS	F
Species	1	6.27	3.70
Error	8	1.69	

Appendix Table A.32. Analysis of variance table for digestible energy intake by goats and sheep in Experiment 2.

Source	df	MS	F
Species	1	1292	8.53*
Error	8	151	

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