The Physiology of Eating and the Energy Expenditure of the Ruminant at Pasture

P. O. OSUJI

Highlight: *Large areas of the world are marginal lands and extensive grazing of moderately good or poor pastures is the major avenue for producing meat and milk. As the world population increases, the future supply of meat and milk for man would of necessity have to come from the utilization of existing marginal lands in grazing systems.*

Conventional estimates of the energy required for maintenance have been made with animals housed indoors in respration chambers. Animals at pasture walk longer distances, and usually up gradients and ingest herbage of usually low dry matter content. Consequently, they spend considerably more time eating and foraging for food than conventionally housed animals. These extra muscular activities, over and above those observed indoors, might increase the maintenance energy requirements of animals on range by 25–50%.

It is suggested that this increased requirement might be due to the energy cost of eating, walking to graze, and the "work of digestion" done by the gut in handling bulky pasture materials.

The energy requirements of animals indoors have been estimated by the use of direct calorimetry (Pullar, 1969; Blaxter, 1967; Benzinger and Kitzinger, 1949; Braman, 1933) or indirect calorimetry (Blaxter, 1967; Blaxter et al., 1954; Kleiber, 1935; Flatt et al., 1958; Wainman and Blaxter, 1958, 1969), and by the comparative slaughter technique (Lofgreen, 1965). However the energy requirements of the free ranging animal have been more difficult to estimate because of the complications of environmental factors. Indications are that animals on range have maintenance requirements appreciably higher than those indoors.

Blaxter (1967) reported that activity by sheep at maintenance and in a thermoneutral environment would

increase their total energy expenditure by 11%. For cattle he suggested that they expend about 15% more energy out-of-doors than indoors. Other workers determined the maintenance requirements of animals at pasture from the intake of digestible organic matter required to maintain them at constant liveweight. Corbett et al. (1961) found that when cows were strip-grazed, their maintenance requirements did not differ greatly from what would be expected indoors. The average cow required 12.1 Mcal metabolizable energy (ME) per day. Reid (1958) reported that the maintenance needs of average dairy cows at pasture was 18.6 Mcal/day. Wallace (1955) found that dairy cows at pasture required 21.1 Mcal/day for maintenance. Similar values by Hutton (1962) ranged from 18.4-25 Mcal/day. Some of these estimates would indicate that cows at pasture have maintenance needs 50 to 100% greater than similar cows indoors.

The increased requirements of sheep at pasture have ranged from about 25% (Langlands et al., 1963; Coop and Hill, 1962) to about 100%

(Lambourne and Reardon, 1963). Values for penned sheep were 1.6 Mcal/day (Langlands et al., 1963) and 1.4 Mcal (Coop, 1962). However the outdoors maintenance requirements reported by the various workers were 2.3 to 2.7 Mcal ME/day (Coop and Hill, 1962) and 2.1 Mcal/day (Lambourne and Reardon, 1963). Blaxter (1967) suggested that such high maintenance requirements for sheep at pasture might be due to increased costs of body movement at pasture, the effects of the outdoor environment, or errors due to the measurement of organic matter intake. It is suggested that the increased energy expenditure at pasture might be due to increased overall costs associated with grazing, especially the costs of walking to and harvesting the herbage, which depend on the availability of pasture and environmental stresses (Osuji, 1973).

Recently Young and Corbett (1972) developed methods for estimating the energy requirements of sheep at pasture. They used either a "Mobile Indirect Calorimeter" (Corbett ct al., 1969) or the carbon dioxide entry rate technique (Young et al., 1969). With these apparently improved techniques the energy requirements of sheep at pasture were 60 to 70% greater than those for housed sheep of similar body weight (Yougn and Corbett, 1972). These values are all 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 animals at pasture.

Graham (1964, 1965) reported that the energy expended in muscular work by a sheep at pasture could be up to six times that of a housed sheep due to standing, walking, eating, the energy cost of rumination, and the secretory activities associated with feeding (Ustjanzew, 1911; Graham, 1962, 1964; Agr. Res. Council, 1965; Young, 1966; Osuji, 1971; Webster, 1972). The energy cost of eating has been said to constitute an appreciable part of the extra maintenance requirement of the grazing animal (Osuji, 1971; Webster, 1972). The muscular activities of prehension and mastication plus the secretory activities associated with feeding are essential components of this complex. Therefore, the study of the marked changes associated with eating, especially their contributions to the total heat increment of an animal, may lead to a better understanding of the physiology of forage utilization, particularly with regard to energy requirements and the effect of the physical form of the diet on the productivity of ruminants.

Studies of the physiological changes associated with feeding in animals at pasture are very difficult. Therefore, Osuji (1973) attempted to study in the calorimeter the changes associated with the ingestion of fresh herbage and the same material dried. It was hoped that this would give a clue as to such changes in animals eating the same fresh material in the field. It was found that the ME requirement of sheep given fresh grass was 12% higher than that of sheep given dried grass.

Energy Cost of Muscular Activity

Standing vs Lying

When an animal is fasted in a respiration chamber, the energy the animal expends in minor movements (standing, drinking, and scratching) is usually very small (Blaxter, 1967). In cattle, Forbes et al. (1927) found, as did Blaxter (1967), that under the conditions obtainable in respiration chambers, the activity of cattle was much the same whether they were fed or fasted. Fasting steers spent on average 7.2 hours/24 hours standing as compared to 7.8 hours for the fed animal.

It is difficult to ascertain to what extent the levels of activity in animals observed in respiration chambers

Table 1. Energy cost (kcal/kg/hour) of standing over lying.

Species	Energy cost of activity	Reference
Sheep	0.06	Osuji (1973)
	0.12	Hall and Brody (1933)
	0.07	Joyce and Blaxter (1963)
	Metabolism increased by 70%	Pullar (1962)
	0.38	Armsby and Fries (1915)
	0.34	Graham (1964)
	0.12	Webster and Valks (1966)
Cattle	0.09	Hall and Brody (1933)
	0.12	Forbes et al. (1927)
	0.06	Blaxter and Wainman (1962)
	0.10	McLean (1962)

reflect their activity under normal feeding conditions or under range or pasture conditions where the area available for movement is greatly increased, especially when pasture availability is limited. With both cattle and sheep, there is a linear increase in grazing time as pasture availability decreases (Lofgreen et al., 1957; Arnold, 1960).

Not surprisingly, these reports show that animals grazing poor or sparse pastures spend more time standing and walking about than do conventionally housed animals. The increased energy expended by an animal at pasture over that expended in a calorimeter depends, therefore, on the energy cost of the different activities at pasture and the time spent in pursuit of them additional to that in the calorimeter. Young and Corbett (1972) in a recent experiment showed that as pasture availability decreased from 2800 to 370 kg/hectare, grazing time increased from 8.2 to 12.3 hours.

Estimates of the increased energy cost of standing over lying made in respiration equipments are summarized in Table 1.

Walking

The energy cost of horizontal locomotion has been determined by various workers for various species of animals. Clapperton (1961, 1964) found that the energy cost of horizontal walking in sheep increased with speed and was on average 0.59 cal/horizontal kg meter. Values of 0.54 for man (Smith, 1922), 0.58 for the dog (Lusk, 1931), and 0.39 cal/horizontal kg m for the horse (Brody, 1945) have also been reported. Clapperton (1961) with sheep found that the energy cost of vertical work decreased with speed but was independent of gradient. He found a value of 6.45 cal/vertical kg m. This

could be compared to 6.92 cal/kg vertical m found for man by Lusk (1931). The amount of food given to the sheep had no effect on the cost of work.

Since the work of ascent is about 10 times as costly as walking on a horizontal plane (Clapperton, 1961) it suggests that an animal grazing a hill pasture expends more energy walking to find the herbage in addition to the other muscular activities. In an area where animals face drought conditions for a greater part of the year and have to travel long distances to graze or drink, the energy cost of walking could be high. Such problems are experienced for example by the nomadic Fulannis and Masai who herd their cattle across the rangelands of Africa.

Energy Cost of Eating

The Agricultural Research Council of the United Kingdom (1965) stated that the heat increment of feeding in ruminants is in the main accounted for by the heat of fermentation and the energy cost of metabolizing the volatile fatty acids (VFA). The energy cost of eating they considered was negligible. In other words, the energy cost of grazing, as distinct from the energy cost of standing and walking to graze, should be no different from the energy cost of eating the same amount of food energy when provided in a convenient and readily accessible form in a calorimeter. As indicated earlier, this conclusion now seems unlikely (Osuji, 1971; Webster, 1972); it is probable that grazing is energetically more expensive than eating prepared and accessible food, and the cost of grazing may explain the differences between published accounts of the maintenance energy requirement of the grazing animal.

It has been shown that the energy cost of eating is a direct function of the time spent eating (Osuji, 1973). Therefore, animals at pasture spending 8 to 10 hours (Tribe, 1949; Hughes and Reid, 1951; Arnold, 1960; and Graham, 1965) per day eating would expend an appreciable amount of energy as a direct consequence of eating. Therefore, it is of interest to include in an examination of the factors contributing to the total heat increment of feeding an estimate of the energy cost of eating.

Estimates of the energy cost of eating have been reported by Ustjanzew (1911), Blaxter and Joyce (1963), Graham (1964), Young (1966), Webster (1967), Webster and Hays (1968), and Osuji (1971, 1973). These have been gathered together in Table 2.

Ustjanzew (1911) using mask and tracheostomy techniques measured the respiratory exchange of sheep which were fasted for 13 to 14 hours and then offered various types and preparations of food. The energy cost of eating hay was the same whether it was fed in the long form or chopped and steamed. Metabolic rate during the course of the meal increased by 60%.

The energy expended during consumption of green feed (pea haulms and lucerne) was greater than that during the consumption of an equivalent amount of dry matter fed as hay. This was due mainly to the increased amount of time that the sheep required to achieve the same dry matter intake when eating fresh material.

Graham (1964) dug small areas of turf from pasture and relaid them on the floor of a respiration chamber. Sheep were allowed to graze this material for 1-2 hours. Prepared meals were offered to the sheep between grazing periods. He found that the rates of food intake varied with types of food. Sheep weighing about 40 kg ate 0.5-1 kg of fresh herbage (60-120 g DM) per hour when grazing and 2-3 kg cut fresh herbage (300-400 g DM) and 400-800 g hay per hour; i.e., the rate of eating during grazing was lower than the rate of eating comparable cut fresh grass. Not surprisingly, when sheep were offered poor pasture or given prepared food *ad lib,* their rate of intake was very low; but when given small meals after long periods without food they had the fastest eating rate.

Table 2. Estimates of the energy cost (cal/kg/min) of eating.

Animal	Feed	Cost	Reference
Sheep	Long timothy hay	14.7	Ustjanzew (1911)
"	Timothy hay (wet) soaked	13.42	"
"	Long clover hay	14.73	"
"	Dry pea or lucerne	12.35	"
"	Green lucerne	11.08	"
"	Red clover (green)	7.01	"
"	Oat grain	15.15	"
"	Lucerne hay	10.94	"
Ox	Hay	7.06	Dahn (see Ustjanzew (1911)
Sheep	Cut grass	9.0 (4.9-13.2)	Graham (1964)
"	Uncut sward	9.0 (4.0-16.4)	"
"	Chopped dried grass	10.3	Osuji (1973)
"	Pelleted dried grass	4.4	"
"	Fresh pasture grass	7.5	"
"	Lucerne chaff	5.4-12.4	Young (1966)
"	Wheaten chaff	8.08	"
"	Concentrate	6.4-7.0	"
"	Dried grass	22.0	Webster (1967)*
"	Alfalfa/brome hay	13.8 (11.7-15.5)	Webster and Hays (1968)
"	Chopped alfalfa		Christopherson (1971)
"	Brome grass hay	8.05	"

*Estimate based on heart rate used as an index of heat production.

The rate of energy expenditure during eating was not affected by the size of meals or by the length of time between them. It was suggested that there was "*a tendency* for the cost of any given activity to vary in the same direction as the rate of intake." This statement should not necessarily be taken to mean that the energy cost of activity (eating) is directly related to the rate of eating. Graham's experiments were not particularly designed to answer this question. Graham (1964) estimated the energy cost of grazing as 0.54 kcal/hour/kg wt (range, 0.29-0.79). The corresponding value for eating prepared meals was 0.54 (range, 0.24-0.98).

Blaxter and Joyce (1963) reported that the increased metabolic rate (50-60%) associated with eating in sheep did not continue into the post prandial period. They partly ascribed this to the excitement of animals anticipating their regular feed. However, Osuji (1973) found that heat production during the 2 yours preceding feeding was often not significantly different from the base line values.

Young (1966) offered diets of various types to sheep and found that the increased energy expenditure per gram of diet ingested varied with the type of diet. The energy cost of eating (cal/kgw/g) was 0.3-0.6 for a concentrate diet and 1.2-1.9 for lucerne or wheaten chaff diet. The rates at which the foods were eaten were about 12 g/min for the chaff and

more than 40 g/min for the concentrate diet. His results would, therefore, show contrary to Graham's (1964), that the energy cost of eating was inversely proportional to the rate of eating. Young (1966) also attributed the initial rapid rise in the metabolic rate of the sheep when food was given to psychic factors and claimed that during eating there was a slight increase in respiratory frequency, but this may have been an artefact.

He also used sheep fitted with oesophageal fistulas and found that when the sheep were sham-fed such that 77% of the food was recovered from the oesophageal fistula, there was no difference in the metabolic rate between normally and sham-fed sheep. This finding thus discounted the possibility that the presence of food in the rumen acted as the metabolic stimulus. Young therefore concluded that the increased heat productions observed during eating originate mainly from the act of prehension and mastication.

Webster and Hays (1968) have reported that the increased metabolic rate associated with eating is not mediated through the sympathetic nervous system. They showed that propranolol (a beta-adrenergic blocking agent) almost totally inhibited cardioacceleration in sheep following exposure to a moderate cold stress but only slightly reduced the cardioacceleration observed in sheep during feeding.

Table 3. The daily energy expenditure of a 50 kg sheep at pasture compared to that of a similar sheep kept indoors.

Activity	Duration of activities		Housed		Energy cost of activities		Cost of activity in kcal/kg body wt.
	Unit of measure	No. of units	Unit of measure	Total cost	Grazed		
					Unit of measure	Total cost	
Eating (chopped dried grass)	hour	1	kcal/day	31.0	—	—	0.62/hour
Grazing (fresh pasture)	"	9		—	kcal/day	202.5	0.45/hour[1]
Ruminating	"	8	"	12.0	"	12.0	0.03/hour
Standing							
Housed	"	2	"	6.0	—	—	0.06/hour
Grazed	"	12	—	—	"	36.0	0.06/hour
Walking							
Housed	km/day	1	"	29.5	—	—	0.00059/m
Grazed	km/day	6.1	—	—	kcal/day	180.0	0.00059/m
Total energy cost of muscular work			"	78.5	"	430.5	
Resting metabolic rate[2]			"	1200.0	"	1200.0	
Total daily energy expenditure							
Amount			"	1278.5	"	1630.5	
Increase in energy expenditure due to:							
(1) Muscular activity			%	6.6	%	35.9	
(2) Eating/grazing			"	2.6	"	16.9	
(3) Ruminating			"	1.0	"	1.0	
(4) Standing and walking			"	3.0	"	18.0	

[1] From Osuji (1973).
[2] Resting metabolic rate = Basal metabolic rate (BMR) + heat increment of feed at maintenance.

Young (1966) also estimated that the energy cost of eating for housed animals accounts for 2-3% of their daily energy expenditure. For free ranging animals grazing for 8 to 9 hours a day, the energy cost of eating could constitute an appreciable part of the maintenance requirement (Osuji, 1971; Webster, 1972). The contribution of eating to the daily energy expenditure of an animal grazing poor pasture would be considerably greater, since it has been reported (Arnold, 1960) that the time spent grazing is greatly increased when animals graze very poor pasture. Graham (1964) reported that a sheep grazing poor pasture has a maintenance requirement 40% greater than that of a caged animal.

This estimate agrees more closely with the predictions of increased energy requirements of sheep out-of-doors made on the basis of organic matter intake (Coop and Hill, 1962; Langlands et al., 1963; Lambourne and Reardon, 1963). But it is considerably in excess of the value of about 15% referred to by the Agr. Res. Council (1965) on the basis of Blaxter's (1967) prediction of the allowances for extra muscular activities out-of-doors. This did not include the energy cost of eating, as this was considered negligible. There is, therefore, a strong suggestion on the basis of the foregoing arguement that the energy cost of eating makes a significant contribution to the energy

requirements of animals, especially those at pasture.

Results from recent experiments (Osuji, 1973) indicate that eating definitely results in increased heat production in ruminants as has been observed by other workers. The precise relationship between eating and heat production, especially in relation to the effect of the physical form of the diet, has not been clearly defined.

The trials reported by Osuji (1973) suggest:

1) that eating is associated with an increase in heat production and the increased rate often varies with the physical form of the diet but does not seem to vary with the size of the meal;

2) because dried roughage diets take longer to eat, the increase in heat production associated with their ingestion is considerably greater. Pelleting has the effect of markedly increasing the rate of food intake, and since pelleting reduces the particle size of a diet, the eating of pelleted diets does not result in appreciable increases in heat production attributable to trituration during eating;

3) when fresh grass is given to sheep, their rate of intake of dry matter is much slower, even though they eat an equivalent weight of wet matter more rapidly. This is mainly because of the enormous amount of water in the herbage which they must ingest to attain the same level of dry matter intake as that from dried grass.

Consequently, the energy cost of eating (cal/g DM) the same grass is about twice as great when the fresh than when the dried grass is given;

4) the energy cost of eating varies directly with the time spent eating (r = 0.86). For animals eating, for example, 8 hours a day at pasture, the energy cost of eating would contribute significantly to maintenance requirement. These observations could also explain the low energy costs associated with the eating of prepared meals by housed animals, as these usually consume their day's meal in 1-2 hours.

The same experiments showed that the energy cost of rumination is very small. Therefore, the value of rumination to animals that chew the cud might lie in the great saving in energy during rumination as opposed to eating. For example, the energy cost of eating for a sheep at pasture eating for 16 hours instead of for 8 hours a day, would amount to 22% of the maintenance energy requirement. By eating for only 8 hours, the sheep would at least halve this amount of energy expenditure.

On the basis of calorimetric estimates it has been calculated that a grazing animal would need 10-15% more energy for maintenance than the housed one (Blaxter, 1967). This allowance was made for the increased muscular activity of the grazing animal, mainly standing and walking. However, allowing for activities like

standing, walking, and rumination does not explain the wide discrepancies between the maintenance energy requirement of the housed compared to the free-grazing animal. It is suggested that the energy cost of eating *per se* could partly explain such discrepancies. Webster (1972) and Graham (1964) have reported that the energy cost of eating could account for 25-50% of the extra maintenance requirement of the grazing animal.

It is also probable that the "work of digestion" involved in handling the bulky fresh grass might account for an appreciably high fraction of the total heat increment of feeding observed in ruminants. Osuji (1973), for example, found that visceral heat increment due to aerobic gut metabolism in sheep accounted for about 66% of the increased heat production of the portal drained viscera disregarding the type and physical form of diet.

Table 3 attempts to summarize the contribution of various factors to the increased energy requirement of sheep at pasture as compared to the housed animal. This table clearly shows that the sheep at pasture has a maintenance requirement about 30% higher than that of a comparable animal indoors. This extra requirement is due to the muscular activities of eating, rumination, standing, and walking. While energy expenditure due to eating (foraging?) amounts to about 50% of the total expenditure due to muscular activity in the grazing animal, the corresponding percentage for the housed animal eating a prepared meal is 39%. The contributions of the other activities, except standing and walking, are not appreciable when compared to the eating component.

The maintenance requirement of the animal at pasture has been said to be 25-100% higher than that of a similar animal indoors. This is within the range (30%) calculated in Table 3. It is however being suggested that the "work of digestion" i.e., the work done by the gut in "handling" the bulky pasture material could be the other major component of the increased energy expenditure of the free ranging animal (Osuji, 1973). This is an area that needs further study.

Fluid and Electrolyte Changes during Eating

Dobson et al. (1966) reported that when sheep were changed from high potassium (K), low sodium (Na) grass to hay and diets of medium K and Na contents, the excretion of Na in the urine fell and there was a net retention of Na. When the animals were returned to the grass diet, the Na retained during the previous regime was rapidly lost in the urine. They ascribed these changes to the water and electrolyte content of the gut and suggested that the different physical forms of the diets and their different osmotic activities might have played some part. Stacy and Warner (1966) showed that the rate of absorption of Na from the rumen into the blood was influenced by the potassium concentration of the rumen fluid. The rumen has been said to dominate the response of the animal to changes in the electrolyte content of the diet. When potassium chloride (KCl) was added to a maintenance diet (700 m-eq/day), the K content of the rumen increased and the Na content decreased, due possibly to an increased absorption of Na across the rumen wall (Warner and Stacy, 1972a). Warner and Stacy, (1972b) also found that when saliva was replaced by a synthetic solution, the rate of water movement across the rumen wall was a linear function of the osmotic pressure and concluded that the rate of K and Na absorption tended to depend on the immediate nutritional state of the animal. The morphology of the rumen epithelium underwent extensive changes when the rumen contents were made highly hypertonic.

During feeding, an increased volume of fluid leaves the plasma and extracellular fluid space (ECF) and enters the gut. Stacy and Warner (1966) reported an increase of 0.29-0.85 liters/hour in the flow of fluid from the ECF to the rumen during the consumption of dry feed and ascribed this to an increased salivary flow. A decrease of 10% in the ECF volume was noted by Ternouth (1968) in sheep given 350 g of lucerne chaff. He ascribed this to an increased salivary flow and to the transfer of plasma fluid across the rumen wall during eating. Blair-West and Brook (1969) showed a rapid fall in the plasma volume of sheep within 15 minutes of starting to eat. Plasma volume in sheep given 1 kg of chopped alfalfa-brome hay declined sharply by 300 ml at the beginning of the meal and recovered slowly after feed was removed. Changes in ECF volume estimated from thiosulphate disappearance was variable but showed a significant fall of 1-1.5 liters during eating (Christopherson and Webster, 1972).

Blair-West and Brook (1969) showed that plasma renin concentration rose throughout the duration of a meal and indicated that the renin-angio-tensin system was activated during eating, leading to retention of Na and water when appreciable quantities of fluid were being lost from the ECF to the gut. Feeding has also been shown to stimulate the release of the antidiuretic hormone in sheep.

While it is difficult to make any precise quantitative estimates of the effects of the quantity and quality of food eaten on the flow of electrolytes into and out of the gut, it is clear that these effects are considerable. Webster (1972) therefore postulated that the increased metabolic rate associated with eating could be attributed to these marked increases in the rate at which body fluids were redistributed between the extravascular and vascular compartments and the lumen of the gut. The association of angio-tensin with active transport suggests a possible hormona stimulus to thermogenesis during eating. Because of this, it seems that the effect of eating fresh grass on fluid and electrolyte changes in animals needs more researching.

Cardiovascular Changes Associated with Eating

Heart rate is known to be related to oxygen consumption (Brody, 1945; Webster, 1967) and this relationship has been used to predict the metabolic rates of animals (Blaxter, 1948; Webster, 1967; Brockway and McEwan, 1969). Webster (1967) used the heart rate to predict the metabolic rate of sheep during eating and exposure to cold. Within limits, the relationship between heart rate and oxygen consumption could in some animals, be used to predict energy expenditure. In three out of four sheep the errors associated with the prediction were less than 10%. However in the experiments of Brockway and McEwan (1969) heart rate could not be used adequately as a

predictor of energy expenditure in sheep during eating because of the large errors associated with the prediction equations.

Marked increases in the heart rate of sheep during eating have been reported (Young, 1966; Webster, 1967; Webster and Hays, 1968; Berzins, 1969; Christopherson and Webster, 1972). Ingram and Whittow (1962) also reported an increased heart rate during eating in cattle. Young (1964) attributed the initial increase in heart rate in sheep to the release of adrenaline. The increased heart rate associated with eating was not abolished by beta-adrenergic blockade. It was concluded, at that time, that the cardioacceleration during feeding could not be attributed to excitement (Webster and Hays, 1968). Hays and Webster (1971) later showed that most of the increase in heart rate observed when sheep ate a meal in a thermoneutral environment could be attributed to reduced vagal inhibition. When the stimulatory effects of colds and eating were superimposed, heart rate was often considerably higher than 110 beats/minute, the intrinsic rate of the denervated sheep's heart, even when sympathetic cardioaccelerator fibres were blocked with propranolol. Hays and Webster (1971) suggested from these observations that at this time heart rate was accelerated in part by a non-autonomic factor, possibly angio-tensin, known to be released during eating (Blair-West and Brook, 1969).

During eating both arterial and venous CO_2 tensions and free plasma HCO_3 increased while blood pH decreased; (Christopherson and Webster, 1972) arterial oxygen tension (PO_2) did not change significantly during eating but venous oxygen tension (PvO_2) fell significantly. The fall in oxygen (O_2) saturation of venous blood was related to the decline in pH. The arteriovenous difference in oxygen content increased from 4.4 ml/100 ml before feeding to 6 ml/100 at the end of the meal.

The beginning of the meal was associated with a significant increase in haematocrit and this persisted and only declined slowly afterwards. Blood haemoglobin increased from 8.6 to 9.4 g/100 ml but this was attributed entirely to the increase in haematocrit levels. Cardiac output increased by 17% and stroke volume declined throughout the meal from 67 to 52 ml per heart beat (Christopherson and Webster, 1972).

Apparently eating is associated with a lot of cardiovascular changes. It is to be expected therefore that increased activity by these various systems during eating will contribute to the elevated metabolic rate associated with eating. Therefore for animals on range, the increase in the activities of these systems would be considerably greater and these would increase their maintenance requirement appreciably. Additional increases are suggested as coming from the increased "work of digestion" involved in the handling of the bulky pasture materials.

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