

Metabolic Components of Energy Expenditure in Growing Beef Cattle - Review -

J. S. Caton^{1*}, M. L. Bauer¹ and H. Hidari²

¹ Department of Animal and Range Sciences, North Dakota State University, Fargo, ND 58105, USA

² Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Hokkaido 080, Japan

ABSTRACT : A large portion of total energy expenditure associated with ruminant livestock production goes towards maintenance. Approximately 55% of whole body energy use is consumed by visceral tissues (including internal organs) with the majority of this going to the liver and gastrointestinal tract. Muscle and adipose tissues consume about 27% of total body energy expenditure. Metabolic components within the viscera responsible for the majority of energy consumption include ion transport, protein turnover, substrate cycling, and urea synthesis (liver). Within muscle tissue of growing animals ion transport and protein turnover account for most of the energy expenditure. Protein synthesis consumes approximately 23% of whole body energy use and visceral tissues account for proportionally more of whole body protein synthesis than skeletal muscle. Research efforts focused on improving energetic efficiency of the tissues and metabolic mechanisms responsible for the majority of whole animal energy expenditure should provide information leading to more efficient production of an edible product. (*Asian-Aus. J. Anim. Sci.* 2000. Vol. 13, No. 5 : 702-710)

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INTRODUCTION

Concepts of energy expenditure and measurement have their roots in the classic work of Armsby and Fries (1915), Brody (1945), Klieber (1961), Blaxter (1962), and Lofgreen and Garrett (1968). Identifying and partitioning energy expenditure to various tissues and metabolic processes within tissues is of considerable interest to scientists, allied industries, and livestock producers. Proper identification of tissues and metabolic processes that consume energy associated with both maintenance and production should provide avenues for more focused research. End results should be management practices which conserve energy expenditure by tissues or processes within tissues which are maintenance or service oriented (Baldwin et al., 1980) resulting in proportionally more available energy for product formation. Unlike non-ruminants, a high proportion of metabolizable energy use in ruminant species (>50%) goes to maintain parent populations (Webster, 1989). In addition, over 70% of whole-herd energy expenditure in beef cattle can be associated with maintenance (Ferrell and Jenkins, 1985). The objectives of this paper are to review and summarize existing scientific literature regarding metabolic components of energy expenditure in ruminant livestock. Emphasis will be placed, where possible, on beef cattle. It is hoped that this review will assist in design of future experiments directed towards improving energetic efficiency of beef cattle production.

MAINTENANCE CONSIDERATIONS

Data summarized by Webster (1989; table 1) demonstrates that there are vast differences between ruminants and non-ruminants in the amount of energy expended on maintaining the parent populations. Unlike non-ruminant species, parent populations of ruminant livestock consume over 50% of the total energy associated with product formation. Total herd energy expenditure for maintenance can range from 60 to 90% of total energy use (Caton and Dhuyvetter, 1996). Maintenance energy expenditure is defined as the energy needed for basal processes plus some minimal amount of work; or, as the amount of energy needed to maintain energy balance in the absence of product formation (Ferrell, 1988; Baldwin, 1995).

Table 1. Estimation of yearly proportion of metabolizable energy (ME) use for maintenance of the parent population and slaughter generation of livestock (Adapted from Webster, 1989)

Item	Poultry	Pigs	Sheep	Beef cattle
	—— % of ME use/year ——			
Parent population	4	20	70	52
Progeny	96	80	30	48

Tracking maintenance energy expenditures and requirements in ruminant species is further complicated by grazing. Reid et al. (1980) reported that maintenance requirements may be 10 to 90% greater

* Address reprint request to J. S. Caton. Tel: +1-701-231-7653, Fax: +1-701-231-7590, E-mail: caton@plains.nodak.edu.

Table 2. Energy expenditure of various activities in sheep

Reference	Animal	Treatment	Energy expenditure of activity (% total)					Digestive tract
			Standing	Walking	Eating	Ruminating	Fermentation	
Osuji, 1974	Sheep	Confined	0.5	2.3	2.4	0.9		
		Grazing	2.2	11.0	12.4	0.7		
Webster, 1980	Sheep	Chopped hay						
		Below maintenance			6.0	1.4	24.1	9.4
		Above maintenance			3.6	0.1	13.6	26.0
		Barley pellets						
		Below maintenance			0.1	-	11.8	11.4
		Above maintenance			0.05	-	6.3	30.0

Table 3. Energy expenditure by various tissues (% of whole body energy use)

Reference	Animal	Physiological state	Nervous tissue	Skin	Heart	Kidney	Digestive tract	Liver	Muscle	Adipose
Ferrell, 1988	Sheep	Mature	12.0	2.7	10.0	5.0	15.0	20.5	23.0	7.0
Smith & Baldwin, 1974	Dairy cow	Non-lactating	17.0 ^a	3.5	10.0	-	12.2	22.5	26.0 ^b	-
Webster, 1989	Sheep	Mature	-	-	-	-	24.0	28.0	15.0	-
Webster, 1981	Rats		14.0	11.0	-	14.0	8.0	12.0	20.0	-
Baldwin, 1995	Dairy cow	Lactating	-	-	-	-	-	-	-	5.6
Range			14.0-17.0	2.7-11.0	10.0	5.0-14.0	15.0-24.0	12.0-28.0	15.0-26.0	5.6-7.0
Mean			14.0	5.7	10.0	9.5	14.8	21.0	21.0	6.3

^a Includes kidney; ^b Total carcass (includes bone and adipose).

in grazing compared with pen-fed situations. Data reported by Osuji (1974) indicated that grazing sheep had 30% greater daily energy expenditures when compared with pen-fed controls. Moreover, Robbins (1993) reported that cost of locomotion adds substantially to maintenance cost in grazing ruminants. Data calculated from Osuji's (1974; table 2) work demonstrates that combined functions of standing, walking, eating and ruminating consume 26.3% of total body energy use in grazing sheep. Conversely, in confined sheep, these functions account for only 6.1% of total energy use. Energy expenditure associated with walking and eating represented the majority of the increased energy use associated with grazing. In later work with sheep, Webster (1980; table 2) demonstrated that energy expenditure (% of total) associated with eating chopped hay fed either below or above maintenance was greater when compared with sheep fed barley pellets. In addition, energy expenditure associated with eating, was less in sheep fed above compared with below maintenance. Webster (1980) also demonstrated that fermentation and gastrointestinal tract (GIT) tissue account for a large portion of whole body energy expenditure. This indicates that as energy intake increases GIT energy use also increases. In addition, this response was observed independent of

diet type (chopped hay or barley pellets). These results agree with data comparing the effect of energy intake level on GIT energy use (Reynolds et al., 1991) and demonstrate the central role of the GIT in whole body energy expenditure.

TISSUE ENERGY EXPENDITURES

In summarizing work from several authors (table 3) it can be concluded that, on the average, the viscera and internal organs (heart, kidney, digestive tract, and liver) consume 55% of total energy use in ruminant species. This figure is impressive when one realizes that the same tissues represent only 6 to 7% of empty body mass (Ferrell, 1988). On the other hand, muscle, while representing over 40% of empty body mass appears to account for 21% (15 to 26%) of total energy use. When these data are expressed per gram of tissue, the differences between visceral and muscle energy expenditure is tremendous. Combined muscle and adipose tissue energy expenditures represent 27% of total energy use. Most energy expenditure data are from mature animals. Estimates of tissue energy expenditure in growing ruminants are limited; however, in pre-ruminant calves the liver, portal-drained viscera, and hind limbs represented 14.2, 19.4 and 23.6% of

Table 4. Energy expenditures associated with the liver and gastrointestinal tract (% of whole body energy use)

Reference	Animal	Physiological state	Tissue energy expenditure, %	
			Liver	GIT ^a
Ferrell, 1988	Sheep	Mature	20.5	15.0
Thompson et al., 1975	Rams	Mature	13.9	
Thompson et al., 1978	Rams	Mature	21.5	18.5
Huntington et al., 1985	Steers		25.0	
Huntington and Tyrrell, 1985	Dairy cows	Nonlactating		18.0
Reynolds et al., 1986	Dairy cows	Lactating	25.2	20.4
Webster, 1980	Ruminants	Maintenance		20.0
		Twice maintenance		23.0
Ferrell et al., 1976	Beef heifers	Pregnant and nonpregnant	21.7	
Smith and Baldwin, 1974	Dairy cows	Nonlactating	22.5	12.2
Huntington et al., 1988	Dairy steers			25.0
Reynolds and Tyrrell, 1989	Beef heifers		21.0	25.0
Reynolds et al., 1991	Beef heifers	Mature		
		Alfalfa/low intake	18.5	25.8
		Alfalfa/high intake	26.3	27.5
		Concentrate/low intake	20.6	23.8
		Concentrate/high intake	21.6	22.6
Eisemann & Nienaber, 1990	Beef steers	Mature		
		Fed	20.6	22.7
		Fasted	25.8	18.9
Webster, 1989	Sheep		28.0	24.0
Burrin et al., 1989	Lambs	Maintenance	22.0	19.0
		Ad libitum (compensating)	41.0	28.0
Huntington et al., 1990	Beef steers	Growing		
		Fed	23.5	24.0
		Fasted	30.9	22.5
Range			13.9-41.0	12.2-28.0
Mean			24.0	22.0

^a Majority of data included here is from the portal-drained viscera which also includes pancreas and mesentery.

total energy use, respectively (Martin et al., 1991). These estimates for hind limb energy use in growing calves are similar to total muscle energy use in mature animals (table 3).

Using a mathematical model, Gill et al. (1989a) estimated energy expenditure of combined muscle and adipose tissues in growing sheep to be 27.1% of total energy expenditure. This estimate is similar to data presented in table 3. Interestingly, the model of Gill and coworkers (1989a) predicts that adipose consumes, on a proportion basis, more of total energy expenditure than muscle (24.6 and 2.5% for adipose and muscle, respectively). These specific estimates of total energy use do not fit well with other data (table 3) and likely reflect inadequacies in the model. Their model also projects visceral energy (heart, kidney, digestive tract, liver) use at 72.1% of total in growing sheep. This estimate is somewhat higher than data presented in table 3. While the model of Gill et al. (1989a) may provide estimates of specific tissue energy use that do not always agree with existing

data, the concept of modeling tissue energy expenditure under various physiological conditions is worthy of attention and, if fully developed, could provide useful insight into the area of whole animal energetics.

Liver and gastrointestinal tract

Research conducted during the past 25 years evaluating liver and GIT (PDV) energy expenditure in relation to whole body energy use is summarized in table 4. Most of the studies used oxygen consumption as a measure of energy expenditure, used multiple catheter techniques, and measured entire portal drained viscera rather than the GIT. For an excellent review of the multi-catheter technique readers are referred to Huntington et al. (1989).

Across all studies included in table 4, the liver and GIT consume 24 (13.9 to 41%) and 22% (12.2 to 28.0%) of whole body energy expenditure, respectively. In both cases, liver and GIT energy expenditure in compensating sheep were on the highest end of the

ranges. This indicates that, in compensating sheep, the metabolic processes associated with energy consumption are enhanced above non-compensating levels. This is particularly evident when evaluating liver energy use in maintaining (22.0%) and compensating (41.0%) sheep (Burrin et al., 1989). Likewise, in the same study, the energy expenditure of the PDV followed a similar pattern (19.0 and 28.0% for maintaining and compensating sheep, respectively). It seems that in order to compensate, these sheep needed to have the necessary metabolic machinery in place (GIT and liver) to accomplish this compensatory growth.

Intake, particularly in higher roughage diets (Reynolds et al., 1991), has a major effect on liver energy expenditure. In beef heifers fed alfalfa diets at low and high intake levels, liver energy use was 18.5 and 26.3% of total, respectively (Reynolds et al., 1991). In the same study the PDV tissues demonstrated a less pronounced response (25.8 to 27.5 for low and high intake, respectively). These changes in liver and PDV energy use are likely resulting from shifts in visceral organ weights. Dietary restriction can reduce visceral organ mass (Burrin et al., 1990; Rompela et al., 1991; Swanson, 1996). In studies with growing and mature beef cattle (Eisemann and Nienaber, 1990; Huntington et al., 1990) it has been shown that liver energy expenditure (% of total) is less in the fed when compared with fasted state (table 4). Conversely, the PDV tends to consume less of total energy in the fasted compared with fed state. Their data agrees with Webster (1980) who reported that feeding ruminants twice maintenance resulted in greater PDV energy use, as a proportion of total, when compared with maintenance fed animals (23.0 and 20.0%, respectively). Moreover, lactation appears to increase energy use by the PDV (and liver) over non-lactation (McBride and Milligan, 1984; Kelly et al., 1991). Therefore, it appears that as physiological demand for production increases, energy expenditure by visceral tissues also increases. This stands to reason as the liver and PDV are metabolically highly active tissues. Clearly the viscera (mainly the liver and GIT) consume substantial amounts of total body energy expenditure across a wide range of physiological states. Attempts at understanding and manipulating whole animal energetics towards more product formation and less maintenance cost must consider these highly active visceral tissues.

Metabolic components of GIT and liver energy expenditure

In an excellent review by Huntington and McBride (1988) it was suggested that 62 to 95% of PDV tissue energy use (oxygen consumption) was accounted for by ion transport (principally Na^+ , K^+ -ATPase;

maintenance of membrane potential) and protein turnover (combined synthesis and degradation). When specific estimates for ion transport and protein turnover are included in the estimate, percentage of whole body energy consumption (table 5) arising from PDV (GIT) is 12.4%. This is somewhat less than the 22% summarized in table 4. Reasons for this discrepancy are diverse and could include everything from changing physiological states to inherent variation associated with these types of measurements. Conservatively, a fair assessment would be that Na^+ , K^+ -ATPase and protein turnover account for at least 50% of total gut tissue energy use. Other metabolic components of energy expenditure within gut tissue include metabolic reactions, digestive enzyme secretion, absorption, and minor ion transport associated with tissue functions like HCl formation. Huntington and McBride (1988) suggested that RNA/DNA and phospholipid turnover may contribute significantly to overall gut energy use. A small portion of gut energy use is also likely accounted for by substrate cycling.

Estimates of gut tissue energy use derived by Huntington and McBride (1988) appears to differ considerably from those of Baldwin (1995). In his review (Baldwin, 1995), protein turnover represented 42%, enzyme secretions 24.2%, and active transport 17.2% of total ruminant GIT energy expenditures (table 6). Ion transport by Baldwin's (1995) calculation represented only 10% of total GIT energy use whereas Huntington and McBride (1988) reported that GIT Na^+ , K^+ -ATPase consumed 28.5 to 61.0% of GIT energy expenditure. Differences in these estimates are likely explained by the multiple uses of the membrane potential generated by the Na^+ , K^+ -ATPase system. Its likely that much of the energy consumed by the Na^+ , K^+ -ATPase system (Huntington and McBride, 1988) is partitioned to other functions in the calculations of Baldwin (1995). Moreover, the work of Baldwin (1995) is focused on basal energy expenditures and is calculated or theoretical, while Huntington and McBride (1988) summary includes considerable *in vitro* data which may or may not reflect *in vivo* responses.

Within the liver, Na^+ , K^+ -ATPase, protein synthesis, urea synthesis, and substrate cycling represent the majority of energy expenditure (81 to 135%; table 5). Principle systems contributing to energy use categorized as substrate cycling include glucose to glucose 6-phosphate, glycogen to glucose 6-phosphate, fructose 6-phosphate to fructose 1,6-bisphosphate, phosphoenol pyruvate to pyruvate to oxaloacetate, and acetate to acetyl CoA (Rabkin and Blum, 1985). Calculations of minimal contribution of Na^+ , K^+ -ATPase, protein synthesis, substrate cycling, and urea synthesis in liver tissue to whole body energy use (Huntington and McBride, 1988; table 5) indicates

Table 5. Metabolic energy expenditure in ruminant gastrointestinal tract and liver and relationship to whole animal oxygen consumption (modified from Huntington and McBride, 1988)

Item	% Tissue oxygen consumption		% Whole body oxygen consumption ^h		
	Gut	Liver	Gut	Liver	Gut plus liver
Na ⁺ , K ⁺ -ATPase	28.5-61.0 ^a	22.5-55.3 ^a	5.7	4.5	10.2
Protein synthesis	20.2 ^b	15.5-24.4 ^c	4.0	3.1	7.1
Protein degradation	13.7 ^c		2.7		2.7
Substrate cycling		18.0-30.3 ^f		3.6	3.6
Urea synthesis		25.0 ^b		5.0	5.0
Total	62.4-94.9	81.0-135.0	12.4	16.2	28.6

^a Original data from McBride and Milligan, 1985a.^b Original data from McBride (unpublished).^c Original data from Seims et al., 1984.^d Original data from McBride and Milligan, 1985b.^e Original data from McBride, 1986.^f Original data from Rabkin and Blum, 1985.^g Original data from Huntington and Reynolds, 1987.^h Assumes gut and liver each consume 20% of whole body oxygen.**Table 6.** Energy expenditure within the ruminant gastrointestinal tract

Item	% of total GIT energy use
Ketone body formation from butyrate	5.8
Triglyceride synthesis	0.8
Digestive enzyme secretions	24.2
Protein turnover	
Mucosa	28.8
Other	13.2
Active transport in absorption	17.2
Ion transport	10.0
Total	100.0

^a Adapted from Baldwin (1995).

that these processes represent 16.2% of energy expenditure. With GIT and liver tissues combined, five primary metabolic components of energy expenditure (Na⁺, K⁺-ATPase, protein synthesis, protein degradation, substrate cycling, and urea synthesis) represent a minimum of 28.6% of total body energy use. In situations where one would expect higher GIT and liver oxygen consumption (like growth or lactation), the proportion of energy consumed by those five metabolic components would likely increase. Therefore, research focusing on methods to reduce energy use by or improve efficiency of these metabolic processes should, if successful, allow more energy for product formation within growing beef cattle.

GROWTH CONSIDERATIONS

Energy is used by beef cattle with differing efficiencies for maintenance and gain (growth) functions (NRC, 1981, 1984). After energy is consumed for maintenance by both product and support tissues, then energy is moved into metabolic pathways that result in product formation and accretion. Principle tissues comprising growth are

muscle, adipose, and bone. Relationships between protein synthesis and degradation make protein accretion a metabolically expensive process. In fact, on a caloric basis protein accretion is 0.62 times as efficient as lipid accretion; however, because of the large amount of water associated with lean tissue compared with adipose accretion, fresh lean tissue is deposited with less energy cost than adipose (Owens et al., 1995). As animals approach maturity protein accretion decreases; however, fat accretion may continue in mature animals and is dependent upon available energy and efficiency of metabolic processes. From an intensive livestock production standpoint growth of lean tissue is desirable; thus, young animals are usually slaughtered before reaching maturity and high planes of nutrition dictate fat deposition. Therefore, energetic expenditures associated with protein synthesis should be of considerable importance to overall growth efficiencies of beef cattle.

Protein synthesis

Energetic expenditures for protein synthesis in growing and mature animals averages 23% of whole animal energy expenditure (table 7). Data from Millward et al. (1976) and Davis et al. (1981) indicate that protein synthesis is a somewhat larger proportion of total energy costs in growing compared with mature animals. The overall energetic expenditure associated with protein synthesis (23%) is in the same general area as that attributed to the liver (24%) and GIT (22%; table 4). Moreover, the review of Huntington and McBride (1988) indicate that protein synthesis within GIT and liver tissue accounts for approximately 20% of energy expenditure within each tissue (table 5). This leaves 10 to 15% of total body energy expenditure to be attributed to protein synthesis in non-splanchnic, tissues.

Data summarized in table 8 indicates that GIT and liver tissues combined account for 37.5% of total body protein synthesis, while muscle and total carcass

Table 7. Energetic costs of protein synthesis

Reference	Species	Physiological state	% Whole animal
Lobley et al., 1980	Beef heifers	Growing	14-31
Davis et al., 1981	Lambs	Growing	42
Millward et al., 1976	Sheep	Mature	5- 7
	Lambs	Growing	25
Gill et al., 1989b	Lambs	Growing	19
Rolfe and Brown, 1997	Mammals	Mature	25-30
MacRae and Lobley, 1986	Livestock	Mature	17-25
Summers et al., 1986	Livestock	Mature	15-25
Range			5-31
Mean			23

Table 8. Tissue contribution to whole body protein synthesis

Reference	Species	Physiological state	% of total protein synthesis				Total carcass
			Muscle	GIT	Liver	Skin	
Gill et al., 1989a	Lambs	Growing	21-26	25-26	13-14	23-26	-
Lobley et al., 1980	Beef heifers	Growing	12-23	32-46	4- 8	9-21	32-33
Early et al., 1990	Beef heifers	Growing	20-23	12-16	5- 6	-	-
Davis et al., 1981	Lambs	Growing	-	18-34	7- 9	19-21	12-24
Lobley et al., 1994	Lambs	Growing	-	25-35	-	-	-
Ferrell, 1988	Pigs	Growing	24-28	20-23	16-17 ^a	6- 7	-
Attaix et al., 1988	Lambs	Suckling	29	11.5	12	13	-
Webster, 1980	Rats	Lean	14	41	18	28	-
Range			12-29	12-41	5-18	6-28	12-33
Mean			21.9	26.1	11.4	17.8	25.3

^a Includes pancreas and kidney.

account for approximately 22 and 25%, respectively. Combined estimates of protein synthesis in GIT, liver, skin, and total carcass accounts for approximately 80% of whole body protein synthesis. Edible product likely represents less than one fourth of whole body protein synthesis (table 8). Conversely, the largest portion of protein synthesis is associated with those tissues considered to have support or service functions.

Research efforts focused at enhancing efficiency of protein synthesis would appear to have greater impact on whole animal protein turnover and energetics if support or service tissues (viscera, nerve, and skin) were targeted. Or, to put it another way, those tissues that we, as animal scientists have often considered relatively unimportant likely have a greater impact on whole body protein synthesis than edible product tissues. This concept becomes more important when we consider that the viscera (minus fill), skin, and nervous tissue represent approximately 14.5% of empty body weight. Moreover, these tissues account for roughly 70% of whole body energy expenditure (table 3) and over 55% of whole body protein synthesis. Research leading to a clear understanding of metabolic processes within these tissues should provide insight

towards methodologies that would enhance overall energetic efficiency of livestock production.

Metabolic components of energy expenditure in muscle tissue

Within muscle tissue, specialty tasks (standing, walking, and other contraction) were once thought to consume a small percentage of whole body energy expenditure (Webster, 1978; Milligan and Summers, 1986). However, more recent work (table 9) indicates that specialty tasks associated with muscle work can account for approximately 33% of muscle tissue energy use. Based on data in table 3, this could account for 5 to 9% of total body energy expenditure. This estimate agrees well with the data of Osuji (1974) and Webster (1980) presented for confined sheep in table 2. In grazing situations, where most of the world's ruminant livestock are kept, the proportion of energy use by specialty tasks of muscle can be substantially higher (Osuji, 1974; Robbins, 1993). Therefore, it follows, that from the energetic perspective of the animal, management practices which reduce muscular work associated with acquiring food should reduce energy loss and enhance animal

Table 9. Energetic costs of metabolic processes in muscle tissue

Reference	Species	Physiological state	% of tissue energy use					
			Na ⁺ -K ⁺ -ATPase	Ca ⁺⁺ transport	Substrate cycling	Protein synthesis	Protein degradation	Specialty tasks
Greg and Milligan, 1982	Calves	Growing	39-43 ^a			2-3		
Harris and Lobley, 1991	Sheep	Maintenance	34-35	9-10	7-8	19-20	7-8	31-32
Lobley, 1990	Ruminant	Various	18-23		5-8	15-25	5-10	30-50
Summers et al., 1988	Various	Maintenance	17-46	7-13	0.5	15-23		26
Range			17-46	7-13	0.5-8	2-25	7-10	26-50
Mean			32	10	5	15	8	33

^a Includes calcium transport.

energetic efficiency. In extensive grazing situations, economics dictate that ruminant animals must use energy to harvest at least portion of their own feed.

From a metabolic standpoint, after specialty tasks associated with muscle tissue have been removed, energy expenditure can be separated into two major categories. The first being ion transport and the second being protein turnover. Major mechanisms involved appear to be Na⁺, K⁺-ATPase and Ca⁺⁺ transport (Ca⁺⁺ ATPase and other Ca⁺⁺ fluxes). These processes combined account for approximately 42% (24 to 59%) of total energy expenditure associated with muscle tissue (table 9). Protein turnover (the combined affects of protein synthesis and degradation), when positive, results in protein accretion. Within muscle, tissue protein synthesis represents approximately 15% and degradation 8% of total muscle tissue energy expenditure. Combined, the cost of protein turnover in muscle tissue is around 23% (9 to 35%) of total tissue energy use. From a research standpoint, considerably more emphasis has been placed on protein synthesis than degradation. Successful manipulation of either process could have a net effect of enhancing energetic efficiency of product formation. Unlike liver tissue, substrate cycling is a relative small component of overall energy use in muscle.

IMPLICATIONS

The majority of energy expenditure by beef cattle is accounted for by tissues and metabolic processes not directly associated with product formation. Research efforts focused on non-product tissues and the metabolic processes of ion transport, substrate cycling, and protein turnover have the potential to result in improved energetic efficiency of product formation. If improvement in whole herd energetic efficiency as it relates to product formation is a goal, then investigations with both growing and parent populations would seem equally warranted. Improved efficiency resulting from new techniques could result in either greater product production with constant

inputs or static product formation with less inputs. Final application would depend upon production goals and product demand.

REFERENCES

- Armsby, H. P. and F. A. Fries. 1915. Net energy of feeding stuffs for cattle. *J. Agric. Res.* 3:435.
- Attaix, D., E. Aurousseau, A. Manghebati and M. Arnal. 1988. Contribution of liver, skin and skeletal muscle to whole-body protein synthesis in the young lamb. *Br. J. Nutr.* 60:77-84.
- Baldwin, R. L. 1995. *Modeling Ruminant Digestion and Metabolism.* Chapman and Hall, London.
- Baldwin, R. L., N. E. Smith, J. Taylor and M. Sharp. 1980. Manipulating metabolic parameters to improve growth rate and milk secretion. *J. Anim. Sci.* 51:1416-1428.
- Blaxter, K. L. 1962. *The energy metabolism of ruminants.* Charles C. Thomas Publishing Co. Springfield, IL.
- Brody, S. 1945. *Bioenergetics and growth, with special reference to the efficiency complex in domestic animals.* Reinhold Publishing Corp. New York.
- Burrin, D. G., C. L. Ferrell, R. A. Britton and M. Bauer. 1990. Level of nutrition and visceral organ size and metabolic activity in sheep. *Br. J. Nutr.* 64:439-448.
- Burrin, D. G., C. L. Ferrell, J. H. Eisemann, R. A. Britton and J. A. Nienaber. 1989. Effect of level of nutrition on splanchnic blood flow and oxygen consumption in sheep. *Br. J. Nutr.* 62:23-34.
- Canes, R., J. J. Romero and R. L. Baldwin. 1982. Maintenance energy requirements during lactation in rats. *J. Nutr.* 112:1878.
- Caton, J. S. and D. V. Dhuyvetter. 1996. Manipulation of maintenance requirements with supplementation. In: *Proc. 3rd Grazing Livestock Nutrition Conference.* Proc (Ed. M. B. Judkins and F. T. McCollum III). West. Sec. Amer. Soc. Anim. Sci. 47(Suppl. 1):72-82.
- Davis, S. R., T. N. Barry and G. A. Hughson. 1981. Protein synthesis in tissues of growing lambs. *Br. J. Nutr.* 46:409-419.
- Early, R. J., B. W. McBride and R. O. Ball. 1990. Growth and metabolism in somatotropin-treated steers: III. Protein synthesis and tissue energy expenditures. *J. Anim. Sci.* 68:4153-4166.
- Eisemann, J. H. and J. A. Nienaber. 1990. Tissue and whole-body oxygen uptake in fed and fasted steers. *Br.*

- J. Nutr. 64:399-411.
- Ferrell, C. L. 1988. Energy metabolism. In: *The Ruminant Animal. Digestive Physiology and Nutrition* (Ed. D. C. Church) Prentice Hall, Englewood Cliffs, New Jersey, USA. p. 250.
- Ferrell, C. L. and T. G. Jenkins. 1985. Cow Type and the Nutritional Environment: Nutritional Aspects. *J. Anim. Sci.* 61:725-741.
- Ferrell, C. L., W. N. Garrett, N. Hinman and G. Grichting. 1976. Energy utilization by pregnant and non-pregnant heifers. *J. Anim. Sci.* 42:937-950.
- Gill, M., J. France, M. Summers, B. W. McBride and L. P. Milligan. 1989a. Mathematical integration of protein metabolism in growth lambs. *J. Nutr.* 119:1269-1286.
- Gill, M., J. France, M. Summers, B. W. McBride and L. P. Milligan. 1989b. Simulation of the energy costs associated with protein turnover and Na⁺, K⁺-transport in growing lambs. *J. Nutr.* 119:1287-1299.
- Gregg, V. A. and L. P. Milligan. 1982a. *In vitro* energy costs of Na⁺, K⁺ ATPase activity and protein synthesis in muscle from calves differing in age and breed. *Brit. J. Nutr.* 48:65-71.
- Harris, P. M. and G. E. Lobley. 1991. Amino acid and energy metabolism in the peripheral tissues of ruminants. In: *Physiological Aspects of Digestion and Metabolism in Ruminants* (Ed. T. Tsuda, Y. Sasaki and R. Kawashima). London. Academic Press. pp. 201-230.
- Huntington, G. B. 1990. Energy metabolism in the digestive tract and liver of cattle: influence of physiological state and nutrition. *Reprod. Nutr. Dev.* 30:35-47.
- Huntington, G. B. and W. McBride. 1988. Ruminant splanchnic tissues-energy costs of absorption and metabolism. In: *Biomechanisms Regulating Growth and Development*, Dordrecht. Kluwer Academic. pp. 313-327.
- Huntington, G. B., J. H. Eisemann and J. M. Whitt. 1990. Portal blood flow in beef steers: Comparison of techniques and relation to hepatic blood flow, cardiac output and oxygen uptake. *Anim. Sci.* 68:1666-1673.
- Huntington, G. B. and C. K. Reynolds. 1987. Oxygen consumption and metabolite flux of bovine portal-drained viscera and liver. *J. Nutr.* 117:1167-1173.
- Huntington, G. B. and H. F. Tyrrell. 1985. Oxygen consumption by portal-drained viscera of cattle: Comparison of analytical methods and relationship to whole body oxygen consumption. *J. Dairy Sci.* 68:2727-2731.
- Huntington, G. B., G. A. Varga, B. P. Glenn and D. R. Waldo. 1988. Net absorption and oxygen consumption by Holstein steers fed alfalfa or orchardgrass silage at two equalized intakes. *J. Anim. Sci.* 66:1292-1302.
- Huntington, G., G. Varga, D. Waldo and B. Glenn. 1985. Oxygen consumption by portal-drained viscera and whole body of Holstein steers fed alfalfa or orchard grass at two intakes. *J. Anim. Sci.* 61(Suppl. 1):448.
- Kelly, J. M., M. Summers, H. S. Park, L. P. Milligan and B. W. McBride. 1991. Symposium: Nonmammary metabolism in support of lactation and growth. *J. Dairy Sci.* 74:678-694.
- Kleiber, M. 1961. *The fire of life: an introduction to animal energetics*. John Wiley & Sons Inc. New York.
- Lobley, G. E. 1990. Energy metabolism reactions in ruminant muscle: responses to age, nutrition and hormonal status. *Reprod. Nutr. Dev.* 30:13-34.
- Lobley, G. E. 1993. Species comparisons of tissue protein metabolism: Effects of age and hormonal action. *J. Nutr.* 123:337-343.
- Lobley, G. E., A. Connell, E. Milne, A. M. Newman and T. A. Ewing. 1994. Protein synthesis in splanchnic tissues of sheep offered two levels of intake. *Br. J. Nutr.* 71:3-12.
- Lobley, G. E., V. Milne, J. M. Lovie, P. J. Reeds and K. Pennie. 1980. Whole body and tissue protein synthesis in cattle. *Br. J. Nutr.* 43:491-502.
- Lofgreen, G. P. and W. N. Garrett. 1968. A system for expressing net energy requirements for beef cattle. *J. Anim. Sci.* 27:793.
- Lomax, M. A. and G. D. Baird. 1983. Blood flow and nutrient exchange across the liver and gut of the dairy cow. *Br. J. Nutr.* 49:481-496.
- MacRae, J. D. and G. E. Lobley. 1986. Interactions between energy and protein. In: *Control of Digestion and Metabolism in Ruminants* (Ed. L. P. Milligan, W. L. Grovum and A. Dobson). Prentice Hall, Englewood Cliffs, NJ. pp. 367-385.
- Martin, C., I. Ortigues, D. Durand and M. Vermorel. 1991. Contribution of three tissues to energy metabolism in preruminant calves. In: *Energy Metabolism* (Ed. C. Werk and M. Boessinger). European Association of Animal Production Publ. #58: pp. 28-31.
- McBride, B. W. 1986. Cellular energy expenditure on Na⁺, K⁺ transport and protein synthesis in hyperthyroid sheep. *J. Dairy Sci.* 69(Suppl. 1):194.
- McBride, B. W. and L. P. Milligan. 1985a. Influence of feed intake and starvation on the magnitude of Na⁺, K⁺-ATPase-dependent respiration in duodenal mucosa of sheep. *Brit. J. Nutr.* 54:293-303.
- McBride, B. W. and L. P. Milligan. 1985b. Magnitude of ouabain-sensitive respiration in the liver, of growing, lactating and starved sheep. *Br. J. Nutr.* 54:293-303.
- McBride, B. W. and L. P. Milligan. 1984. The effect of lactation on ouabain-sensitive respiration of the duodenal mucosa of cows. *Can. J. Anim. Sci.* 64:817-824.
- Milligan, L. P. and M. Summers. 1986. The biological basis of maintenance and its relevance to assessing responses to nutrients. *Proc. Nutr. Soc.* 45:185-193.
- Millward, D. J., P. J. Garlick and P. J. Reeds. 1976. The energy cost of growth. *Proc. Nutr. Soc.* 35:339-349.
- NRC. 1981. *Nutritional Energetics of Domestic Animals*. National Academy Press. Washington, DC, USA.
- NRC. 1984. *Nutrient Requirements of Beef Cattle* (6th Ed.). National Academy Press, Washington, DC, USA.
- Osuji, P. O. 1974. The physiology of eating and the energy expenditure of the ruminant at pasture. *J. Range Manage.* 27:437.
- Owens, F. N., D. R. Gill, D. S. Secrist and S. W. Coleman. 1995. Review of some aspects of growth and development of feedlot cattle. *J. Anim. Sci.* 73:3152-3172.
- Rabkin, M. and J. J. Blum. 1985. Quantitative analysis of intermediary metabolism in hepatocytes incubated in the presence and absence of glucagon with a substrate mixture containing glucose, ribose, fructose, alanine and acetate. *Biochem. J.* 225:761-786.
- Reid, J. T., O. D. White, R. Anrique and A. Fortin. 1980.

- Nutrient energetics of livestock: Some percent boundaries of knowledge and future research needs. *J. Anim. Sci.* 51:1393.
- Reynolds, C. K., G. B. Huntington, H. F. Tyrrell and P. J. Reynolds. 1986. Splanchnic tissue and whole animal oxygen consumption by lactating Holstein cows. *J. Dairy Sci.* 69(Suppl. 1):193.
- Reynolds, C. K., H. F. Tyrrell and P. J. Reynolds. 1991. Effects of diet forage-to-concentrate ration and intake on energy metabolism in growing beef heifers: Whole body energy and nitrogen balance and visceral heat production. *J. Nutr.* 121:994-1003.
- Robbins, C. T. 1993. *Wildlife Feeding and Nutrition*. Academic Press. San Diego, CA.
- Rolfe, D. F. S. and G. C. Brown. 1997. Cellular energy utilization and molecular origin of standard metabolic rate in mammals. *Physiological Reviews.* 77:731-758.
- Rompala, R. E., D. E. Johnson, W. V. Rumpler, H. W. Phetteplace, S. M. Specht and C. F. Parker. 1991. Energy utilization and organ mass of targhee sheep selected for rate and efficiency of gain and receiving high and low planes of nutrition. *J. Anim. Sci.* 69:1760.
- Seims, W., W. Dubiel, R. Dumbey, M. Muller and S. M. Rapoport. 1984. Accounting for the ATP-consuming processes in rabbit reticulocytes. *European J. Biochem.* 134:101-107.
- Summers, M., B. W. McBride and L. P. Milligan. 1988. The components of basal energy expenditure. In: *Aspects of Digestion Physiology in Ruminants* (Ed. A. Dobson and M. Dobson). Comstock Books, NY (in press).
- Swanson, K. C. 1996. Influence of Dietary Factors on Visceral Growth in Sheep. M. S. Thesis. North Dakota State Univ., Fargo.
- Thompson, G. E., J. W. Gardner and A. W. Bell. 1975. The oxygen consumption, fatty acid and glycerol uptake of the liver in fed and fasted sheep during cold exposure. *Quart. J. Exp. Physiol.* 60:107-121.
- Thompson, G. E., W. Maneson, P. L. Clarke and A. W. Bell. 1978. Acute cold exposure and the metabolism of glucose and some of its precursors in the liver of the fed and fasted sheep. *Quart. J. Exp. Physiol.* 63:189-199.
- Webster, A. J. F. 1978. Prediction of the energy requirement for growth in beef cattle. *World Rev. Nutr. Diet.* 30:189-227.
- Webster, A. J. F. 1980. Energy costs of digestion and metabolism in the gut. In: *Digestive physiology and metabolism in ruminants* (Ed. Y. Ruckebusch and P. Thivend). AVI publishing Inc. Westport, CT. pp. 469-484.
- Webster, A. J. F. 1981. The energetic efficiency of metabolism. *Proc. Nutr. Soc.* 40:121-128.
- Webster, A. J. F. 1989. Bioenergetics, bioengineering and growth. *Livestock Production.* 48:249-269.