Changes in Liver and Gastrointestinal Tract Energy Demands in Response to Physiological Workload in Ruminants[1,2]

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ABSTRACT **Liver and gastrointestinal tract weights (ingesta- and adipose-free) appear to increase or decrease in direct proportion to dietary intake within and across physiological stages of maintenance, growth, fattening or lactation. Liver and gut mass increase ~15 and 30 g per unit of liveweight raised to the 0.75 power ($Wt^{0.75}$) for each multiple of 500 kJ/$Wt^{0.75}$ [~1 × maintenance (M)] increase in metabolizable energy (ME) intake, with linearity indicated up to the highest recorded level (4.5 × M). Extrapolation from in vivo arteriovenous O_2 measurements across splanchnic tissues and from the previously cited weight information indicates that liver and gut tissue oxidize ~3.5 and 1.0 kJ of ME/g of fresh tissue daily, in contrast to whole-animal rates of 0.1 kJ/g. Thus, energy use by the relatively small amount of liver and gut accounts for 45 to 50% of whole-animal heat energy. On a differential basis, increases in energy use by these tissues appear to account for up to 70% of the heat increment of ME use above maintenance.** *J. Nutr.* **120:649–655, 1990.**

INDEXING KEY WORDS:

• *energy* • *visceral organ* • *ruminants*

This paper characterizes changes in visceral organ mass and parallel changes in energy use by these tissues in sheep and cattle in response to changing diet intake. The functional workload concept, simplified largely as metabolizable energy intake, is considered as an explanation of the changes in mass, function and resulting energy consumption by these tissues. Related reviews concerning the importance of visceral organ mass in animal energetics (1–3) and in gastrointestinal tract adaptation and growth (4, 5) have also recently appeared.

GASTROINTESTINAL HYPERTROPHY

The presence of food in the gut evokes a host of responses, including peptide hormonal stimulation, induction of specific amino acid and sugar transporters and generalized increases in the mass of mucosal and related gut tissue. The ability of the gastrointestinal tract to change is dramatically illustrated in the newborn (6). Sections of the baby pig small intestine increase in weight by 41 to 72% in just 24 h and continue to an approximately fourfold increase in weight after 10 d of suckling (**Table 1**). Length of the baby pig small intestine increases ~80% during this 10-d period. Mucosal mass nearly doubles the first day, with only small increases during the following 9 d. The adaptability of gut mucosa is also evident following gut resection. If the upper half of the small intestine is removed, the remaining half can double its glucose transport per unit length of intestine (7) by increasing villus height and functional absorptive surface (8).

The concept that tissues in the body expand or regress in response to their functional workload has been considered for many body organs and has been described as an economy of nature (9). An interesting illustration of this concept has been developed in a comparison of gut adaptations in mammals compared to reptiles (10). Mammals the same size as reptiles require 5 to 10 times more feed for maintenance and move food through the gut 10 times faster, and yet they digest nutrients with equal efficiency. Mammals also have a sevenfold higher

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TABLE 1

Gut development in the newborn pig[1]

Age	Empty body wt	Jejum		Ileum	GIT
		Total	Mucosa		
	kg	*g*		*g/EBW*$^{0.75}$	
Birth	1.2	13	8	14	34
24 h	1.3	22	14	21	47
10 d	3.8	52	16	57	58

[1]Adapted from Widdowson (6). Values for ileum and gastrointestinal tract (GIT) are expressed as grams per empty body weight (EBW) (measured in kilograms) raised to the 0.75 power.

capacity for glucose and proline uptake in the small intestine, and yet each functional unit, the enterocyte, appear to function remarkably similarly in the two types of animals. The evolution of the mammal produced a sixfold increase in gastrointestinal surface area through an amplification of mucosal mass roughly proportional to food requirements.

The mechanism(s) by which food or nutrient complexes in the gut induce intestinal mucosal hypertrophy is not known. In the small intestine, however, responses relate to absorption rather than metabolism. When actively absorbed but nonmetabolized nutrients (e.g., lactose, methylglucoside and sodium chloride) were infused into isolated intestinal sacs from rats, they stimulated hypertrophy similarly to glucose (11). However, when a nutrient that was not actively absorbed but that was metabolized (e.g., mannose) was infused, no hypertrophy occurred. Hydrolysis of disaccharides also stimulates intestinal hypertrophy (12). Disaccharide infusions stimulated hypertrophy more than monosaccharides did, but not if hydrolysis was blocked. Thus, disaccharidase function appears to add to functional workload stimulation.

INTAKE-INDUCED CHANGES IN ORGAN WEIGHTS

To investigate the relationship between visceral organ hypertrophy and diet, we examined data from four sheep and three cattle experiments in which nonadipose organ mass was measured at varying but surmisable metabolizable energy (ME) intakes, which stabilized for at least 21 d before slaughter (**Table 2**). For comparison purposes, organ weights and intakes were expressed in ratio to empty body weight in kilograms raised to the 3/4 power (EBW$^{0.75}$). Moderate to high concentrate diets (10 to 45% roughage) were generally fed at low and high planes of nutrition [~1 and 2 × maintenance (M)] in the seven growing-fattening trials, but diets were fed at up to 4.5 × M in the lactation trial.

Lambs and steers fed at levels near maintenance had liver weights of ~30 and 40 g/EBW$^{0.75}$. High planes of nutrition increased these to 50 or 60 g/EBW$^{0.75}$ for the growing animals. The livers in the lactating Holsteins were about twice as large when expressed on this scale. The total weight of empty and largely fat-free gastrointestinal tract (GIT) averaged about 120 g/EBW$^{0.75}$ in steers and lambs fed near maintenance whereas weights in lactating Holstein cows started at more than double this level. Although most of this high GIT weight in lactating cows appears related to their much higher ME intake, it is not clear whether this accounts for all of the difference from growing animals. Prior measurements with dry cows (ME intake not specified) indicated relatively heavy GIT weights of ~200 g/EBW$^{0.75}$ in Holstein and Jersey breeds (19).

Less than half as much organ weight response to changing intake was found in the extensive plane of nutrition experiment with lambs by Ferrell et al. (15). Many factors are possibly involved such as gut dissection technique, animal age, diet, etc.; however, the 72-h fast before slaughter in their experiment probably caused a leveling effect across prior planes of nutrition. The 3-d fast may have depressed organ weights to a greater degree for those animals on high as compared to low planes of nutrition (15). In other research, a 50% decrease in intake from ad libitum levels reduced sheep liver and gut weights 25 and 12%, respectively, in just 5 d (14).

In spite of the heavier GIT noted for the one all-roughage diet (ref. 14, pelleted dehydrated alfalfa) in the present summary, varying forage levels at constant ME intake appears generally to have no effect on liver and GIT tissue weight. Varying diet grain equivalent from ~15 to 85% had no effect on the empty, fat-free GIT weights of several bovine genotypes (20). Also, constant ME intake for 45 d of diets containing 10, 45 and 95% chopped alfalfa produced no changes in liver or GIT tissue weights of steers at slaughter (16) even though gut fill was markedly elevated. One forage treatment in this experiment (80% native grass) did elucidate GIT tissue weight by 20 to 25%. An attempt by our laboratory to repeat this observation with sheep fed another batch of native hay as compared to alfalfa was unsuccessful (unpublished data). Although errors and varied techniques may be responsible for the discrepancies, the possibility of forage-associated GIT hypertrophic factors cannot be ruled out.

The change in organ weight per unit of change in diet energy intake was similar across most of these experiments with lambs, steers and lactating cows (Table 2; **Fig. 1, 2**). Averaged across all experiments, liver weight increased 29 g and GIT weight increased 61 g for each dietary ME increase of 1 MJ. Because 500 kJ (120 kcal)/EBW$^{0.75}$ approximates 1 × M, increasing consumption by one multiple of maintenance is expected to increase liver and GIT weight by ~14 and 28 g/Wt$^{0.75}$.

The magnitude of variation in weight in these very active organs across changing physiological situations suggests parallel energetic variations.

ORGAN OXYGEN CONSUMPTION IN VITRO

The development of biopsy procedures (21, 22) and the use of cell homogenates (23–25) to examine the response of liver and GIT in vitro to alterations in prior animal ME intake have provided important information about how the oxygen consumed by those tissues is partitioned to various productive functions (14, 21, 22, 26, 27). Despite differences in methodology or media composition, these data demonstrate the dynamic nature of the gastrointestinal mucosa and liver tissue. The proportion of energy associated with nutrient and ion transport has paralleled energy intake (14, 21, 22, 23, 24, 25) in nearly all cases. Sheep switched from a fasted state to twice maintenance energy intakes showed a 2.5-fold increase in the proportion of respiration attributable to the Na^+/K^+-ATPase pump in duodenal biopsies (22). This same response has been seen in sheep hepatocytes, with 62% lower oxygen consumption from Na^+/K^+-ATPase in fasted than in fed sheep (22).

Despite these changes in the activity of Na^+/K^+-ATPase or in protein synthesis and degradation seen with alterations in physiological state or energy intake, few if any of these studies have shown a change in total respiration rate (**Table 3**). This is perhaps due to the specific techniques used. Krebs (29) demonstrated large differences in respiration rates with the same tissue incubated in different media. Levin and Syme (30) demonstrated 60-fold differences in respiration rates from everted jejunal sacs in the presence of high or low oxygen tensions. Burrin et al. (28), using isolated hepatocytes from fed and fasted rats, found higher total energy use levels in fed rats, but they were unable to show differences in total oxygen consumption when expressed per gram dry weight. When expressed per milligram DNA, however, the fasted rats had signifi-

TABLE 2

Liver and gastrointestinal tract (GIT) organ mass responses to changing plane of nutrition in sheep and cattle

Ref	Animal type	Empty body wt	Energy intake	Liver wt	GIT wt	Organ wt/ME intake[1]	
						Liver	GIT
		kg	*kJ/EBW$^{0.75}$*	*g/EBW$^{0.75}$*	*g/EBW$^{0.75}$*	*g/MJ*	
13	Lamb	30	987	39	150	25.8	52.1
		32	975	39	154		
		39	1192	50	162		
		30	456	29	124		
un[2]	Lamb, ram	56	1121	48	149	23.1	53.1
		49	556	35	119		
14	Lamb	25	1016	59	223	39.4	78.9
		20	506	39	183		
15	Lamb, ram	21 to 45	326 to 1648	29 to 45	99 to 133	14.3	21.7
16	Hereford steer	493	515	41	111	33.5	71.0
		524	916	55	138		
		533	515	39	116		
		563	812	47	142		
17	Angus steer	325	1067	60	162	28.6	53.9
		325	473	43	140		
18	Holstein, lactating	470 to 620	1757 to 3138	85 to 133	283 to 395	26.3	56.9
					Average[3]	29	61

[1]Calculated by regression across experimental group means except for ref. 18, which examined the slope across 19 individual cows where r^2 = 0.61 and 0.47 for liver and GIT mass related to ME intake, respectively. ME = metabolizable energy.

[2]Unpublished data, Johnson, D. E., Metabolic Lab., Colo. State Univ. (Targhee ram lambs fed two levels of an 80% alfalfa, 20% cracked corn diet as a pellet).

[3]Average response excluding ref. 15; see text.

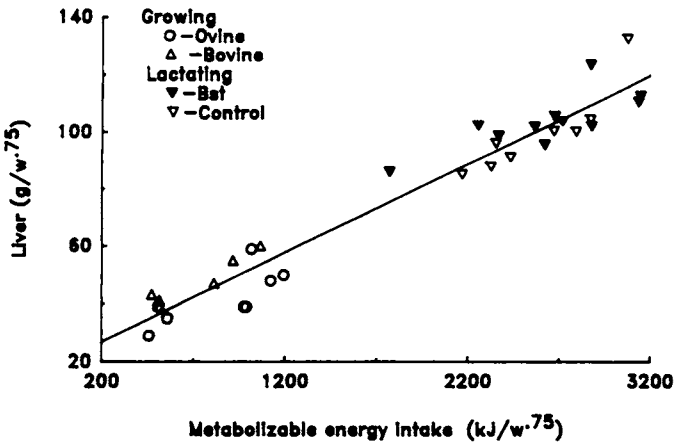

FIGURE 1 Relationship of mean liver weights to mean metabolizable energy intakes reported in several experiments for growing sheep and cattle and for 19 lactating cows (data from Table 2). Bst = bovine somatotropin.

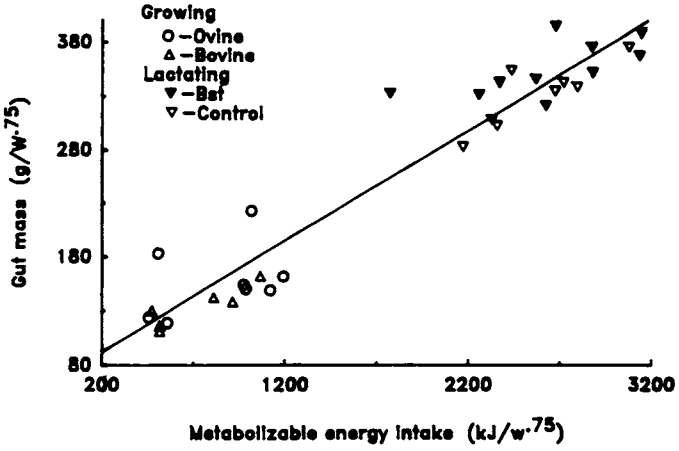

FIGURE 2 Weights of gastrointestinal tract tissue related to metabolizable energy intake in growing sheep and cattle and in lactating cows (data from Table 2). Bst = bovine somatotropin.

cantly lower respiration rates. Nevertheless, the overall data, combined with significant reductions in liver weight and total liver respiration rate, indicate that the reduction in oxygen consumption by the liver is a result of decreased liver size rather than a decline in liver metabolic activity per unit weight.

Relating in vitro estimates of respiration to whole-organ in vivo measurements has proven successful for gut but not for liver tissue. Burrin et al. (13) found that in vitro ovine liver O_2 uptake rates in vitro were only 9–13% of those measured with portal and hepatic catheters in vivo. Also, as presented by McBride et al. (27), bovine liver in vitro O_2 uptake equaled only ~10% of in vivo rates. Daily energy use in vitro averages about 0.7 kJ/g for liver and about 1.2 kJ/g for gut mucosa.

Huntington and McBride (3) related in vitro estimates of the relative proportion of O_2-consuming functions to in vivo whole-body O_2 consumption and concluded that Na^+/K^+-ATPase activity and protein synthesis in the gut and liver accounted for ~17% of whole-body O_2 consumption. Twenty-nine percent of whole-body O_2 consumption could be accounted for when protein degradation and urea cycling were factored into their estimate.

TABLE 3

Liver and intestinal mucosa energy use as measured by in vitro oxygen uptake

Animal (ref)	Diet/stage	Energy use intensity[1]	
		Liver	Mucosa
		kJ/(g·d)	
Sheep (22)	Fasting	0.5	1.0
	Low[2]	NA[3]	1.1
	High[2]	0.7	1.2
Sheep (22, 25)	Low	0.5	2.1
	High	0.5	2.2
Sheep (24)	High-J[4]	NA	1.3
	High-C[4]	NA	0.9
Ov/bov[5] (22, 21)	Lact-1	0.8	0.7
	Lact-2	0.8	0.9
	Dry	0.8	0.8
Rat (28)	Low	3.3	NA
	High	3.1	NA

[1]Converted to kJ (@ 20.5 kJ/L O_2) per gram fresh tissue (dry matter and protein from ref. 13).

[2]Low and high dietary intake.

[3]Not applicable.

[4]Mucosa sampled in the jejunum (J) or colon (C).

[5]First third (Lact-1) and last third (Lact-2) of lactation; measurements on ovine (ov) liver (22) and bovine (bov) mucosa (21).

EVALUATING SPLANCHNIC TISSUE ENERGY USE FROM ARTERIOVENOUS O_2 DIFFERENCE IN VIVO

Portal blood flow increases acutely with an elevated workload of feeding (31, 32); it has also been shown to increase with a chronically raised workload (i.e., increased ME intake). Webster (33) and Lomax and Baird (34) found a curvilinear increase in portal blood flow with increased ME intake, but Huntington (35) and Weighart et al. (36) found this relationship to be linear. Portal blood flow also increases with increasing concentrate intake (37) and is faster in lactating than in nonlactating cattle (34, 38–40).

TABLE 4

Liver and portal-drained viscera (PDV) energy use measured in vivo by arteriovenous oxygen difference technique

Ref	Animal type	ME intake	Energy use		Differential[1]	
			Liver	PDV	Liver	PDV
		kJ/Wt$^{0.75}$	*kJ/Wt$^{0.75}$*		*kJ/MJ*	
13	Lamb	400	92	90	297	79
		804	212	122		
47[2]	Beef heifer	601	107	135	173	153
		1006	17	197		
		605	92	112	198	119
		1009	172	160		
48[3]	Holstein steer	738		166		108
		1051		200		
		715		161		290
		877		208		
49	Cow, lactating	1732		172		224
		1808		189		
50	Beef steer	0		82		
		872		125		

[1]In tissue energy use per change in metabolizable energy (ME) intake above maintenance.
[2]Low and high concentrate diets.
[3]Alfalfa and orchardgrass diets.

Hepatic circulation is in series with the gastrointestinal tract and in parallel with the hepatic artery. The hepatic artery in dogs provides approximately one-third of the total liver blood flow but 50% of the O_2 extracted (41). Oxygen extraction of uptake is well regulated in the liver (42), with maintenance of constant O_2 uptake even with 50% reductions in hepatic flow (43). Amino acids and glucose infusion (44), gastrointestinal hormones and glycogenolytic hormones all increase liver blood flow (45, 46).

Energy use, calculated from O_2 consumption of the portal-drained viscera (PDV) also increases with increased ME intake (**Table 4, Fig. 3**). Changes with intake tend to parallel whole-body changes in energy use. Thus, the PDV energy use as a fraction of whole-body use remains remarkably constant, near 24% in several experiments. Data with sheep (13, 31, 32), pigs (51) and lactating dairy cattle (52) on various levels of intake all fall within a range of 16 (49) to 29% (48). There may be important dietary factors that change the fraction, however. Reynolds and Tyrrell found a significant effect of diet on this percentage, with a high concentrate diet having a lower proportion of PDV energy cost than was found with a low concentrate diet (47).

In vivo arteriovenous difference measurements show liver energy consumptions similar in magnitude to those by PDV (Table 4), averaging an additional 20% at 1 × M. Increasing the level of energy intake affected liver O_2 consumption, blood flow and percentage liver O_2 uptake/total body O_2 uptake (47). Liver O_2 consumption as a percentage of whole-body O_2 consumption has ranged from 18 (47) to 41% (13), with most estimates falling between 20 and 26% (13, 31, 47, 48, 52). During fasting, hepatic blood flow and O_2 consumption decline, as one would expect (50, 53), but the percentage of liver

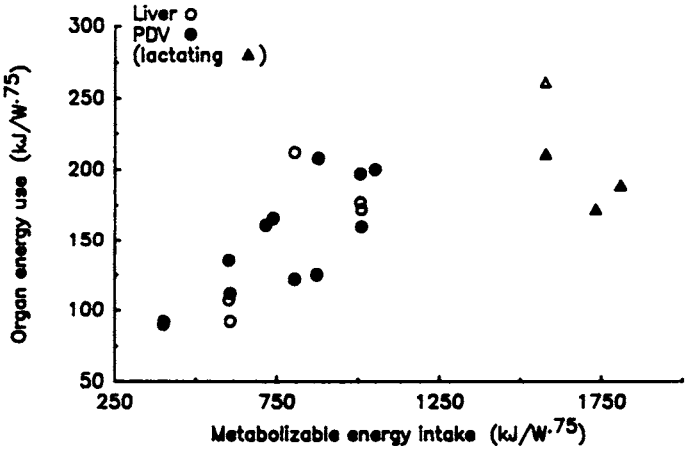

FIGURE 3 Energy use by liver and gastrointestinal tract tissues (PDV, portal-drained viscera) related to metabolizable energy intake by growing and lactating animals (data from Table 4 and ref. 52).

TABLE 5

Liver and gastrointestinal tract (GIT) energy use intensity

Situation/reference	Organ energy use	
	Liver	GIT
	kJ/(g·d)	
In vivo A-V:[1]		
1 × M	2.4	0.9
2 × M	3.7	1.3
In vitro[2]	0.7	1.2
Prior summary[3]	1.6	0.2

[1]Extrapolated from data in Tables 2 and 4, portal-drained viscera (PDV) energy use divided by GIT weights. A-V = arteriovenous difference technique. M = maintenance.

[2]Averaged from Table 3.

[3]Compiled from pre-1971 literature summary and extrapolated to cattle (19).

O_2 to whole-body O_2 consumption remains similar (53, 54).

The differential increase in energy use by liver and PDV averaged 223 and 162 kJ, respectively, per each megajoule of increased ME intake (Table 4). Within the limitations of measurement error, these differentials can be compared to a conventionally measured heat increment of ME use above maintenance. Some 45 to 70% of the heat increment of these diets appears to be accounted for by energy-consuming events in these two tissues.

The in vivo energy consumption data of Table 4, in $kJ/Wt^{0.75}$, can be divided by the tissue weights of Table 2, in $g/Wt^{0.75}$, after adjusting to common intake to yield estimates of energy use intensity and to allow comparison to in vitro data (**Table 5**). At maintenance, liver and GIT use 2.4 and 0.9 kJ/(g·d), in contrast to whole-animal rates of about 0.1 kJ/(g·d). In vitro and in vivo O_2 consumption rates of mucosa are comparable for GIT, but in vitro incubations of liver have grossly underestimated in vivo rates. It should be noted that the in vivo rates for GIT are likely biased high because O_2 measures were for PDV, which includes visceral adipose and pancreas, which were not included in the GIT weights. The estimates compiled from the early in vitro and in vivo blood flow literature (19) are intended to apply to animals at maintenance. The values have been widely quoted to illustrate the high relative energetic intensity of splanchnic tissue; however, those values appear to still underestimate the tissue's joulic fury.

The definition of factors that control or influence splanchnic energy or nutrient delivery to tissue may provide methods to understand and possibly control efficiency and composition of animal production.

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