

Metabolism and Metabolic Body Size: A Study With Cattle and Sheep

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DR. K. L. BLAXTER--BIOGRAPHY

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METABOLISM AND METABOLIC BODY SIZE: A STUDY WITH CATTLE AND SHEEP

By K. L. Blaxter

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Samuel Brody's genius lighted on and illuminated many aspects of biological thought. His very versatility of mind brought order from the chaos of unrelated fact and observation in many fields of endeavour. It is indeed difficult for anyone to say what was his greatest contribution, for the greatness of what he did lay in the integration of biological information rather than in any isolated experiment of classical beauty. Like all men he was dependent on those who went before him, but few have embellished, extended, and rationalized so many of what can be called the general and eternal problems of biology, namely the relations between body size and body function, between part and whole, between the organism and its environment, and between food resources and animal growth, form and function. He was, above all, a man in the forefront of the great humanistic and liberal tradition of scientific thought.

Much of what Brody accomplished reflects credit on this University, on the Herman Frasch Foundation and on other sources of support. He was early recognized as a man who needed freedom. Academic freedom and academic discipline are both essential to greatness. The one can be given, but the other is innate in the man. To refuse the one, or to tie remuneration and facilities to a narrow utilitarianism will not dim the intellect but must of necessity prevent its full fruition. The University, those who financed his work, and those who discussed, analysed, talked, argued and wrangled, and disagreed with him, have the satisfaction that they all helped to make a great man and thereby to augment the well-being of mankind.

One of Brody's abiding interests was in size of animals. Size intrigued him, in its relationship to energy metabolism, N metabolism, growth rates, lactation, food intake, and climatic variables. This interest can be seen in all his work and much of his experimentation was designed to elucidate the general and specific biological effects of size and of age of organism. In this lecture I wish to deal with the studies which my colleagues and I have made in recent years which bear on these perennial problems, using as starting points some of Brody's generalizations. The scope of our investigations is small when compared with his, for we have been concerned, almost entirely, with adult castrated male cattle and sheep. This restriction to two species, I hasten to add, in no way reflects a narrowness of outlook on the part of the British Agricultural Research Council. Rather it reflects our own limitations.

Brody's analysis of the relation between body size and the fasting, minimal, or basal metabolism of mature species of mammal is certainly one of his greater contributions. Brody and Proctor (1932) found that basal metabolism did not vary with the two-thirds power of weight as might be assumed from an elementary dimensional analysis but with a power of weight closer to three-fourths. He coined the term 'metabolic body size' to refer to body weight raised to the power 0.73, and this was early adopted as a reference base in energy metabolism studies (Anon, 1935). The equation he ob-

tained on analysis of data for species ranging in size from the 20 g mouse to the 4000 kg elephant was

$$M = 70.5 W^{0.734}$$

His subsequent work dealt with the effect of increases in the size of an individual species on its metabolism. In general, he found there was a tendency for metabolism per unit metabolic size to be greater for the young animal than for the adult.

Brody's equation was clearly a generalization and associated with an error in the statistical sense of this term. It was criticised by Benedict (1938) on the grounds that the deviations of the metabolism of certain species from the generalizations were real and not to be countenanced by Brody's purely statistical approach. To this Brody replied (1945) that one of the two species cited by Benedict which had a very low metabolism relative to its metabolic body size was the marmot a hibernator, and the other was a hypopituitary and hypothyroid dwarf mouse. In those species such as the intact boar, bull, and elephant, which Benedict found to have very high metabolic rates relative to their metabolic body size, technical difficulties probably account for the high rates. In the present context of sheep and cattle Brody's data show that the metabolism of adult sheep deviates on average by -7 percent and that of adult cattle by +4 percent from the values computed from the 0.73 power of their weight. How far these deviations are real is of considerable interest.

Our own experiments have some bearing on this problem. We have carried out some hundreds of experiments to determine fasting metabolism in adult wether sheep and adult steers. Each experiment consisted of fasting the animal for 112 hours and measurement of metabolism from the 64th to the 112th hour of fast. All estimates of the metabolism of sheep were considerable lower than the inter-species mean established by Brody and that all the estimates of the metabolism of cattle were above the inter-species mean. The mean value for sheep aged more than 2 years was 55kcal/24 h/kg $W^{0.73}$ (Blaxter, 1962 a) and for cattle 80kcal/24h/kg $W^{0.73}$ (Blaxter & Wainman, 1961 a, 1961 b, 1964; Blaxter, Davidson & Wainman, 1964). Our experiments thus suggest that sheep have a metabolism 22 percent lower, and that cattle have a metabolism 13 percent higher than the inter-species mean of 70.5 kcal/24 h/kg $W^{0.73}$ would suggest. These deviations are greater than those Brody found.

The absolute validity and reliability of these measurements must be examined before they are accepted. First, the considerable variation evident in Tables 1 and 2 must be examined; secondly, the possibility that the remarks made by Brody about Benedict's species with a high metabolism might apply to the results with cattle and; lastly, the possibility exists that the length of fast was not sufficient to allow the true fasting metabolism to be reached in sheep but it was in cattle.

In the course of a series of fasting experiments with sheep, it was noted that considerable individual variation occurred in the metabolism of individuals of about the same size. Two individuals were therefore selected from the group, one the sheep with the highest and the other with the lowest metabolism, and, at intervals over two and half years, their fasting metabolism was determined. The results are shown in Table 1

TABLE 1 - HEAT PRODUCTION DURING FASTING OF TWO SHEEP SELECTED ON THE BASIS OF INITIAL MEASUREMENTS TO HAVE THE HIGHEST AND THE LOWEST METABOLISM OF A GROUP OF SHEEP

Date of Fast	Heat Production kcal/ kg W ^{0.73}	
	Sheep Z	Sheep Y
September 1959	47.4	56.1
March 1960	47.2	58.1
July 1960	50.4	57.8
April 1961	49.5	57.8
January 1962	45.4	54.2
Mean	48.0	56.8
Coefficient of variation	±4.1	±2.9

where it is evident that the difference in the metabolism of these two sheep persisted, and that the coefficient of variation of the measurement in the individual was only three to four percent. Sheep Z had an average metabolism per unit of body size of 48 kcal/24 h, which is 32 percent lower than the inter-species mean, while sheep Y had a metabolism of 57 kcal/24 h, which is 19 percent lower than the inter-species mean. These results show that there are real differences between individual sheep in their metabolism and that the variation is not indicative of inaccuracy but of an individual variation which when expressed as a coefficient of variation amounts to ±11 percent of the mean value.

Sheep are more nervous animals than steers and it seems unlikely that the high results for fasting cattle could stem from technical difficulties of training them to acquiesce to experimental conditions. In this regard, the diminution with continued training in the fasting metabolism of the untrained sheep is proportionally greater than that of the untrained steer; training in this instance meaning the removal of an individual animal from a commercial stock and its subsequent confinement in a pen or cage in close proximity to man. This might be taken as evidence that the "technical problems" adduced by Brody still apply to the steer, but repetition of experiments with individually trained cattle does not result in a progressive lowering of their fasting metabolism.

In each of the experiments, metabolism was measured for four consecutive 24 h periods during the fast using closed circuit respiration chambers. With both sheep and cattle, the respiratory quotient was 0.73 or below on the third and fourth days of fast, and methane production in both species was then less than 5 percent of that recorded before the fast began. These results suggest that the experiments with the two species were fully comparable. It must, however, be realized that the choice of the optimal length of fast to use to secure a valid estimate of minimal metabolism is somewhat arbitrary since heat production falls at a faster rate than does body weight during fasts of up to 11 days duration in sheep and of up to five days in cattle. The choice of the 64th hour

of fast as marking the beginning of the post-absorptive state in both species is justified solely on the basis of the low RQ then obtained, the constancy of the ratio of the methane production that has by then occurred. With closed circuit respiration chambers, the determination of the 24 hour production of methane is a very accurate measurement and production of as little as 100 ml CH₄/24 h by a sheep can be measured. Amounts of methane slightly greater than this can be detected even after 10 days starvation, which suggests that cessation of methane production may not be an adequate index of the post absorptive state.

It would seem from these considerations that there is no reason to doubt on technical or biological grounds the validity of the conclusion that wether sheep have a low metabolism relative to the mass of mammalian kind and that steers have a relatively high one. The conclusion seems rather different to expectation because the sheep is an alert, sensitive animal while the steer is rather stolid and phlegmatic.

Further information relating to the validity of the conclusion that the sheep has a low and the steer a high metabolism comes from studies of the N metabolism of sheep and cattle, both during fasts and when diets free of N are given. The results of these studies are summarized in Table 2. They show that the losses of N in urine on fasting and on feeding N-free diets, when expressed per kg metabolic body size, are greater for cattle than they are for sheep. These losses of N when expressed/kcal fasting metabolism are lower for cattle than they are for sheep. Brody found that between species minimal urinary N metabolism was 146 mg N/kg W^{0.72} (Brody, Proctor & Ashworth, 1934). It will be noted that the cattle and more particularly the sheep produced less urinary N than might be expected from this generalization based on all mature species. Both species produced less N/basal calorie than might be inferred from the Terronine-Sorg Matter Law (1928) as modified by H. H. Mitchell (1962) which states that the minimal N metabolism of all mammals is 2.0 mg N/basal calorie, a value which Brody confirmed and showed from his inter-species generalizations to decline slightly with increasing body size.

It is now of some interest to examine the differences between these economically important species in their minimal requirements of energy and protein in terms of effects on food utilization and efficiency and also in terms of effects on the animal's reaction to its environment. This necessarily involves considerations of the comparative utilization of food by sheep and cattle, a subject which Professor Kleiber dealt with in a theoretical way in the first Brody Memorial Lecture (1961).

We have carried out two series of calorimetric experiments in which sheep and steers have been given the same food mixtures (Blaxter & Wainman, 1961 b, 1964). The results for six different diets are summarized in Table 3. They show that at the maintenance level of nutrition, that is, when energy retention is zero, and particularly with low quality diets, sheep tend to lose slightly more energy in feces and slightly less energy in urine and methane than do cattle. The differences are, however, small. The efficiencies of utilization of metabolizable energy for maintenance and for fattening are virtually the same in cattle and in sheep. These results suggest, therefore, that cattle and sheep differ very little in their ability to digest different diets when these are given at the maintenance level of nutrition and that the metabolizable energy they so obtain is used by them with virtually the same efficiency for both maintenance and adult growth and fattening.

TABLE 2 - FASTING AND MINIMAL N METABOLISM OF SHEEP AND CATTLE

	Sheep	Cattle
Percentage of fasting heat production accounted for by protein oxidation*	23.8 ± 1.5	22.6 ± 1.0
Mean N excretion in fasting mg/basal calorie*	8.3	7.9
Mean N excretion in fasting mg/kg W ^{0.73} *	456	632
Mean endogenous N excretion on N-free or N-low diets mg/kg W ^{0.73} **	85	113
mg endogenous N/basal calorie**	1.6	1.4

* Based on 23 determinations with sheep and 12 with cattle (Hannah Institute data)

** The values for cattle are those summarized by Blaxter (1958). The values for sheep are those of Harris & Mitchell (1941), Sotala (1930), Johnson *et al.* (1948) and Ellis *et al.* (1956) which average 33 mg/kg weight expressed on a metabolic size basis

*** Endogenous N (row 4) divided by 55 kcal (sheep) or 80 kcal (cattle).

TABLE 3 - THE UTILIZATION OF THE ENERGY OF SIX DIFFERENT RATIONS BY SHEEP AND CATTLE

		Ration					
		1	2	3	4	5	6
Fecal loss of energy at maintenance kcal/100 kcal	Sh	38.9	30.7	24.9	24.5	14.5	27.8
	St	35.2	30.4	24.2	22.2	16.6	28.2
Urine loss of energy at maintenance kcal/100 kcal	Sh	4.1	4.3	3.4	3.9	3.4	4.8
	St	5.0	4.7	4.3	3.6	3.6	5.7
Loss of energy as CH ₄ at maintenance kcal/100 kcal	Sh	6.7	8.7	8.9	9.1	9.9	10.6
	St	7.8	8.6	9.0	9.3	8.6	9.2
Metabolizable energy at maintenance kcal/100 kcal	Sh	51.3	56.4	62.7	62.9	72.2	56.4
	St	52.0	56.2	62.3	65.0	71.1	56.1
Partial efficiency for maintenance	Sh	70.4	73.3	69.7	74.7	77.6	80.4
	St	70.0	74.4	74.9	79.3	81.1	80.4
for production	Sh	27.5	35.4	44.0	47.1	53.3	53.5
	St	31.4	32.8	42.1	47.6	54.2	51.4

Similar studies to the above can be made with respect to the protein nutrition of cattle and sheep. The apparent digestibility of the N-containing compounds in the six diets given at a maintenance level referred to was the same in cattle as it was in sheep. Since metabolic fecal N is the same in both species at 4.5 g N/kg dry matter ingested, the true digestibility of N-containing compounds must be very similar in both species. The biological value of protein which is a measure indicative of the efficiency with which protein is used to meet minimal needs, is lower in sheep than it is in cattle. An analysis of results of metabolic trials made with cattle at the Hannah Institute and at Wisconsin Experiment Station (Blaxter, 1958) shows that the biological value of protein for cattle is on the average, 75 percent with a standard deviation of ± 4.6 . Studies with sheep (Turk, Morrison & Maynard, 1934; Miller, Morrison & Maynard, 1937; Smuts & Marais, 1938; Miller & Morrison, 1939; Harris & Mitchell, 1941; Johnson, Hamilton, Mitchell & Robinson, 1942) indicate, however, that the average biological value of protein in sheep is 64 percent with a standard deviation of ± 8 percent. The mean values for the two species, each derived from many experiments, clearly differ and the most likely explanation is that the sheep requires considerable sulphur-containing amino acids to synthesize the keratins of its wool.

From the observations above, maintenance energy and protein needs of the two species can be assessed. This has been done in Table 4. The maintenance energy needs of steers, expressed as the amount of metabolizable energy they require per unit of metabolic size, are over 40 percent greater than those of sheep, but their protein needs

TABLE 4 - THE ENERGY AND PROTEIN REQUIREMENTS OF ADULT CATTLE AND SHEEP FOR MAINTENANCE EXPRESSED PER KG METABOLIC BODY SIZE

Values/kg $W^{0.73}$	Sheep	Cattle	$\frac{\text{Cattle}}{\text{Sheep}} \times 100$
Basal metabolism kcal/24 h	55	80	145
Maintenance energy requirement as kcal metabolizable energy*	75	110	145
Corresponding dry food intake as hay (metabolizable energy 2.5 kcal/g)	30	44	145
Endogenous metabolism of N (mg)	85	113	133
Metabolic fecal N (0.45 g/100 g dry food)	135	198	
Maintenance available protein requirement (mg N)**	343	415	121

* Efficiency of utilization of metabolizable energy 73 percent in both species.

** Sum of endogenous N metabolism and metabolic fecal N divided by the biological value expressed as a decimal. The biological value for sheep was 64 percent and for cattle 75 percent.

are only about 20 percent greater. These conclusions are not greatly altered by the slight tendency for cattle to digest low quality rations more efficiently than sheep. Sheep on this basis obviously require diets containing a slightly higher percentage of protein to maintain themselves than do cattle. It is also evident from Table 3 that what was true of the estimates of minimal protein and energy metabolism is equally true of maintenance needs.

Both Brody (1945) and Kleiber (1961 b) have emphasized the importance of the intake of food in determining what Brody termed "gross efficiency," that is, the ratio

$$\frac{\text{Output of energy (as milk or eggs or meat or work)}}{\text{Input of energy (as metabolizable energy)}}$$

Our first observations related to this problem were made with sheep (Blaxter, Wainman & Wilson, 1961) and they established that as the nutritive value of unit food (as judged by the apparent digestibility of its energy) increased, so the voluntary intake of food increased. A second series of experiments was then undertaken with steers (Blaxter & Wilson, 1962). It was noted that the relation between the voluntary intake of food and the apparent digestibility of the energy of food was very similar in cattle to the relationship found in sheep, cattle possible eating up to 15 percent more than the sheep. The fact that when the apparent digestibility of food was the same, cattle per kg metabolic body size consumed only up to 15 percent more food than did sheep, together with the observations that the cattle have maintenance costs per kg of metabolic size which are more than 40 percent greater than those of sheep necessarily implies that the sheep is the more efficient species of the two when given access ad libitum to food.

A fallacy exists, however, in this argument. It is necessarily assumed that when intake of food is maximal, the metabolizable energy of food is the same in both species, that is, that the small differences in digestive efficiency noted at the maintenance level of nutrition are equally small when food is taken to appetite. To use the apparent digestibility of food as the independent variable in establishing regressions to examine species differences in voluntary intake is legitimate only if each species digests each particular food equally well.

A series of experiments was therefore made in which the same foods were given to both sheep and cattle (Blaxter, Davidson & Wainman, 1964). The fasting metabolism, the voluntary intake of food, and the apparent digestibility of food when intake was maximal were determined with each animal. These observations allow estimation of the digested energy taken in relative to maintenance needs of digested energy in each species. Table 5 summarizes the results of some of these experiments. It shows that the cattle used in this experiment had a mean fasting metabolism per kg metabolic body size more than 50 percent greater than that of sheep. The cattle consumed more of the foods per kg metabolic size. Cattle also digested each food better than did sheep. The final answer in terms of efficiency was that the feeding level attained was much the same in each species. If anything, sheep were able to attain a higher feeding level when given the poorer quality foods than were cattle, and with very high quality foods the cattle tended to excel.

TABLE 5 - UTILIZATION OF THREE FOODS WHEN GIVEN AD-LIBITUM TO SHEEP AND STEERS (means of 4 animals/food)

		Food		
		Oat straw	Hay	Artificially dried grass
Apparent digestibility of dietary energy %	Sheep	43.4	52.8	75.0
	Steers	51.0*	55.6N	78.3N
Voluntary intake of dry matter/day, g/kg W ^{0.73}	Sheep	48.7	70.1	96.6
	Steers	56.0*	88.8*	134.2**
Basal metabolism kcal/kg W ^{0.73}	Sheep	48.4	51.0	51.7
	Steers	79.2**	79.7**	77.2**
Digested calorie intake kcal/kg W ^{0.73}	Sheep	91	158	310
	Steers	132*	217**	464**
Intake relative to maintenance requirement±	Sheep	1.10	1.83	3.55
	Steers	1.00N	1.60N	3.68N

N not statistically significant

* significant when $0.05 > P < 0.01$

** significant when $P < 0.01$

± Maintenance requirements in terms of digested energy were taken to be 1.7 x the fasting energy expenditure

These experiments suggest that sheep when given unlimited access to food consume more dry matter than they might be expected to consume from their maintenance requirements of dry matter but they digest this food dry matter rather poorly. Cattle on the other hand stop eating when they have consumed a rather low amount of dry matter relative to their maintenance needs of dry matter, but the food they do consume is digested very well. Both species appear to digest food equally well at the maintenance level of nutrition, though even then, with poor quality food, sheep tend to have a lower digestive efficiency. In this regard we have shown in other experiments that the major factor accounting for the decline in the partial efficiency of food utilization ($E_p = \frac{dG}{dI}$ where G is gain of energy to the body and I is food intake) is the decline in the digestibility of food as intake increases (Blaxter, 1961). We have shown, and so have workers in East Germany (Nehring & Schiemann, 1961), that the efficiency of utilization of metabolizable energy above the maintenance datum does not decline as intake of food decreases.

Brody's studies showed that for milk production (Brody & Nisbet, 1938; Brody & Proctor, 1935; Brody & Cunningham, 1936) and for work production (Hall & Brody, 1934; Brody, 1945) total or gross energetic efficiency of food utilization was independent of body size. Kleiber (1933, 1935) concluded from theoretical studies much the same. These studies with steers and sheep provide further confirmation of the generality but in so doing demand a more rigorous definition of terms in Kleiber's generalization about ef-

efficiency. Kleiber has stated (1961 a) "since neither partial efficiency nor relative food capacity are consistently related to body size, the total efficiency of food utilization is independent of body size." For a particular food sheep have a greater relative food capacity in terms of dry food intake than have cattle but sheep have a lower partial efficiency expressed in terms of calories retained per gram of dry food than have cattle, provided partial efficiency is measured at maximal food capacity. Furthermore, these two determinants of efficiency change with the type of food given. Relative food capacity in ruminants is related to, if not determined by, partial efficiency, and the nature of the relationship is not precisely the same in cattle as it is sheep.

I now wish to turn to another aspect of this problem of the relation of metabolism to size of ruminant animal and to examine its implications in relation to the tolerance of sheep and cattle to heat and to cold. Here a schematic approach is very helpful, as shown in Fig. 1. This shows a cross section of an animal with a hair coat. Heat is produced internally, is transferred to the skin surface by convective transfer by the blood where part of the heat is used to evaporate moisture (H_E) and part, the sensible heat (H_N), is transferred by a process analogous to conduction through the coat to the coat surface where it is dissipated by convection and radiation to the environment. We thus have $H = H_E + H_N$. The internal temperature, T_R , the skin surface temperature, T_S , the coat surface temperature, T_F , and the air temperature, T_A , can all be measured and the resistance to the flow of heat described in terms of "insulations." We can thus define firstly the tissue insulation or internal insulation, I_T , as

$$I_T = \frac{T_R - T_S}{H}$$

the coat insulation as

$$I_F = \frac{T_S - T_F}{H_N}$$

the air insulation as

$$I_A = \frac{T_F - T_A}{H_N}$$

In fact, it is not particularly easy to measure the temperature of the surface of the coat as indeed Brody found (Thompson, Worstell & Brody, 1952) and so the last two insulations are conveniently combined to give the external insulation

$$I_E = \frac{T_S - T_A}{H_N}$$

Furthermore, it must be recognized at the start that the ambient air temperature is not the sole index of the "coldness" or "warmness" of the environment and that I_A will necessarily vary with air movement and with the radiation sinks and sources surrounding the animal.

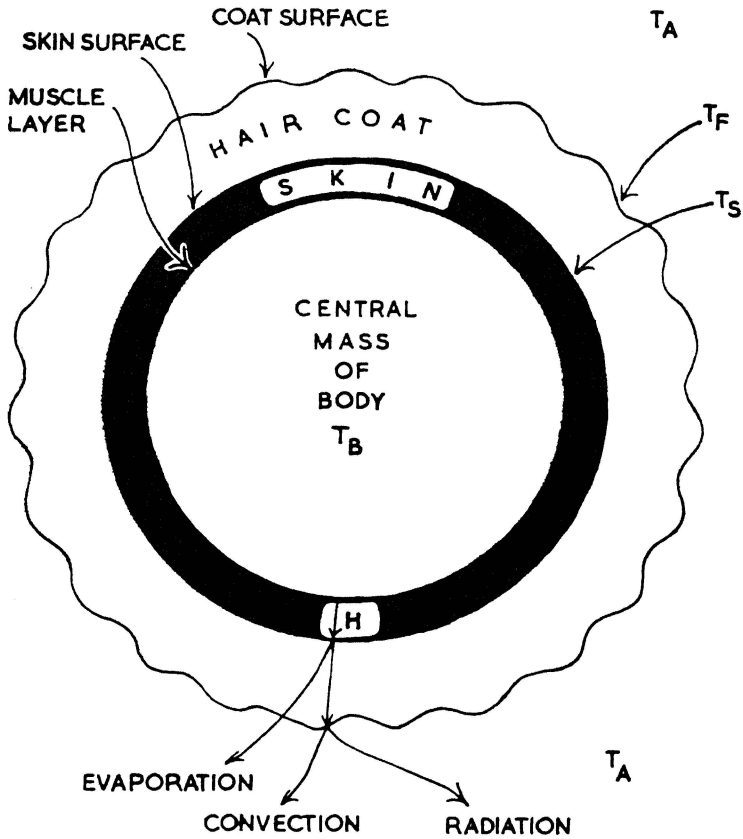


Figure 1 . Schematic analysis of the heat losses of an animal. Heat is produced centrally where the temperature is T_B . It passes through the skin to the skin surface, which has a temperature T_S . Here part is lost to the atmosphere by vaporization of water at the skin surface. The remaining sensible heat flows by processes of conduction and convection through the coat to the coat surface, which has a temperature T_F . Here part is lost by convection and part by radiation. The temperature of the air is T_A .

The distinction between external and internal insulations and between evaporative and sensible losses of heat make it possible to compare species one with another in terms of their ability to resist cooling or heating. Our measurements have been made largely in respiration chambers in which sheep and cattle can be confined for long periods but, lately, we have been making measurements over shorter periods using mask and tracheostomy techniques to determine the heat production. Most of our work has been concerned with the effects of the coldness of environments for Scotland is a cold country. It is interesting that Brody's work evolved in a similar way for when explaining his extensive use of short-term measurements of metabolism using masks he states that he found chamber methods "too expensive and too slow and the data obtained usually not sufficient for statistical analysis". We agree with his opinion about expense but have overcome the remaining difficulties by operating seven instruments continuously as a routine operation. The combination of the short-term and long-term approaches seems to us ideal and the results of the approaches agree absolutely.

We have measured the tissue insulation of both sheep (Blaxter, Graham, Wainman and Armstrong, 1959; Armstrong, Blaxter, Clapperton, Graham and Wainman, 1960; Joyce and Blaxter, 1964) and cattle (Blaxter and Wainman, 1961 a; Blaxter and Wainman, 1964 b; Gonzalez Jimenez and Blaxter, 1962), and found that once an animal is below its critical temperature, tissue insulation is virtually constant and the evaporative heat loss is constant also. Vasoconstriction appears to approximate an all or none relationship. Table 6 summarizes some of the results we have obtained under these cold conditions. The results show that apart from low values in very young cattle, two very

TABLE 6 - THE TISSUE INSULATION OF CATTLE AND SHEEP IN COLD CONDITIONS AND THE MINIMAL LOSS OF HEAT BY VAPORIZATION OF WATER IN THESE CIRCUMSTANCES

Class of Animal	Tissue Insulation °C/Mcal/24 h/m ²	Minimal Loss of Heat by Vapourizing Water Mcal/m ² /24 h
Ayrshire calves 4 days	3.3 ± 0.3	0.34
21 days	5.8 ± 0.4	0.34
Ayrshire steers	6.7	0.35
Galloway steers	6.7 ± 1.1	0.35
Cheviot sheep	6.8 ± 1.2	0.25
Blackfaced sheep	5.7 ± 0.4	0.24
Downcross sheep	3.5 ± 0.3	0.32
Man	3.5	0.29

* Errors are standard deviations not standard errors.

young cattle, two very dissimilar breeds of cattle have the same tissue insulation of 6.7 units and that the basal evaporative loss of moisture is remarkably constant at 0.34 Mcal/m²/24 h in both. With sheep, however, it seems that breed differences exist and that the Down crosses we have used have low tissue insulations compared with the Cheviot and Scottish Blackface which are mountain breeds. Under very warm conditions, it has been found that vasodilation reduces tissue insulation to about a third of the values obtained in the cold.

External insulation is markedly affected by coat length and to make comparisons between the two species, a coat length must be specified. In Table 7 coat length or, rather, the depth of the insulating layer of hair or wool has been specified as 20 mm, corresponding to a winter coat in cattle and to a short autumn fleece in sheep. This table shows that when the air is still there are virtually no differences between the species in their external insulation, low values for Ayrshire calves largely being accounted for by the sparseness and wispy nature of their erected hair coats. In gentle breezes of less than 2 m.p.h., however, the sheep's coat is a better insulator than is the steers coat of the same depth. This difference no doubt stems from the coherence of the individual wool fibres in the sheep fleece, which prevents wind access. Even so, a wind of only 9 m.p.h. destroys about 40 percent of the insulation of a sheep fleece. It is difficult to separate coat insulation I_F from air insulation I_A which together make up the external insulation except under still air conditions. Studies with calves and sheep kept in the same type of respiration chamber show that in sheep the I_A is 5.7 units and in calves it is 7.1 units. The difference may be real but the technical difficulties encountered in determining the temperature of the surface of the coat make such a conclusion doubtful: both values are similar to those noted in experimental species as diverse as the mouse, the pig, and man (Blaxter, 1962 b).

It would thus appear that differences between sheep and steers in the basic parameters which determine heat loss are not great, particularly when hill breeds of sheep are compared with cattle. As might be expected, the insulation external to the skin is virtually independent of size of animal, and, provided the air is still, of the type of coat, while it is only with Down sheep that any gross divergence of the tissue insulation from an interspecies mean can be inferred.

We have defined the lower critical temperature more rigorously than Brody did (Worstell & Brody, 1953) as that air temperature below which the animal must increase its heat production if it is to maintain its deep or internal body temperature. It can be shown by manipulation of the heat flow equations that in the steady state, the critical temperature T_C is given by the expression

$$T_C = 39.0 - H (I_T + I_E) - V_B I_E$$

where, restating terms and units,

T_C = critical temperature (centigrade degrees)

H = heat production (Mcal/m² body surface/24 h)

I_T = tissue insulation (° C/Mcal/m²/24 h)

TABLE 7 - EXTERNAL INSULATION OF SHEEP AND CATTLE UNDER DIFFERENT CONDITIONS OF AIR VELOCITY; COAT DEPTH WAS 20 MM

Conditions	External Insulation °C/Mcal/m ² /24 h		
	Sheep	Cattle	Calves
Still air, wind velocity 0.4 - 0.6 m.p.h.	14.0	14.3	13.7
Mild breeze 1.6 m.p.h.	12.5	10.9	-
Strong wind 7.5 m.p.h.	9.9	-	-

TABLE 8 - THE CRITICAL TEMPERATURES OF SHEEP AND CATTLE BOTH HAVING A COAT 20 MM IN DEPTH AND BOTH GIVEN A MAINTENANCE RATION

Environmental conditions	Adult Galloway steers	Adult Scottish Blackface sheep
	Critical temperatures °C	
Still air	-4	+16
Wind 1.6 m.p.h.	+3	+18
Wind 7.5 m.p.h.	-	+22

I_E = external insulation ($^{\circ}\text{C}/\text{Mcal}/\text{m}^2/24\text{ h}$)

V_B = basal loss of heat by fully vasoconstricted skin and minimal pulmonary exchange ($\text{Mcal}/\text{m}^2/24\text{ h}$).

In this expression the critical temperature is defined as an air temperature. It is necessarily qualified by the conditions of convection and radiation used to establish external insulation. In view of the preceding discussion which shows that variation in the numerical magnitude of I_T , I_E , and the product $V_B I_E$ as between sheep and cattle is for the most part small, any major variation in T_C can only arise from variation in the magnitude of H . The heat production of sheep, when expressed on the basis of metabolic body size, is considerably lower than is that of cattle similarly expressed. The species difference in heat production per unit of surface area must necessarily be greater because the surface area of animals varies with a smaller power of weight than the 0.73 power. We have always used, and this is a convention in most environmental studies, surface area computed by the Meeh formula, $A = kW^{2/3}$, and have used as coefficient a value of 0.09 ($\text{m}^2, \text{kg} W^{2/3}$), which derives from studies by Professor H. H. Mitchell. For an adult sheep weighing 50 kg, heat production at the maintenance level of nutrition is 1.00 $\text{Mcal}/\text{m}^2/24\text{ h}$. For an adult steer weighing 500 kg at the same nutritional level, heat production is 1.82 $\text{Mcal}/\text{m}^2/24\text{ h}$. These values were derived from Table 3 and show that at the maintenance level of nutrition the heat production of cattle/ m^2 of its conventional surface exceeds that of sheep by 80 percent.

Table 8 shows the results of computation of critical temperature for the conditions given in Table 7. From this table it can be concluded that cattle are cold tolerant animals and sheep are not. The difference between them stems largely from the large difference in the amount of heat they produce per unit of their surface rather than from differences in the basic physiological mechanisms governing the flow of heat and moisture from the deep tissues of the body to the environment. Kibler and Brody (1954) found much the same reasons to account for the low tolerance of nonlactating Brahman cattle to cold and wind compared with lactating Jerseys and Holsteins.

It can be argued, and quite legitimately, that it is unfair to compare these two species when their coats have the same depth, because the depth of the winter coat of the sheep is so much greater than that of cattle. It can be computed from the equation defining critical temperature and from our data relating external insulation to coat depth, that in still air the critical temperatures of the two species would be the same when the sheep carried 5.5 cm fleece and the steer 2 cm. To combat cold under natural conditions the sheep relies on the high external insulation its wool provides while the steer relies on its high heat production.

Similar considerations apply to the tolerance of these two species to heat. As environmental temperature rises, the amount of heat which can be lost by radiation and convection falls. This amount of heat is much the same in sheep and cattle, for their tissue insulations when completely vasodilated are very comparable and their external insulations do not, of course, change. To maintain deep body temperature constant, heat produced in metabolism which cannot be dissipated by convection and radiation must be used to evaporate water from the skin surface and respiratory passages. This necessarily means that at comparable nutritional planes, cattle must dissipate consider-

ably more heat as water vapor than sheep. Our results with sheep suggest that when the water vapor pressure of the surrounding air is 20 mm, they can evaporate $1.8 \text{ Mcal/m}^2/24 \text{ h}$ without an increase of rectal temperature (Blaxter, 1962 b). Brody's studies (Kibler & Brody, 1952) with cattle suggest that under similar conditions cattle can evaporate about $2.5 \text{ Mcal/m}^2/24 \text{ h}$. Sheep can dissipate heat equivalent to about $1.8 \times$ their maintenance heat production and cattle can dissipate heat equivalent to about $1.4 \times$ their maintenance heat production. It would be expected that sheep would be more heat tolerant than cattle. Brody in his extensive climatic studies showed that milking cows started refusing food in the face of thermal stress at environmental temperatures of 24° C and that heifers refused at temperatures of 35° C (Worstell & Brody, 1953). Our experiments showed that maintenance rations were refused by steers kept continuously at temperatures of greater than 33° C , but sheep were able to consume rations which resulted in considerable body gains even at environmental temperatures of 39° C . The high heat production of cattle and the low heat production of sheep relative to their metabolic size or their surface area appears therefore to be the single most important factor determining the differences in their tolerance to heat and to cold. Sheep are heat tolerant animals and have a sub-equatorial distribution over the earth's surface largely because of their low metabolism relative to their size. European type cattle are cold tolerant animals and are most commonly found in temperate climates, largely because of their high heat production relative to their size.

In this lecture I have taken as my starting point Brody's concept of metabolic body size as a reference base to which the metabolism and function of all mammalian species can be referred. It has been shown that the two ruminant species of greatest economic concern to man, sheep and cattle, deviate considerably and significantly from this great generality. To conclude from this disparity that the concept of metabolic body size is wrong or misleading is to misunderstand completely the value of inter-species generalizations, what are loosely called biological laws and the attitude of mind of Samuel Brody. Generalities in zoology are of immense importance because they provide the only sure basis whereby the attributes of an individual species can be set in the true perspective of the wealth of mammalian kind, and the consequences of its nonconformism examined. Brody's generalization makes it possible to make a more useful statement about the metabolism of sheep and cattle than that 7.8 sheep weighing 50 kg produce as much heat during fasting as does one steer weighing 500 kg! It enables the statement to be made that the sheep has a very low metabolism relative to other species of the same size and that the steer has a slightly high one. The generalities of the relationships between minimal N metabolism and body size of mammals enable one to state that ruminants have a low urinary endogenous N excretion relative to their size, but have a very large fecal N loss. The primary observations now have a scientific merit as well as a factual worth for they engender new processes of induction in the mind of the experimenter, they pose new questions and raise new implications, which, if answered, advance our knowledge. Fact alone is sterile: hypothesis and integration are the very stuff of science.

I have attempted to explore the consequences of the difference between the metabolic rates of these two species as they affect efficiency of food utilization and the tolerance of the species to heat and cold. Both species achieve about the same total or gross energetic efficiency but they apparently do so in rather different ways. These results again raise further questions about the effects of size of the ruminant gut

on the fermentation of food in the rumen, on the rate of flow of digesta and on digestive efficiency. The two species differ in their innate tolerance to both cold and heat and this difference stems fairly directly from differences in their heat production. This result again raises questions but these are of a different, more philosophical kind. They are concerned with the evolution of species, with the survival value of a low metabolic rate in hot countries and the relative survival value in cold countries of a high metabolic rate or a thick pelage. These latter questions so difficult to answer would certainly have interested Brody.

In conclusion, I would like to say that I am very grateful to have had this opportunity to express my admiration for Samuel Brody. I am not alone in this. Much of the work we are doing in Scotland stems directly from Brody's researches, notably much of our own calorimetric work, and many of the researches by Dr. J.D. Findlay on the effects of thermoregulatory mechanisms in cattle. Indeed this renown and his example now encompass the world.

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