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The fasting metabolism of cattle

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1. The metabolism of seventeen steers was determined on forty-nine occasions during fasts of either 112 or 136 h duration. 2. Faeces continued to be produced during fasts of up to 136 h duration at rates which were 15–20% of those noted before the fasts began. 3. Carbon dioxide production and oxygen consumption fell continuously throughout with animals weighing less than 200 kg but changed little after 88 h in animals weighing more than 200 kg. Methane production was considerably reduced during fasting but did not disappear. Urinary nitrogen excretion changed very little. Of the total loss of energy from the body, the loss of protein accounted for 25%. This was unaffected by age or size of animal. 4. With individual Ayrshire steers, metabolism increased during growth with body-weight raised to the power 0.68 ± 0.05. No greater precision of estimate was obtained from logarithmic regressions of metabolism on body-weight than from linear ones. 5. Seven Ayrshire steers had a mean fasting metabolism of 100 ± 1.6 kcal/kg $W^{0.73}$ 24 h, eight Black cattle of the Aberdeen Angus type a fasting metabolism of 81 ± 1.5 kcal/kg $W^{0.73}$ 24 h and two Ayrshire × Beef Shorthorn steers a fasting metabolism of 96 ± 2.9 kcal/kg $W^{0.73}$ 24 h. Variation in the fasting metabolism of an individual steer from time to time, expressed as a coefficient of variation, was $\pm 7.4\%$. 6. The results are discussed in relation to interspecies generalizations about the relation between fasting metabolism and body-weight.

According to Ritzman & Benedict (1938), the first determinations of the fasting metabolism of steers were made by them in 1919 at Durham, New Hampshire, and in the following year Armsby conducted similar experiments with cows in the respiration calorimeter at the State College, Pennsylvania. Relatively few determinations of the fasting metabolism of cattle have been made in the ensuing 45 years, largely because few laboratories have been equipped with calorimeters or respiration chambers. The determinations made by Ritzman & Benedict (1938), by Kleiber, Regan & Mead (1945), by Forbes and his associates (Forbes, Fries, Braman & Kriss, 1926; Forbes, Kriss & Braman, 1927; Forbes, Swift, Bratzler, Black, Wainio, Marcy, Thacker & French, 1941; Cochrane, Fries & Braman, 1925) and by Mitchell and his associates (Mitchell, Hamilton & Haines, 1940, 1941; Mitchell, Hamilton, McClure, Haines, Beadles & Morris, 1932) were relatively few, and for the most part did not embrace a wide range of size or breed of cattle. The results of the fifty-eight determinations traced as having been made up to 1962 were summarized by Blaxter (1962). Extensive observations made by Benedict & Ritzman (1927) with four steers were not included because oxygen consumption was not determined, heat production being calculated from carbon dioxide production using an assumed respiratory quotient. Brody's (1945) determinations of resting metabolism by short-term measurement of the respiratory exchange helped, however, to delineate effects of age and breed on metabolism. Since that summary was made workers in Japan (Hashizume, Kaishio, Ambo, Morimoto, Masubuchi, Abe, Horii, Tanaka, Hamada & Takahashi, 1962; Hashizume, Morimoto,

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Masubuchi, Abe, Horii, Hamada, Tanaka, Takahashi, Kaishio & Ambo, 1964) have made fifteen determinations of the basal metabolism of native cattle and six determinations of the metabolism of European-type cattle. In addition Flatt & Coppock (1963) have briefly reported the results of a number of determinations with six cows. The total number of experiments to determine the fasting metabolism of cattle that have been traced to date is thus in the region of 100 only. The purpose of this paper is to summarize the results of a further forty-nine determinations of the fasting metabolism of seventeen cattle with reference to the effects of age and breed. The results of some of these have been published (Blaxter & Wainman, 1961 *a*, *b*, 1964; Blaxter, Wainman & Davidson, 1966); the remainder have not.

EXPERIMENTAL

Animals. Seventeen steers, including seven Ayrshire steers (nos. 1, 2, 3, 4, 5, 6 and 7), two Ayrshire × Beef Shorthorn steers (Kr and Bg) and eight Black cattle of the Aberdeen Angus type (As, Ay, C, E, F, I, J and H) were used. The animals were purchased from commercial sources. The Ayrshires were undoubtedly pure-bred but the Black cattle were not. Some of the latter, from their appearance, included Galloway blood and others had white flecking suggesting some further breed admixture in their ancestry. All the Black animals were, however, animals bred for beef production rather than as dairy animals. They are referred to as Black cattle. The number of determinations made with each varied, as can be seen from Table 4. With seven animals (1, 2, 3, 4, 5, As and Ay), four or more determinations were made at different times. While some animals were better subjects for respiration experiments than others, all were docile and appeared unaffected by the experimental conditions imposed.

Method of determination of fasting metabolism. Before the fast began all the animals were given a ration of hay or of hay and oats calculated to be sufficient to prevent them losing or gaining weight. They were given their last meals at 17.00 h on the day preceding the experiment. Metabolism measurements were commenced at 09.00 h the following day and continued either until 09.00 h 4 days, or, in six experiments, 5 days later. In some but not all experiments with adult cattle, 30 g MgO were given on the 2nd day of fast because of the finding by Robertson, Paver, Barden & Marr (1960) that fasting can lead to hypomagnesaemia. No tetany was observed in animals not given MgO, and the MgO can be assumed to have had no effect on metabolism. The environmental temperature at which the determinations were made was always 22° or above and the air velocity was 0·4 miles/h. This environment is well above the critical temperature of the steer (Blaxter & Wainman, 1961 *a*). On each day of the fast, carbon dioxide production, methane production and oxygen consumption were determined using closed-circuit respiration chambers. The steers were weighed at the beginning and end of the fasts and usually also after 64 h of fast. The fasting metabolism was taken to be the mean heat production per 24 h measured 64–112 h after food, a period referred to as the 3rd and 4th days of fast. The analytical and other methods were the same as those described for sheep (Blaxter, 1962). Two respiration chambers were used. That of Wainman & Blaxter (1958) was used to measure the metabolism of animals weighing more than about 250 kg, and the metabolism of smaller animals was determined in a closed-circuit respiration chamber operating on similar principles but with an animal chamber of 4000 l. capacity rather than the 9000 l. of the larger instrument and in which CO_2 was absorbed in a solution of potassium hydroxide rather than with solid soda lime.

RESULTS

Faecal excretion. As first reported for adult oxen by Grouven (1864), faeces continued to be produced throughout the fasts by all the animals. Table 1 shows the mean weights of dry faeces produced during fasting by cattle weighing 200 kg or less and indicates that even on the 5th day of fast, dry faeces weighing 15–20 % of the amounts excreted before the fast began were produced. As described for adult steers by Benedict & Ritzman (1927), the moisture content of the faeces fell with increased length of fast and the faeces were usually in the form of pellets. The N content of the dry faeces changed very little with length of fast.

Table 1. *Mean excretion of dry matter and concentration of nitrogen in the faeces of young Ayrshire steers during fasting*

Steers	Age (weeks)	Mean body-weight (kg)	Before fasting	Day of fasting				
				1	2	3	4	5
			Dry matter (g/24 h)					
4, 5, 6	16	70	494	149	149	58	74	—
4, 5, 7	34	97	787	446	278	135	116	—
1, 2, 3	31	145	865	372	224	182	191	135
1, 2, 3	46	182	950	507	352	231	143	175
			% N in faeces					
4, 5, 6	16	70	2·87	3·05	3·21	2·89	2·94	—
4, 5, 7	34	97	2·34	2·37	2·45	2·54	2·40	—
1, 2, 3	31	145	2·84	3·12	2·80	2·74	2·44	2·71
1, 2, 3	46	182	2·90	2·89	2·73	2·55	2·53	2·51

About a third of the weight loss in fasting cattle can be accounted for by a loss of digestive-tract contents, as demonstrated by the continued production of faeces. For example, steers 1, 2 and 3 when fasted for 5 days at a body-weight of 160–170 kg produced respectively 6·0, 5·8 and 3·5 kg fresh faeces in the 5-day period. Their weight losses during the same interval were 17·7, 21·3 and 12·7 kg respectively.

Metabolism on successive days of fasting. Table 2 summarizes the results of twenty-eight experiments made with Ayrshire steers, classified according to their weight after 112 h of fast. CO_2 production and O_2 consumption fell continuously throughout the fasting periods in animals weighing less than 200 kg, but with animals weighing more than 200 kg little change took place after the 3rd day. The mean respiratory quotient on the 3rd and 4th days of fasting was, with one exception, accounted for by a single aberrant value for CO_2 production on the 3rd day of fast, very close to 0·73. Methane production fell throughout the fasts and on the 4th day ranged from a mean of 4·0 l./24 h for animals weighing on average 79 kg to 7·3 l./24 h for animals weighing 345 kg. The amounts of methane produced when the animals were given normal maintenance diets before they were fasted were about 80, 130, 170 and 220 l./24 h for the four groups of animals weighing 50–100, 100–200, 200–300 and 300–400 kg respectively. On two occasions steers 1, 2 and 3 were each fasted for 5 days when they weighed less than 250 kg. The mean amounts of CH_4 produced on the 3rd, 4th and 5th days were 6·65, 3·95 and 2·88 l. CH_4/24 h respectively, which suggest a long continuance of CH_4 production after cessation of feeding. Urinary N excretion changed very little during the course of the experiments in any of the groups.

Table 2. *Metabolism of Ayrshire steers when fasted for* 112 *h*

No. of steers	Weight range (kg)	Measurement	Day of fast				Observations on 4th day of fasting as a percentage of those on the 1st
			1	2	3	4	
5	50–100	O_2 consumption (l./24 h)	645·4	588·5	544·6	519·5	80·2
		CO_2 production (l./24 h)	530·4	449·1	399·4	376·3	70·9
		CH_4 production (l./24 h)	17·7	8·7	5·6	4·0	22·5
		Urine N (g/24 h)	23·1	22·1	18·5	18·5	80·0
		Body-weight (kg)	86·1	82·6	81·0	79·2	92·0
		Heat production (kcal/24 h)	3089	2778	2555	2432	78·7
		Respiratory quotient	0·822	0·763	0·733	0·724	—
8	100–200	O_2 consumption (l./24 h)	1104·1	985·5	902·8	868·2	78·6
		CO_2 production (l./24 h)	903·6	756·0	661·0	607·0	67·2
		CH_4 production (l./24 h)	31·6	13·4	6·8	4·2	13·3
		Urine N (g/24 h)	26·9	28·5	27·9	23·8	88·5
		Body-weight (kg)	169·2	163·5	160·7	158·3	93·6
		Heat production (kcal/24 h)	5274	4648	4221	4062	77·0
		Respiratory quotient	0·818	0·767	0·732	0·700	—
8	200–300	O_2 consumption (l./24 h)	1342·5	1214·6	1135·2	1137·7	84·7
		CO_2 production (l./24 h)	1182·8	914·5	811·4	822·8	69·6
		CH_4 production (l./24 h)	50·0	17·6	9·8	6·1	12·2
		Urine N (g/24 h)	42·4	49·0	50·6	43·0	101·4
		Body-weight (kg)	249·5	240·5	—	234·5	94·0
		Heat production (kcal/24 h)	6518	5720	5306	5321	81·6
		Respiratory quotient	0·881	0·753	0·715	0·723	—
7	300–400	O_2 consumption (l./24 h)	1773·3	1623·5	1495·6	1503·1	84·8
		CO_2 production (l./24 h)	1698·8	1334·0	1179·6*	1096·6	64·6
		CH_4 production (l./24 h)	54·0	21·7	11·3	7·3	13·5
		Urine N (g/24 h)	51·4	53·0	46·8	50·6	98·4
		Body-weight (kg)	365·3	—	—	344·9	94·4
		Heat production (kcal/24 h)	8794	772	7230	7052	80·2
		Respiratory quotient	0·958	0·821	0·788*	0·729	—

* One anomalous value for CO_2 production accounted for this high value.

Heat production was usually but not invariably lower on the 4th day than on the 3rd day of fasting. As with sheep (Blaxter, 1962), the choice of time after cessation of food at which to measure metabolism is thus arbitrary, since CH_4 production in steers, as in sheep, does not cease even after 5 days without food, and metabolism and weight decline continuously during fasts. The mean of the values obtained on the 3rd and 4th days of fasting (64th–112th h) which coincides with respiratory quotients of 0·73 or less have been used in subsequent calculations.

Body size and metabolism. Fig. 1 summarizes the individual observations on fasting heat production as related to body-weight with Ayrshire cattle or Ayrshire crosses and Black cattle shown separately. All observations were above the line shown in Fig. 1, which is the interspecies mean fasting heat production estimated by Brody (1945) to be 70·5 kcal/kg $W^{0\cdot73}$ 24 h, where W = body-weight.

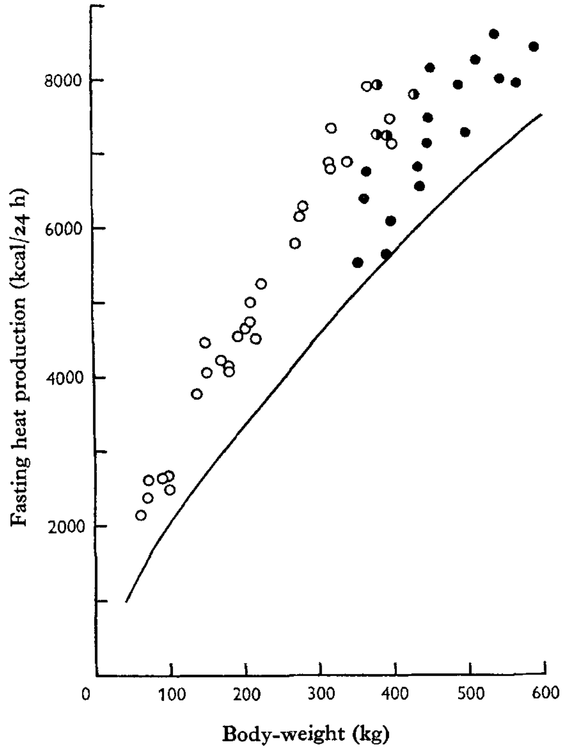

Fig. 1. Heat production of fasted steers in relation to their weight. The line is that which relates fasting metabolism to weight in adults of different species calculated according to Brody's (1945) formula: heat production (kcal/24 h) = 70·5 body-weight $(\text{kg})^{0\cdot73}$. ○, Ayrshire cattle; ●, Black cattle of the Aberdeen Angus type; ◑, Ayrshire × Beef Shorthorn cattle.

With five of the Ayrshire steers fasting metabolism was determined at intervals throughout their lives from 4–8 months to 2½ years of age. The linear regressions and log–log regressions of fasting metabolism on fasted body-weight of these animals are given in Table 3; these demonstrate that metabolism increased with body-weight. All the regressions were statistically significant ($P < 0\cdot01$). The values of F, the variance ratio, were with two steers greater for the logarithmic than for the linear regression, and with three other steers the reverse was true. Prediction of metabolism from a logarithmic regression was thus no more precise than prediction from a linear one.

Fasting heat production calculated from the linear regressions did not differ significantly between animals and the pooled linear coefficient shows that metabolism increased by an average of 16·6 kcal/24 h kg weight gain. The pooled logarithmic regression indicates that the metabolism of these steers varied with weight raised to the power 0·68 ± 0·052. This value was not statistically different from values of 0·73 or 0·75 which are the powers of weight with which the fasting metabolism of different species varies (Brody, 1945; Kleiber, 1961, 1965). No systematic error would thus accrue if the results for animals of different weights were compared by expressing them per unit of metabolic body size, that is, body-weight raised either to the power 0·73 or to the power 0·75, as in Table 4.

Table 3. *Regressions of fasting metabolism* (F, *kcal/24 h*) *on body-weight* (W, *kg*) *of five Ayrshire steers*

			Linear regression		Logarithmic regression	
Steer no.	Weight range (kg)	No. of observations	Equation	Residual standard deviation	Equation	Residual standard deviation*
1	137–319	5	$F = 1111 + 18{\cdot}6\ W$	±286	$F = 91{\cdot}6\ W^{0{\cdot}750}$	±318
2	147–398	6	$F = 2095 + 13{\cdot}4\ W$	±470	$F = 194{\cdot}5\ W^{0{\cdot}610}$	±475
3	152–398	6	$F = 1909 + 14{\cdot}8\ W$	±263	$F = 133{\cdot}0\ W^{0{\cdot}679}$	±217
4	74–340	5	$F = 1083 + 17{\cdot}1\ W$	±240	$F = 172{\cdot}4\ W^{0{\cdot}616}$	±480
5	74–367	4	$F = 857 + 19{\cdot}1\ W$	±135	$F = 86{\cdot}8\ W^{0{\cdot}758}$	±304
All		26	$F = 1356 + 16{\cdot}6\ W$	±363	$F = 128{\cdot}1\ W^{0{\cdot}683}$	±394

* Computed from $\Sigma(F_{\text{obs}} - F_{\text{calc}})^2/(n-2)$, where n is the number of observations and F_{obs} and F_{calc} the observed metabolism and that calculated from the logarithmic regression.

The mean fasting 24 h heat production of the seventeen animals varied from 72·9 to 106·1 kcal/kg $W^{0{\cdot}73}$ 24 h, or from 64·5 to 97·7 kcal/kg $W^{0{\cdot}75}$ 24 h. The errors attached to values for individuals were obtained from analysis of variance of the results of all the trials. Variation in the metabolism of the same animal from occasion to occasion expressed as a coefficient of variation was ± 7·36 % when metabolism was expressed per kg $W^{0{\cdot}73}$ and ± 7·43 % when expressed per kg $W^{0{\cdot}75}$. There was clearly no difference in variation due to choice of reference base. This variation includes all instrumental and analytical error as well as variation of the metabolism of the same animal from occasion to occasion.

Table 4 shows that all the Ayrshire steers had a higher fasting metabolism than the Black steers. The mean values for breed groups given at the foot of Table 4, obtained by giving the mean for each animal an equal weighting, shows that the difference between metabolism of the Ayrshire and the Black cattle was statistically significant. From Table 4, and more particularly from Fig. 1, it is evident that the distribution of body-weight in the two groups was very different. If, however, only those observations made with animals weighing more than 300 kg are included, the mean fasting metabolism of the five Ayrshires (two are excluded) was 90·4 ± 2·4 kcal/kg $W^{0{\cdot}73}$ 24 h, the mean fasting metabolism of the Black cattle remains unchanged and the difference between Black and Ayrshire cattle is reduced to 9·4 ± 2·6 kcal/kg $W^{0{\cdot}73}$ 24 h. This difference was statistically significant ($P < 0{\cdot}01$). The two Ayrshire × Beef Shorthorn crosses which were within the same weight and age range as the Black cattle also had a higher metabolism than the Black cattle ($P < 0{\cdot}01$).

Table 4. *Fasting metabolism of individual steers. Values are means with their standard errors*

Steer	Breed or type	Body-weight range (kg)	Age range (years)	No. of determinations	Mean fasting heat production kcal/kg $W^{0.73}$ per 24 h	Mean fasting heat production kcal/kg $W^{0.75}$ per 24 h
1	Ayrshire	137–319	0·7–2·5	5	102·4 ± 3·2	91·9 ± 2·9
2	Ayrshire	147–398	0·7–2·5	6	98·7 ± 2·9	88·4 ± 2·6
3	Ayrshire	152–398	0·7–2·6	6	100·6 ± 2·9	90·1 ± 2·6
4	Ayrshire	74–340	0·3–2·0	5	97·0 ± 3·2	87·6 ± 2·9
5	Ayrshire	74–367	0·3–2·0	4	100·0 ± 3·5	90·3 ± 3·2
6	Ayrshire	63	0·3	1	106·1 ± 7·0	97·7 ± 6·4
7	Ayrshire	92	0·7	1	96·9 ± 7·0	88·6 ± 6·4
Kv	Ayrshire cross	380–392	1·8–2·4	2	98·4 ± 5·0	87·3 ± 4·5
Bg	Ayrshire cross	379–430	2·4–3·6	2	94·3 ± 5·0	83·6 ± 4·5
As	Black*	490–567	2·0–3·7	4	83·1 ± 3·5	75·5 ± 3·2
Ay	Black	450–594	2·0–3·7	4	82·8 ± 3·5	73·1 ± 3·2
C	Black	363–365	2·0–2·4	2	88·6 ± 5·0	78·7 ± 4·5
F	Black	434–443	2·0–2·4	2	82·0 ± 5·0	74·5 ± 4·5
E	Black	392	2·0	1	72·9 ± 7·0	64·5 ± 6·4
H	Black	439–454	2·0–2·4	2	83·8 ± 5·0	75·9 ± 4·5
I	Black	349	2·0	1	77·0 ± 7·0	68·6 ± 6·4
J	Black	394	2·0	1	77·5 ± 7·0	68·7 ± 6·4
Means						
	Seven Ayrshires				100·2 ± 1·6†	90·7 ± 1·5†
	Five Ayrshires weighing more than 300 kg				90·4 ± 2·4†	
	Two Ayrshire crosses				96·3 ± 2·9†	85·4 ± 2·9†
	Eight Black cattle				81·0 ± 1·5†	72·4 ± 1·5†
Interspecies mean: Brody (1945)					70·5	—
Kleiber (1961)					—	69·0 ± 1·5
Sheep, 3 years of age (Blaxter, 1962)					58·5 ± 1·3	54·1‡

* Black cattle of the Aberdeen Angus type.

† Between-animal standard error, each mean value being given an equal weighting.

‡ Calculated by multiplying metabolism/kg $W^{0.73}$ by $W^{0.02}$, taking a mean value for W of 50 kg.

Protein metabolism. The proportion of the total loss of energy from the body during fasting which derived from oxidation of protein was 26·4 ± 1·2 % for the seven Ayrshire cattle, 23·0 ± 2·1 % for the two crosses and 23·3 ± 1·1 % for the eight Black cattle. These means did not differ significantly one from another nor was the regression of the percentage of the loss of energy from the body which was derived from protein on metabolism per kg $W^{0.73}$ significant statistically. The slightly higher value for Ayrshire cattle compared with Black cattle was not due to the fact that the Ayrshires were younger. In six experiments in which Ayrshire cattle, weighing 100 kg or less, were fasted, 26·7 % of the total energy loss was accounted for by protein oxidation. In six experiments in which Ayrshire cattle weighing over 300 kg were fasted, the mean proportion accounted for by protein was 25·5 %. The small apparent fall was not statistically significant. It appears therefore that on average 24·5 ± 0·8 % of the energy lost from the bodies of the cattle during fasting was derived from protein oxidation.

In similar trials with sheep the loss of energy derived from protein, expressed as a percentage of the total loss of energy, was 23·8 ± 1·5 (Blaxter, 1962), a value not significantly different from that noted with cattle.

DISCUSSION

The determinations of the fasting metabolism of the seventeen steers show that relative to generalizations made with a wide range of other species the steers had a high fasting metabolism for their size. Previous investigations with sheep (Blaxter, 1962) showed that wether sheep aged more than 2 years had a low fasting metabolism of 58·5 kcal/kg $W^{0.73}$ 24 h. The fasting metabolism of Ayrshire steers was 100 kcal/kg $W^{0.73}$ 24 h and that of Black steers 81 kcal/kg $W^{0.73}$ 24 h. The mean metabolism of all species as estimated by Brody (1945) was 70·5 kcal/kg $W^{0.73}$ 24 h. This estimate, however, differs slightly from that determined by Kleiber (1961) which was 69·5 kcal|kg $W^{0.75}$ 24 h.

Kleiber's equation predicts the metabolism of a 50 kg animal to be 7 % greater and of a 500 kg animal to be 12 % greater than does the equation of Brody. When Kleiber's equation with its slightly larger coefficient of W is used as a reference base, the difference in the metabolism of sheep and cattle relative to an interspecies mean is slightly reduced. To obliterate the difference between them entirely, metabolism as between species would have to vary with a power of body-weight greater than 0·9. No investigations of the relation of the metabolism to weight in a series of different species differing in size suggest that the interspecies exponent of W can approach a value of 0·9. The conclusion that relative to all species sheep have a low fasting metabolism and cattle a high one appears, therefore, to be correct.

The evidence that the fasting metabolism of different breeds of cattle may differ supports results obtained by Hashizume *et al.* (1962). They found the mean fasting metabolism of five Japanese Holstein cattle to be 73·1 kcal/kg $W^{0.75}$ 24 h and of four Japanese Black cattle 51·5 kcal/kg $W^{0.75}$ 24 h, the difference being statistically significant. The former value, which is corrected to 24 h lying down, agrees with a mean value reported by Flatt & Coppock (1963) of 73·5 kcal/kg $W^{0.75}$ 24 h with six Holstein cows in the USA. Earlier Ritzman & Benedict (1938) had noted that Jersey cows had a higher fasting metabolism than Holstein cows. Brody's (1945) extensive metabolic investigations suggest, however, that the Jersey cow has if anything a lower metabolism than the Holstein. In addition, he found no large difference between the basal metabolism of Holstein cattle and beef cattle in the United States.

Ritzman & Benedict (1938) drew attention to a considerable variation in the fasting metabolism of cows and steers. In their experiments the heat production of individual animals from occasion to occasion certainly varied more than it did in ours.

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