The fasting metabolism of Brahman, Africander and Hereford × Shorthorn cattle

By J. E. VERCOE

CSIRO Division of Animal Genetics, Cattle Research Laboratory, Rockhampton, Qld 4700, *Australia*

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1. The fasting metabolism of twenty-seven animals, nine Brahmans, nine Africanders and nine Hereford × Shorthorns was measured after fasts of 96 h duration. Urine was collected over successive 24 h intervals and gas exchange was determined 96–103 h after the last meal.

2. Urinary urea decreased and creatinine increased throughout the fasting period. There was no difference between breeds in the urinary excretion of nitrogen, urea and creatinine on the 4th day of fasting (72–96 h). Excretion of nitrogen, urea and creatinine increased by 259, 197 and 45 mg/kg increase in fasted weight and by 8·9, 7·6 and 0·91 mg/kcal increase in fasting metabolism respectively. Protein oxidation accounted for 25·6, 21·7 and 22·7% of the fasting heat production of Brahman, Africander and Hereford × Shorthorn cattle respectively, values which were not significantly different.

3. The breeds differed in fasting metabolism per kg fasted weight ($P < 0{\cdot}05$) and in fasting metabolism adjusted for fasted weight ($0{\cdot}05 < P < 0{\cdot}10$), mainly owing to lower values for the Brahmans. The respective values for the Brahmans, Africanders and Hereford × Shorthorns were 20·7, 25·2 and 24·1 kcal/kg (86·6, 105·4 and 100·8 kJ/kg) and 5·856, 6·947 and 6·600 Mcal/24 h (24·50, 29·07 and 27·61 MJ/24 h) at a fasted weight of 277 kg. The variation in fasting metabolism between animals within breeds, expressed as a coefficient of variation, was 13·7%.

4. The results are discussed in relation to published estimates of fasting metabolism, possible reasons for the breed difference and the relation of fasting metabolism to heat tolerance.

Determinations of fasting metabolism in cattle were summarized by Blaxter (1962), Flatt & Coppock (1965) and Blaxter & Wainman (1966). It was pointed out that relatively few such determinations have been made and these were on a limited number of animals and breeds. Blaxter & Wainman (1966) reported results for seventeen steers at the Hannah Dairy Research Institute and produced evidence for differences in the fasting metabolism of dairy- and beef-type cattle.

There is little information on the comparative fasting metabolism of Zebu and European-type cattle, despite a large number of observations on heat production of Brahman, Holstein, Jersey and Brown Swiss cattle made by workers at Missouri (Kibler & Brody, 1950, 1951; Worstell & Brody, 1953). Unfortunately, the Missouri results do not lend themselves to extrapolation to fasting conditions, since the observations were made under a variety of live weights, physiological states, environmental temperatures and feeding regimes. A comparison of Brahman and Brown Swiss heifers (Worstell & Brody, 1953) made at similar intakes of total digestible nutrients, but with differences between breeds in growth rate and weight, suggested that under similar conditions there may have been a lower heat production in the Brahman heifers. This may have been due to a difference in either fasting metabolism or heat increment. In other comparisons of Brahman, Holstein and Jersey cattle, the lower

heat production of the Brahmans under the conditions in which it was measured was attributed largely to differences in weight, food intake and milk production and, although the possibility of a lower fasting metabolism in the Brahmans was suggested, it was not demonstrated (Kibler & Brody, 1950, 1951, 1954; Worstell & Brody, 1953).

Johnston, Hamblin & Schrader (1958) suggested that the lower heat production of the Red Sindhi × Holstein than of the Jersey and Holstein cows was due to a lower fasting metabolism, but this was not successfully demonstrated.

To obtain more comparative information on the metabolism of Zebu and European-type cattle, studies were made on Brahman, Africander and Hereford × Shorthorn cattle. This formed part of an investigation into the physiology and biochemistry of the adaptation of beef cattle to tropical and subtropical environments (Kennedy & Turner, 1959).

EXPERIMENTAL

Animals. Nine Brahman, nine Africander and nine Hereford × Shorthorn male animals were used, three of each breed in each of the years 1966, 1967 and 1968. In 1966, 1967 and 1968, the animals were 22, 20 and 13 months old respectively. All the animals were bulls with the exception of one Africander steer in 1966 and three Hereford × Shorthorn steers in 1967. The breeding and degree of relationship between the representatives of each breed have been described elsewhere (Frisch & Vercoe, 1969). The animals were trained to the respiration chamber situation but they reacted differently to the fasting procedure; some became very docile whereas others became less placid.

Method of determining fasting metabolism. In 1966 and 1967 the animals had been individually fed *ad lib.* on lucerne hay for a period of approximately 10 weeks before fasting and in 1968 they were given daily, for a period of 4–5 weeks, 5 kg of lucerne hay, which was approximately the amount consumed *ad lib.* by the animal with the smallest appetite. The animals were put in metabolism cages at 10.00 hours, 2 h after feeding, and fasted for 96 h. In the next 7 h gas exchange was measured in the confinement-type respiration chambers described by Turner & Thornton (1966). During this period, three or four determinations of fasting metabolism were made, each lasting approximately 1·5 h. When the result of the first determination was higher than those of the subsequent ones, it was discarded, and the mean of the remaining values was used in the calculation of fasting metabolism. Heat production was calculated from the gas exchange using the factors of Brouwer (1965). Methane production was 3–5 l/24 h, which was ignored in the calculation of heat production. In 1966, owing to a failure of the oxygen analyser, heat production was estimated from the CO_2 production and an assumed RQ of 0·76, which was the mean value determined in the subsequent years. No account was taken of variations in the time spent standing and lying because the animals stood for most of the time. The determinations were made at chamber temperatures of 26–28° and 60% relative humidity.

Live weights were determined after fasting for 96 h when the animals entered the respiration chambers.

Urine was collected during the 1st, 2nd, 3rd and 4th days of fasting in 1966 and 1967,

but in 1968 it was collected over the 2nd, 3rd and 4th days only, owing to the fact that metabolism cage accommodation was not available for the 1st day of fasting.

Analytical methods. The urine collected on the 4th day of fasting was analysed for total nitrogen, and all urine samples were analysed for urea and creatinine. The methods were those described by Vercoe (1967).

In analyses of results the variance was partitioned initially into breeds, years, years × breeds and animals within breeds and years. This analysis was done to eliminate the possibility of a year × breed interaction, caused either by the three Hereford × Shorthorn steers in 1967 or for some other reason. Between animals within breeds, fasted weight was confounded with years, and removal of the year effects therefore removed the variation in fasted weight. In addition, analyses of covariance on fasted weight eliminated the significant effect of years in all variates. It was assumed therefore that the year effects were due almost entirely to differences in fasted weight, and the main analyses, the comparison of the within-breed regressions of the variates on fasted weight, was done ignoring years.

RESULTS

The RQ's measured in 1967 and 1968 had a mean value of 0·76 ± 0·01 and there was no difference between the breeds.

Urinary excretion of urea decreased and that of creatinine increased over the fasting period. Values for all breeds followed the pattern shown in Fig. 1.

The means for each breed and for each year of urinary excretion of total nitrogen,

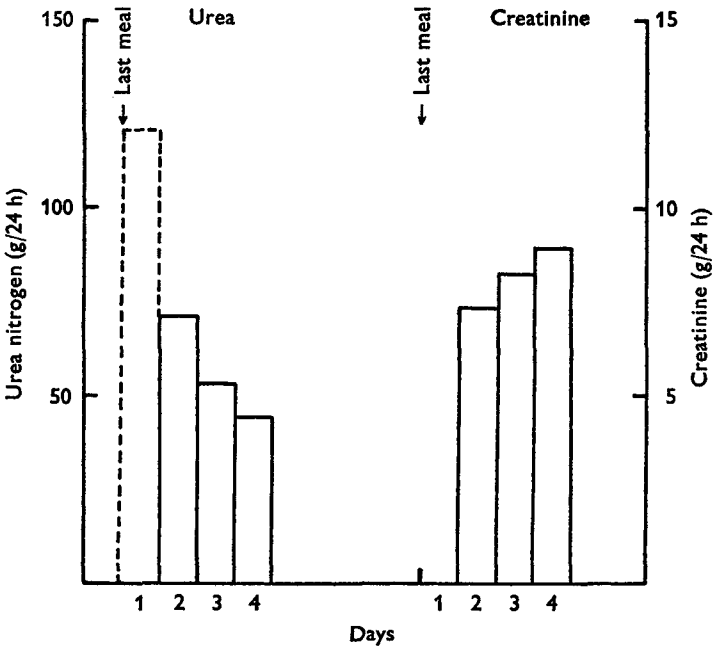

Fig. 1. Mean values for all cattle of urinary excretion (24 h) of urea nitrogen and creatinine for successive days of fasting. Values for day 1 were not obtained in 1968, hence the dotted histogram for urea nitrogen and the omission for creatinine.

urea nitrogen and creatinine, and of fasting metabolism and fasted weight, are shown in Table 1. There were significant differences ($P < 0.01$) between years in all variates and a significant difference ($P < 0.01$) between breeds in fasted weight. There was no significant breed × year interaction in any variate, which indicates that the three Hereford × Shorthorn steers, used in 1967, behaved similarly to the bulls. When fasted weight was used as a covariate the significant effect of years was eliminated, which indicates it is due almost entirely to differences in fasted weight. When years were ignored in the analysis, there was no significant breed difference in fasted weight.

Table 1. *Urinary excretion (g/24 h) of total nitrogen, urea nitrogen and creatinine, and fasting metabolism and body-weight of three breeds of cattle after 96 h of fasting (mean values for three animals)*

Year	Breed	Total N	Urea N	Creatinine	Fasting metabolism (kcal/24 h)	Fasted weight (kg)
1966	Brahman	77·7	59·6	9·92	7051	347
	Africander	67·0	55·3	13·67	7489	308
	Hereford × Shorthorn	59·5	45·0	9·46	7143	314
1967	Brahman	63·8	50·1	11·95	6695	325
	Africander	52·2	44·3	6·99	7356	279
	Hereford × Shorthorn	56·4	43·5	8·31	7253	268
1968	Brahman	36·8	29·4	7·19	5275	236
	Africander	40·3	32·9	6·09	5356	210
	Hereford × Shorthorn	40·6	32·0	6·83	4589	205
	Standard error*	4·2	4·2	0·89	270	5
Means	1966–8					
	Brahman	59·4	46·4	9·69	6340	303
	Africander	53·2	44·2	8·92	6734	266
	Hereford × Shorthorn	52·2	40·2	8·20	6328	262
	Standard error†	5·7	5·0	1·13	471	16

* Based on animal within breed and year variation.
† Based on animal within breed variation.

Comparison of the within-breed regressions of urinary excretion of total nitrogen, urea nitrogen and creatinine on fasted weight (Snedecor & Cochran, 1967) showed that there were no significant differences between the breeds in either slope or elevation. The pooled equations which describe the relation between the urinary constituents and fasted weight are:

$$U = -16{\cdot}9 + 0{\cdot}259\,W \quad (s_b = \pm 0{\cdot}049,\ r = +0{\cdot}74,\ P < 0{\cdot}01), \tag{1}$$

$$UR = -11{\cdot}0 + 0{\cdot}197\,W \quad (s_b = \pm 0{\cdot}048,\ r = +0{\cdot}65,\ P < 0{\cdot}01), \tag{2}$$

$$C = -3{\cdot}5 + 0{\cdot}045\,W \quad (s_b = \pm 0{\cdot}011,\ r = +0{\cdot}65,\ P < 0{\cdot}01), \tag{3}$$

where U = total urinary nitrogen (g/24 h), UR = urinary urea nitrogen (g/24 h), C = urinary creatinine (g/24 h) and W = fasted weight (kg).

For all breeds, therefore, an increase in fasted weight of 1 kg increased the urinary excretion of total nitrogen, urea nitrogen and creatinine by 259, 197 and 45 mg/24 h respectively.

It was similarly shown that, for all breeds, excretion of total nitrogen and urea nitrogen increased by $8{\cdot}9 \pm 2{\cdot}1$ and $7{\cdot}6 \pm 1{\cdot}9$ mg/24 h per kcal increase in fasting metabolism respectively. Creatinine increased by $0{\cdot}9 \pm 0{\cdot}52$ mg/24 h per kcal, but this regression coefficient was not significant.

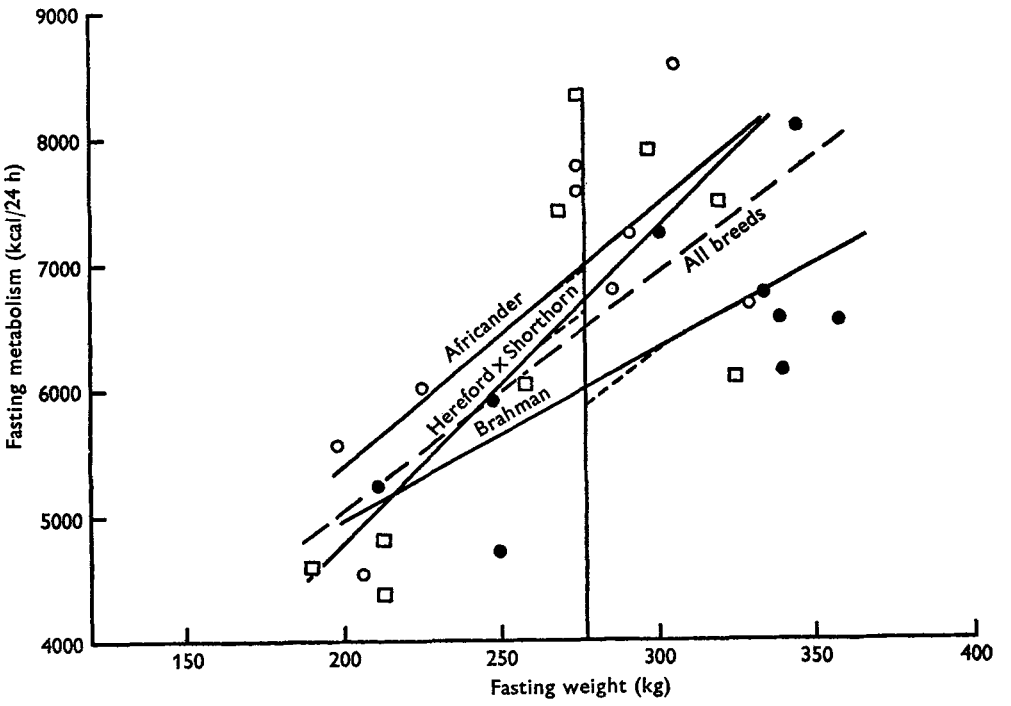

Fig. 2. Fasting heat production (kcal/24 h) of Brahman (●), Africander (○) and Hereford × Shorthorn (□) cattle in relation to fasted weight (kg). The regression lines for each breed (nine animals in each) and for all animals are shown. The vertical line is the weight to which the breeds were adjusted and the short dotted lines join the unadjusted and adjusted means for each breed.

The comparison of the within-breed regression of fasting metabolism on fasted weight is illustrated in Fig. 2. The analysis (Snedecor & Cochran, 1967) showed that the regression coefficients for each breed were not significantly different, and the common one was $18{\cdot}7 \pm 3{\cdot}69$ kcal/kg fasted weight. However, there were differences which approached significance ($0{\cdot}05 < P < 0{\cdot}10$) in elevation and it was calculated that, at a fasted weight of 277 kg, the Brahman, Africander and Hereford × Shorthorn cattle had fasting metabolisms of 5856, 6947 and 6600 kcal/24 h respectively.

There were significant ($P < 0{\cdot}05$) differences in the fasting metabolism per kg fasted weight; the values for the Brahmans, Africanders and Hereford × Shorthorns were 20·74, 25·24 and $24{\cdot}09 \pm 0{\cdot}743$ kcal/kg respectively. The fasting metabolisms per unit metabolic weight ($W^{0{\cdot}75}$) for the Brahmans, Africanders and Hereford × Shorthorns were also different ($0{\cdot}05 < P < 1{\cdot}10$); the respective values were 86·4, 102·5 and $97{\cdot}4 \pm 4{\cdot}20$ kcal/kg $W^{0{\cdot}75}$.

Comparison of log–log regressions of fasting metabolism on fasted weight within breeds showed that there was no difference between the breeds in the exponent ($0{\cdot}85 \pm 0{\cdot}145$) but there was in the coefficient ($0{\cdot}05 < P < 0{\cdot}10$). The logarithmic regressions relating fasting metabolism and weight were:

$$\text{Brahmans} \quad F = 49{\cdot}3\ W^{0{\cdot}85}, \tag{4}$$

$$\text{Africanders} \quad F = 59{\cdot}9\ W^{0{\cdot}85}, \tag{5}$$

$$\text{Hereford} \times \text{Shorthorns} \quad F = 55{\cdot}6\ W^{0{\cdot}85}, \tag{6}$$

where F is the fasting metabolism (kcal/24 h) and W is the fasted weight (kg).

The proportions of the fasting heat production derived from protein oxidation by each breed were 25·6, 21·7 and 22·7% for the Brahmans, Africanders and Hereford × Shorthorns respectively. These values have been derived by multiplying the total urinary nitrogen excreted between 72 and 96 h of the fasting period by 27·5 (Brouwer, 1965), and expressing this as a percentage of the fasting metabolism. Although the Brahmans apparently derived a higher proportion of their fasting metabolism from protein, this apparent difference was not statistically significant. The general mean was 23·3%.

The variability between animals within a breed expressed as a coefficient of variation was ±13·7% for fasting metabolism adjusted for fasted weight and ±13·2% for fasting metabolism per kg $W^{0{\cdot}75}$. These are approximately double the within-animal variation of ±7·4% (per kg $W^{0{\cdot}75}$) reported by Blaxter & Wainman (1966).

DISCUSSION

The relation between urinary nitrogen and fasting weight and metabolism

The mean excretions of total urinary nitrogen per kg of fasted weight and per kcal of fasting metabolism were 195 and 8·5 mg respectively. These values are similar to those reported by Blaxter & Wainman (1966) for Ayrshire cattle weighing between 200 and 300 kg (188 mg/kg and 8·1 mg/kcal).

Oxidation of protein accounted for 23·3% of the fasting metabolism, a value identical with that reported by Blaxter & Wainman (1966) for eight Black cattle of the Aberdeen Angus type. The observed increase in urinary nitrogen with increase in fasting metabolism (8·9 mg/kcal) corresponds to a protein contribution to increased fasting metabolism of 24·5% which is identical with the mean value reported for Ayrshire and Black cattle by Blaxter & Wainman (1966). Although the difference between the breeds was not significant, the Brahmans had a higher value and it is possible that this may be related to a difference in body composition (Graham, 1967).

Fasting metabolism

Blaxter & Wainman (1966) reported mean fasting metabolisms for seven Ayrshire and eight Black steers (Aberdeen Angus type) of 90·7 and 72·4 kcal/kg $W^{0{\cdot}75}$ respectively and Flatt & Coppock (1963, 1965) reported a mean fasting metabolism for six dry non-pregnant Holstein cows of 73·5 kcal/kg $W^{0{\cdot}75}$. The present estimates of 86·4,

102·5 and 97·4 kcal/kg $W^{0·75}$ for the Brahmans, Africanders and Hereford × Shorthorns, with the exception of that for the Brahmans, are higher than these. There are four possible reasons for this difference. First, breed differences in fasting metabolism may be of this order of magnitude. Secondly, the present estimates are higher because the animals had been previously fed *ad lib.*; previous nutritional level can influence the fasting metabolism of sheep (Marston, 1948; Graham, 1967) and my own unpublished results indicate that the same is true for cattle. Thirdly, these measurements were relatively short-term (7 h), with the animals generally standing. The measurements of Blaxter & Wainman (1966) and Flatt & Coppock (1963) were made over 24 h periods when the animals presumably spent some time lying down, which would reduce the fasting metabolism (Blaxter, 1962; Brockway, 1965). Fourthly, and perhaps the most relevant, is that these observations were made mainly on entire male cattle whereas the others have been made on steers or cows. Graham (1968) found that rams had a higher mean fasting metabolism (per kg) than wethers or ewes. However, in spite of these differences a comparison of the metabolism of the three breeds examined in this work is acceptable.

The fasting metabolisms of the three breeds were analysed in four ways; by comparing the within-breed regressions of fasting metabolism on weight, by comparing the breed means for fasting metabolism per unit weight and for fasting metabolism per unit metabolic weight ($W^{0·75}$), and by comparing the within-breed logarithmic regressions of fasting metabolism on weight. The latter three analyses assume zero metabolism at zero weight and therefore are more meaningful physiologically. All the analyses, however, indicate that the Brahmans have a lower fasting metabolism than the other two breeds (significant at $P < 0·05$, or $0·05 < P < 0·10$). While the breed difference must be regarded as marginal because of the level of significance and the nature of the experimental design and statistical analysis, this finding is supported by the observations made by the Missouri workers (mentioned on p. 599) of the heat productions of a number of breeds under a variety of environmental and physiological conditions.

A lower fasting metabolism of the Brahmans may be explained in one of two ways. Either, they have a lower requirement for energy to carry out the functions of basal metabolism, i.e. basal functions are fewer or slower, or, if they have a similar requirement, they are able to use more efficiently the energy released by the biochemical processes occurring at basal conditions, so that less appears as heat. Of these two alternatives, the first seems unlikely. In relation to the second, it may be said that fasting metabolism does not theoretically represent the basal requirement for free energy, but includes an inescapable component of the heat increment arising from metabolism of body tissues. It is known that a multitude of metabolic regulations controls energy metabolism, and their malfunction, e.g. in cases of vitamin or mineral deficiency, lowers efficiency and raises fasting metabolism (Kleiber, 1945; Blaxter, 1962). It is possible therefore that individuals and breeds could also differ biochemically to produce different fasting metabolisms.

A lower heat production has obvious consequences in the maintenance of thermal equilibrium in a hot environment, and it is possible that at least part of the higher heat

tolerance of Brahman cattle observed by the Missouri workers (Kibler & Brody, 1950, 1951, 1954; Worstell & Brody, 1953) was due to a lower fasting metabolism. On the other hand, the heat tolerance of Africanders is known to be higher than that of European breeds (Findlay, 1950) though, judging from comparisons of cross-breds (Rhoad, 1940), it is not as high as that of Brahmans. There may have been less need for Africanders to reduce heat production to assist heat regulation since the area from which they are derived has a hot dry climate where evaporative cooling is effective. However, before it can be categorically asserted that Brahmans have a lower heat production than the other breeds at all levels of feeding in a thermoneutral environment, the heat increment of feeding must be studied. Interest will then be centred on whether the curves for Brahmans and other breeds, relating heat production to metabolizable energy, are parallel or divergent.

Of more direct consequence to this Laboratory is whether the lower fasting metabolism of the pure-bred Brahman is still apparent in its cross with European cattle, since the cross is known to be heat-tolerant (Schleger & Turner, 1965; Vercoe, 1969).

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