# Maintenance requirements in metabolizable energy of adult nonpregnant, nonlactating Charolais cows

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# Maintenance Requirements in Metabolizable Energy of Adult, Nonpregnant, Nonlactating Charolais Cows[1]

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**ABSTRACT:** The objective of this study was to determine the maintenance requirements in metabolizable energy ($ME_m$) of adult, nonlactating, nonpregnant Charolais cows. A feeding trial was conducted using 12 cows fed at one of two feeding levels (75 [L] and 113 [H] kcal of ME·kg $BW^{-.75}$·$d^{-1}$) for 116 d. Body composition was estimated from subcutaneous adipocyte diameter. Body weight changes averaged −468 and +46 g/d, respectively. Diet DM digestibility averaged .496. The L cows spent less time eating and ruminating but had other behavioral characteristics similar to those of H cows. Estimates of $ME_m$ were calculated from BW or body composition changes and amounted to 109 and 124 kcal of ME·kg $BW^{-.75}$·$d^{-1}$, respectively. Heat production (HP) was then measured over 67 d in a second trial on two L and two H cows from the feeding trial and planes of feeding were switched after 14 d. Estimates of $ME_m$ varied from 112 to 105 kcal·kg $BW^{-.75}$·$d^{-1}$. Within animal, day-to-day variations in heat production were high (4.6% on average) and prevented the detection of any precise changes of HP with time on treatment. None of the trials showed any significant effect of level of feeding on $ME_m$.

Key Words: Maintenance Requirements, Metabolizable Energy, Charolais, Cows, Heat Production, Feed Intake

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## Introduction

Maintenance requirements for metabolizable energy ($ME_m$) have been defined as the amount of consumed ME required for zero energy balance (Blaxter, 1962). The $ME_m$ of Charolais cows are not precisely known. Estimates obtained from feeding trials vary from 90 to 130 kcal of ME/kg of metabolic BW ($BW^{.75}$) (Petit et al., 1992) and during the lactation period estimated $ME_m$ are consistently higher than accepted dairy cow requirements by approximately 20% (Agabriel and Petit, 1987). Such discrepancies can arise from differences in the measurement of maintenance (no BW changes, no body composition changes, or zero energy balance). They can also arise from an adaptation of animals with time to different planes of feeding (Turner and Taylor, 1983; Ferrell et al., 1986).

In a first step toward addressing this issue and providing reliable estimates of $ME_m$ for adult, nonlactating, nongestating Charolais cows, an experiment was designed 1) to estimate $ME_m$ from the BW changes of animals fed at a constant plane of feeding (two levels) for 4 mo, 2) to estimate heat production of some of these animals at the end of the feeding trial, and 3) to measure the time necessary for heat production to stabilize after an abrupt change in the plane of feeding. In addition, measurements of body composition, diet digestibility, animal behavior, and concentrations of blood metabolites and hormones were carried out to provide elements for interpretation.

## Materials and Methods

### *Animals*

A total of 12 adult, nonlactating, nonpregnant Charolais cows were used. Animals were 5 to 9 yr of age and averaged 646 ± 8.7 kg in initial BW (mean ± SE) and 4 (± .3) in initial body condition score

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(maximum score = 10; Agabriel et al., 1986). Four of them were ruminally fistulated. Cows were housed indoors in individual stalls.

*Experimental Plan*

Two experiments were conducted consecutively. First, a feeding trial was carried out with all animals during the winter just after the end of the grazing season. It consisted of a 46-d preliminary period and a 116-d experimental period (d 1 to 116). At the beginning of the experimental period, cows were blocked on the basis of their BW, body condition, and fistulated state and were randomly allocated to one of two treatment groups corresponding to the higher (**H**) and the lower (**L**) limits of estimated $ME_m$.

Second, a calorimetry trial was conducted using a total of four animals chosen from both treatment groups on the basis of their acceptance to handling, absence of lameness, and their previous BW changes. This experiment consisted of a 14-d adaptation period to the routine of heat production (**HP**) measurements in respiration chambers. The actual experimental period was 67 d long. During the first 2 wk (d −14 to −1), animals were on the same treatment they had been on in the feeding trial; planes of feeding were then switched abruptly on d 1 such that cows on the L treatment were given the H ration (LH treatment), and vice versa (HL) (d 1 to 53).

*Diet and Feeding*

The diet was composed of orchardgrass (*Dactylis glomerata*) and timothy (*Phleum pratense*) hays in a 50:50 ratio, on an as-is basis. In addition, a commercial mineral-vitamin mixture (100 g/d) was offered to each animal with a minimum and constant amount of soybean meal (89 g of DM/d) to improve palatability. Daily rations were individually distributed in two equal daily meals at 0830 and 1530.

During the first 30 d of the preliminary period of the feeding trial, all animals received 8 kg of hay per day (approximately 11.2 Mcal of ME/d), whereas in the last 16 d feed allowances were adjusted on the basis of individual metabolic BW at the recommended $ME_m$ requirements of 105 kcal of ME·kg $BW^{-.75}$·$d^{-1}$ (INRA, 1978). At the beginning of the experimental period of the feeding trial, cows were fed one of two feeding levels estimated at 90 (L) and 130 (H) kcal of ME·kg initial $BW^{-.75}$·$d^{-1}$. Daily rations remained unchanged thereafter.

At the time the calorimetry trial was started (in May), the weather had become milder and cows refused to eat the poor-quality timothy hay. Consequently, only orchardgrass hay was distributed, after adjustments on a digestible DM basis such that the total digestible DM offered remained unchanged. The actual experimental period and the first HP measurements started 1 wk after this change. After 2 wk of HP measurements (d −14 to −1), the planes of feeding of cows were switched abruptly (LH and HL treatments) on a metabolic BW basis and rations remained unchanged from d 1 to 53.

*Measurements During the Feeding Trial*

*Feed Samples.* The DM of feedstuffs was determined (80°C for 48 h in a forced-air oven) on twice-weekly samples for hays and fortnightly samples for soybean meal. Further subsamples were taken, composited on a monthly (hays) or experimental (soybean meal) basis, ground through a 1-mm screen and analyzed for ash, GE, N, and ADF. Hays were also analyzed for lignin. Different samples were taken daily and composited over the digestibility measurement periods. Feed refusals were collected weekly for chemical analysis.

*Body Weight Gain and Body Composition.* Cows were weighed twice weekly, 4 h after the morning meal, except at the beginning of the experimental period, during which initial BW was taken on three consecutive days. Body condition scores were estimated monthly by a minimum of two persons each time. Body composition was estimated from adipocyte diameter measured in rump adipose tissue biopsies (Robelin et al., 1989) taken initially (d −5) and at the end (d 109) of the feeding trial. Weights of ruminal contents were measured by emptying the rumens of the four cannulated cows, 4.5 h postprandially, before (d −14), at the beginning (d 9), and at the end (d 110) of the experimental period.

*Diet Digestibility.* The DM digestibility of each hay was first measured in a preliminary trial with six adult wether sheep by a 6-d total fecal collection. The results obtained were used for calculating diets.

Whole diet digestibility was then measured in 6 of the 12 cows (3L and 3H) by 12-d total fecal collections at the beginning (d 30 to 42) and end (d 91 to 103) of the feeding trial. The same animals were used in both periods. Daily fecal samples were dried at 80°C for 96 h for DM determination. Further subsamples were frozen, composited on a 12-d basis, freeze-dried, ground through a 1-mm screen, and analyzed for ash, N, GE, and ADF.

*Blood Metabolites and Hormones.* On d −1 and 64, blood was sampled from the tail vein three times daily (immediately preprandially and 2 and 6 h postprandially). On d 88, blood was sampled from jugular catheters every 20 min for a total of 8 h starting 90 min before the morning feeding. Heparin was used as an anticoagulant except for blood samples taken to obtain plasma for growth hormone (**GH**) analysis, for which EDTA was used in combination with a protease inhibitor (iniprol, Laboratoire Choay, Paris, France, 10 μL/mL of blood) to inhibit protease activity. Plasma was frozen immediately and stored (−20°C) awaiting chemical analyses (plasma nonesterified fatty acids [**NEFA**], betahydroxybutyrate, insulin,

cortisol, triiodothyronine [$T_3$], thyroxine [$T_4$], and GH [d 88 only] concentrations).

*Animal Behavior.* Observations on animal behavior were made every 10 min for 48 consecutive hours on d 107 and 108. The following activities of each cow were noted: lying down-head dropped, lying down-head up, lying down-ruminating, standing-inactive, standing-eating, standing-ruminating, and standing-miscellaneous activities (drinking, licking, tail flipping).

### *Measurements During the Calorimetry Trial*

Cows were weighed weekly. Daily sampled feeds were bulked fortnightly for chemical analysis and handled as in the feeding trial. In addition, hay DM was determined daily (105°C, 24 h).

Respiratory exchanges were measured weekly over 2 d in each of the four cows using two indirect, open-circuit respiratory chambers (Vermorel et al., 1973).

Diet digestibility was measured in the respiratory chambers by total fecal collection over 6 d starting 31 d after the switch in plane of feeding. Fecal samples were treated as described for the feeding trial. Urine was collected by aspiration from the fecal collection trays and stored in acid ($H_2SO_4$, 20%) for GE determination.

### *Chemical Analyses*

Organic matter was obtained by difference after ashing at 600°C for 6 h. Kjeldahl N and GE (adiabatic bomb) were determined in all feed and fecal samples. Urinary GE content was measured after freeze-drying urine samples in polyethylene bags. The ADF and lignin were analyzed according to the methods of Van Soest and Wine (1967).

Plasma samples were analyzed for NEFA (automated enzymatic method, Wako Chemicals, Unipath, Dardilly, France) and betahydroxybutyrate (Barnouin et al., 1986) concentrations. Plasma insulin, $T_3$, $T_4$, and GH levels were determined by RIA as previously described (Coxam et al., 1987).

### *Calculations and Statistical Analyses*

Body weight changes, animal behavior results, and plasma GH concentrations were analyzed by analysis of variance according to a randomized block design with a one-way factorial arrangement of treatments. The model included block and treatment. Profile of GH levels was previously treated as described by Merriam and Watcher (1982).

Changes in body condition scores and composition and in plasma hormone and metabolite concentrations with days on experiment (and with sampling hours when relevant) were analyzed by analysis of variance according to a split-plot design with time; animal was nested within treatment group (Gill, 1978). The model included treatment, animal (treatment), day, and treatment × day. The treatment factor was tested by animal (treatment), whereas the other factors were tested by the residual error mean square. The effect of sampling hour was analyzed in this model using the repeated time analysis of SAS (1987). Pre- and postprandial changes in blood data measured on d 88 were also analyzed using the repeated-time analysis of SAS (1987).

Results from the digestibility measurements obtained from three cows in each group were compared using the Student's *t*-test.

Heat production was calculated according to the method of Brouwer (1965) without including the urinary N factor. However a −1% correction in HP was subsequently applied to account for it (McLean, 1986). Thus, HP (kcal) = (3.866 $O_2$ [L, STP (standard temperature and pressure)] + 1.200 $CO_2$ [L, STP] − .518 $CH_4$ [L, STP]) × .99.

## Results

### *Animal Health*

One ruminally cannulated cow, on the L treatment, died of unknown causes on d 23 of the experimental period; it was not replaced. All other animals remained in good health, apart from acute lameness in two cows (one on each treatment). One of these animals was temporarily removed from its stall and put on straw bedding for approximately 2 wk.

### *Feeding Trial*

*Feed Composition and Intake.* Chemical composition of feedstuffs and intakes are presented in Table 1. Actual ME intakes were calculated on the basis of measured cow digestibility and calorimetry results. The latter indicated average proportions of methane and urinary energy losses from GE intake (**GEI**) of .0704 and .0467, respectively. The ME:GE ratio was thus calculated to be .37 instead of .44 as estimated initially, resulting in an ME intake that was lower than initially planned.

*Diet Digestibility.* In sheep, digestibility of the orchardgrass and timothy hays was .594 (SE = .0065, n = 6) and .505 (SE = .0088, n = 6), respectively. In cows, the whole diet was of medium DM digestibility (approximately .50, Table 2). It was on average five percentage units lower than that expected from the sheep results. Overall, diet digestibility remained unaffected by the plane of feeding and was not influenced by the duration of the adaptation to the diet (d 30 vs 91).

*Body Weight Changes.* Rates of BW change were calculated by linear regression on day of experiment (Table 3). Over the whole trial, cows on the L treatment lost weight (−468 g/d), whereas those on the H treatment gained BW slightly (+46 g/d). However, BW did not change regularly with time.

Table 1. Chemical composition of individual feedstuffs (per kg of DM, unless otherwise stated) and average intake (per d and per kg of $BW^{-.75}$ of cows offered a hay diet at two planes of feeding (low [L] and high [H])

| Item | Feedstuff[a] | | | Intake | | | |
|---|---|---|---|---|---|---|---|
| | Orchardgrass hay | Timothy hay | Soybean meal | L | H | SEM[b] | *P*-value[c] |
| Dry matter, g | 850[d] | 852[d] | 875[d] | 46.05 | 69.52 | .170 | .001 |
| Organic matter, g | 919 | 937 | 926 | 42.14 | 63.90 | .157 | .001 |
| Gross energy, kcal | 4,446 | 4,423 | 4,694 | 201.6 | 305.8 | .76 | .001 |
| Metabolizable energy, kcal | — | — | — | 74.6 | 113.2 | .28 | .001 |
| Nitrogen, g | 22.2 | 16.5 | 83.8 | .93 | 1.39 | .003 | .001 |
| Acid detergent fiber, g | 361 | 426 | 84 | 17.67 | 26.90 | .077 | .001 |

[a]Orchardgrass and timothy hays contained 37.6 and 58.3 g of lignin/kg of DM, respectively.
[b]Standard error of treatment means for n = 6.
[c]Statistical differences between treatment means.
[d]Grams per kilogram on an as-is basis.

Three periods could be distinguished upon visual examination of the BW curves.

On d 1 of the feeding trial daily feed allowances were increased by approximately .7 kg of DM for the H treatment and decreased by approximately 2.4 kg of DM for the L treatment relative to the preexperimental allowances. Consequently, BW either remained unchanged (H) or decreased (L) during the first 32 d of the feeding trial. The slight decrease in BW on the H treatment during the first 32 d was mostly due to one animal that lost 574 g/d. The average BW change of the other five animals in that group was $-9 \pm 63.4$ g/d. Subsequently, performances seemed to stabilize; all animals gained weight during the following 48-d period. Body weight gains tended to be higher on the H treatment; however, this difference was not significant. From d 80 onward all cows lost weight, but the L cows lost significantly more. The changes in performance could not be linked to any specific reason.

Ruminal fill was measured on two cows per treatment (or just one cow on the L diet on d 110 as the other had died). From the preliminary period to d 9 of the feeding trial ruminal contents had decreased by 9.4 kg on the L treatment and increased by 1.8 kg on the H treatment, resulting in an average increase of $3.46 \pm .76$ kg (range 1.3 to 5.9, n = 4) per additional kilogram of DMI. Ruminal contents were similar on d 9 and 110. These changes contributed approximately 26% to total BW loss observed in the L cows during the first 32 d. The slight increase in ruminal contents noted in the H cows could have resulted in some underestimation of their BW loss between d 1 and 32.

*Estimates of Body Composition Changes.* Initial body condition scores did not significantly differ between groups; however, the overall range of initial body scores was large, varying from 3 to 6 (Table 3). All cows lost condition linearly during the trial ($P < .001$) and similarly across the L and H treatments. There was a tendency for greater body condition loss in cows that had the highest initial scores.

Table 2. Diet digestibility in cows offered a hay diet at two planes of feeding (low [L] and high [H])

| Item | Dry matter | Organic matter | Gross energy | Nitrogen | Acid detergent fiber |
|---|---|---|---|---|---|
| Days 30 to 42 | | | | | |
| L | .512 | .540 | .498 | .407 | .586 |
| H | .500 | .528 | .486 | .414 | .566 |
| SEM[a] | .0055 | .0082 | .0072 | .0139 | .0125 |
| Significance[b] | NS | NS | NS | NS | NS |
| Days 91 to 103 | | | | | |
| L | .484 | .524 | .489 | .462 | .563 |
| H | .486 | .519 | .476 | .444 | .549 |
| SEM | .0140 | .0108 | .0142 | .0236 | .0098 |
| Significance | NS | NS | NS | NS | NS |

[a]Standard error of treatment means, n = 3.
[b]Statistical differences between treatment means; NS = not significant.

Table 3. Changes in live weights and body composition in cows offered a hay diet at two planes of feeding (low [L] and high [H])

| Item | Plane of feeding | | SEM[a] | Statistical effects[b] |
|---|---|---|---|---|
| | L | H | | |
| n | 5 | 6 | 6 | — |
| Initial live wt, kg | 641 | 645 | 6.8 | NS |
| Live wt gain, g/d | | | | |
| Days 1 to 116 | −468 | 46 | 22.2 | Trt*** |
| Days 1 to 32 | −1,120 | −103 | 73.5 | Trt*** |
| Days 32 to 80 | 153 | 315 | 49.7 | NS |
| Days 80 to 116 | −1,064 | −261 | 43.4 | Trt*** |
| Body condition score | | | | |
| Day −11 | 3.7 | 4.2 | | |
| Day 23 | 2.4 | 3.7 | | |
| | | | .23 | Day*** |
| Day 47 | 2.1 | 3.2 | | |
| Day 109 | 1.3 | 2.5 | | |
| Adipocyte size, μm | | | | |
| Day −4 | 64.0 | 60.8 | | |
| | | | 5.63 | Day*** |
| Day 109 | 36.7 | 51.5 | | |
| Body lipid, kg | | | | |
| Day −4 | 82 | 79 | | Day** |
| | | | 5.6 | |
| Day 109 | 39 | 72 | | Trt × day* |
| Body protein, kg | | | | |
| Day −4 | 100 | 100 | | Day** |
| | | | .4 | |
| Day 109 | 92 | 101 | | Trt × day*** |

[a]Standard error of treatment means.
[b]Trt = treatment effect; Day = day effect; *$P < .05$; **$P < .01$; ***$P < .001$; NS = nonsignificant.

Similar indications were obtained from adipose cell diameter measurements. Cell size decreased during the experimental period for all animals (Table 3). No significant treatment differences were detected because of a large animal variability in the H group. Over 112 d, total lipid loss was calculated to average 43.3 kg (i.e., −386 g/d) and 7.3 kg (i.e., −65 g/d) for the L and H treatments, respectively. This latter value is in the range of error of the technique (standard deviation: 14.6 kg; Robelin et al., 1989) and thus is not different from zero. Over the 112-d experimental period, a small quantity of body protein was calculated to be lost (−8.5 kg, or −76 g/d) or gained (+.8 kg, or +7 g/d) for the L and H treatments, respectively (standard deviation of the technique, 2.8 kg).

*Animal Behavior.* Overall, animals of the two groups spent a similar length of time lying (650 and 675 min/d: SEM = 5.6 for the L and H treatments,

Table 4. Time (in min) spent in different positions or activities by cows fed at two planes of feeding (low [L] and high [H])

| Item | Diet | | SEM[a] (n = 6) | Statistical effects[b] |
|---|---|---|---|---|
| | L | H | | |
| Lying down-head dropped | 145 | 85 | 18.4 | NS |
| Lying down-head up | 325 | 337 | 32.4 | NS |
| Lying down-ruminating | 180 | 253 | 29.2 | NS |
| Standing-inactive | 420 | 277 | 32.8 | NS |
| Standing-eating | 108 | 231 | 20.6 | $P < .01$ |
| Standing-ruminating | 163 | 188 | 24.5 | NS |
| Standing-miscellaneous | 99 | 69 | 18.6 | NS |
| No. of times position was changed | 10.6 | 10.2 | 1.02 | NS |

[a]Standard error of treatment means.
[b]NS = nonsignificant.

respectively) or standing (Table 4). Within each of these positions, there were some differences in activity. There was a tendency ($P < .08$) for the L cows to spend more time lying with their heads down (i.e., sleeping) than the H cows did. During the time spent standing, cows on the L treatment spent a shorter time eating (approximately 2 h less, $P < .01$) than those on the H treatment did. This was counterbalanced by a tendency for a longer time spent standing without being engaged in any specific activity ($P < .06$). Overall, L cows spent less time ruminating (343 vs 441 min/d, SEM = 1.5, $P < .05$, for the L and H treatments, respectively).

When scaling these activities on the basis of DMI, cows on the L treatment ate more rapidly (19.2 vs 25.8 min/kg of DMI) but spent more time ruminating (61.0 vs 49.6 min/kg of DMI).

*Blood Traits.* Animals on the L treatment had higher plasma NEFA concentrations ($P < .01$) than those on the H treatment throughout the experiment (Table 5). During the course of the trial, NEFA concentrations declined markedly in all animals ($P < .05$). The decline was linear in the H cows between d −3, 64, and 88 but quadratic in the L cows, for which concentrations increased between d −3 and 64 but decreased markedly between d 64 and 88. No effect of sampling hour was noted. Similarly, no time trend was noted on d 88 in the concentrations measured from 0700 to 1500.

Betahydroxybutyrate concentrations were not significantly different across L and H cows during the course of the experiment but changed with sampling hours. Two hours postprandially, they were significantly lower in animals offered the H treatment, whereas the reverse seemed to be true 6 h postprandially but only on d 88. Generally, however, variability of the measurements obtained within and across animals was large, such that overall, no significant treatment differences or time trends were detected.

The plasma hormonal balance measured in terms of $T_3$, $T_4$, insulin, cortisol, and GH was not statistically modified by treatment (Table 6). An increase in thyroid hormone concentrations (especially $T_3$) was noted at the end of the experiment, which seemed contradictory to the fact that environmental temperatures had by then become milder (d 88 of the experiment was on April 14, 1988). Linear ($T_3$ and $T_4$) and quadratic ($T_3$) changes of concentrations were noted with sampling hours ($P < .01$). Cortisol concentrations increased ($P < .01$) linearly between d −3, 64, and 88.

## *Calorimetry Trial*

*Intakes and Body Weight Changes.* Feed chemical composition remained relatively unchanged during the experimental period and no instances of feed refusals were observed. The OM, N, GE, and ADF content of feedstuffs averaged 918 g, 22.6 g, 4.45 Mcal, and 361 g/kg for the orchardgrass hay and 926 g, 83.8 g, 4.69 Mcal, and 84 g/kg for the soybean meal, on a DM basis, respectively. Average ME intakes during the same periods amounted to 93.9, 88.3, 132.9, and 136.7 kcal·kg $BW^{-.75}$·$d^{-1}$ before the change and 135.3, 129.7, 89.0, and 94.8 kcal·kg $BW^{-.75}$·$d^{-1}$ from 30 d of adaptation onward for cows 81437, 82387, 80541, and 79316, respectively. The change in plane of feeding corresponded to a sudden increase (cows 81437, 82387; LH treatment) or a decrease (cows 80541, 79316; HL treatment) in intake of approximately 46.7 kcal of ME/kg $BW^{.75}$. It should be noted that because of technical mishaps, the change in plane of feeding was delayed by approximately 7 d for two cows and the subsequent experimental period was reduced to 46 d instead of 53.

Animals lost or gained weight as generally expected from the change in plane of feeding. Body weights of cows 81437, 82387, 80541, and 79316 averaged 562, 569, 582, and 597 kg before the change in plane of feeding and 575, 587, 560, and 574 kg from 30 d of adaptation onward, respectively. A large part of these BW changes could probably be attributed to modifications in ruminal fill (Agabriel and Petit, 1987). Nevertheless, three cows out of the four lost body condition; only one animal on the LH treatment retained its condition.

*Digestibility and Partition of Energy Losses.* Average DM digestibility of the orchardgrass hay was .587 (Table 7), which was very close to the .594 value obtained with sheep. Variability of results among cows was relatively small. Urinary energy losses expressed as a percentage of GEI varied from 3.6 to 6.0%, because of some contamination of urine with feces. However, the ME:GE ratio of the diet remains, by definition, unaffected by such a contamination.

*Heat Production Changes.* Changes in HP with time are shown in Figure 1. On the HL treatment, HP dropped from 15.61 and 15.02 to average 11.54 and 11.47 Mcal/d from 30 d onward after switching the plane of feeding in cows 80541 and 79316, respectively. Most of this overall 25% decrease in HP occurred within the first 10 d. On the LH treatment, conversely, HP increased from 11.79 and 12.25 to 14.26 and 13.81 Mcal/d (cows 82387 and 81437, respectively). This 17% rise in HP was achieved within 10 d after the switch.

No further adaptation of energy metabolism with time on feed could be clearly demonstrated. Indeed, interpretation of data was limited by the fact that HP results were highly variable among days within an animal. Daily variability was calculated as the difference between the two 24-h HP measurements carried out each week. Differences averaged 4.55% of the weekly mean values and ranged from .14 to 9.73%. The variability in the HP measurements mentioned above was not attributable to technical problems in gas flow measurements or g as analysis and could,

Table 5. Postprandial changes in plasma metabolite concentrations as measured on days −3, 64, and 88 in cows offered a low (L) or a high (H) plane of feeding

| Plasma metabolite concentration and time | Plane of feeding: L d −3 | L d 64 | L d 88 | H d −3 | H d 64 | H d 88 | SEM[a] (n = 6) | Statistical effects[b] |
|---|---|---|---|---|---|---|---|---|
| NEFA, $\mu M$ | | | | | | | | |
| 0900 | 102.3 | 132.8 | 28.8 | 52.0 | 29.4 | 16.6 | | Trt** |
| 1100 | 54.2 | 137.7 | 32.8 | 46.7 | 23.3 | 24.4 | 32.75 | Day** |
| 1500 | 91.4 | 123.2 | 17.4 | 67.9 | 63.3 | 13.4 | | Trt × day** |
| β-hydroxybutyrate, $\mu M$ | | | | | | | | |
| 0900 | .19 | .20 | .19 | .18 | .22 | .20 | | |
| 1100 | .23 | .20 | .20 | .25 | .15 | .14 | .021 | NS |
| 1500 | .23 | .19 | .13 | .18 | .19 | .24 | | |

[a]Standard error of treatment means (sampling hours were pooled).
[b]Trt = treatment effect; day = day effect; **$P < .01$; NS = nonsignificant.

thus, be considered entirely as a within-animal variability at fixed intake. For each cow, respiratory quotient values remained quite stable (1.01 and 1.05 on the L and H treatments, respectively) as well as the proportions of energy lost as methane.

On the low plane of feeding, HP (expressed on a metabolic BW basis) averaged 106.1 and 101.2 kcal·kg $BW^{-.75}\cdot d^{-1}$ for cows 81437 and 82387 (LH), and 101.8 and 94.7 kcal·kg $BW^{-.75}\cdot d^{-1}$ (from 30 d of adaptation onward) for cows 80541 and 79316 (HL), respectively. On the high plane of feeding, HP amounted to 131.8 and 125.5 kcal·kg $BW^{-.75}\cdot d^{-1}$ for cows 80541 and 79316 (HL), and 114.3 and 120.4 kcal·kg $BW^{-.75}\cdot d^{-1}$ (from d 30) for cows 81437 and 82387 (LH), respectively.

## Discussion

In low-producing animals such as beef cows, in contrast with high-producing ones (e.g., dairy cows), maintenance energy requirements account for approximately two-thirds of the annual energy requirements (Petit et al., 1992). A precise knowledge of $ME_m$ and of its sources of variation is therefore necessary to improve the evaluation of feed allowances to such animals. Additionally, beef cows often undergo periods of relative underfeeding for economic reasons (Petit et al., 1992). The present study was consequently based on low levels of feeding; the latter were even lower than initially planned because of diet digestibility that was lower in cows than in sheep. The results should thus be interpreted in relation to the low planes of feeding applied.

The $ME_m$ was first calculated by linear regression of MEI on average BW gain and amounted to 109 kcal of ME·kg $BW^{-.75}\cdot d^{-1}$ ($r^2 = .88$). Other $ME_m$ estimates were obtained on the basis of individual body composition changes measured from adipocyte size. It was assumed that the energy contents of body lipid and protein were 9.45 and 5.65 kcal/g, respectively, and that body energy was used or deposited with the following efficiencies initially defined by Blaxter (1974): $k_m = .66$ and $k_f = .29$ (using $q = .37$; INRA, 1978). In these conditions, $ME_m$ averaged 126 (SE = 7.8) and 123 (SE = 10.4) kcal of ME·kg $BW^{-.75}\cdot d^{-1}$ at the low and high levels of feeding, respectively.

Similar calculations were carried out using energy balance measurements in respiration chambers on a small number of animals. Linear regression between MEI and energy balance yielded a $ME_m$ value of 112 kcal of ME·kg $BW^{-.75}\cdot d^{-1}$ ($r^2 = .79$), whereas average $ME_m$ calculated from individual energy balance data amounted to 106 (SE = 3.7) and 105 (SE = 9.7) kcal of ME·kg $BW^{-.75}\cdot d^{-1}$ at the low and high planes of feeding, respectively ($q = .45$, $k_m = .68$, $k_f = .36$; INRA, 1978).

Such an exercise points to two main methodological sources of variation in the estimation of $ME_m$. First, the mode of calculation was shown here to be

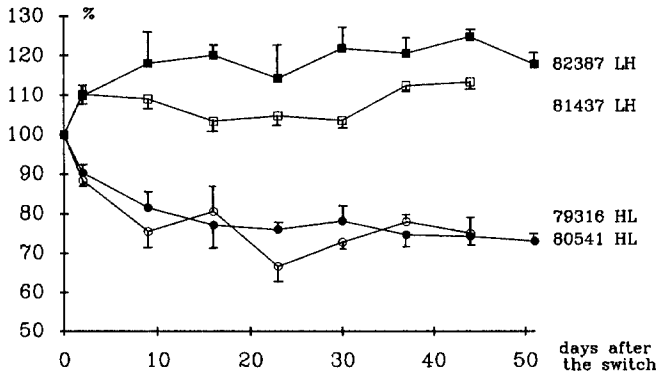


Figure 1. Changes in heat production (expressed as a percentage of the initial level) of cows after a sudden switch in plane of feeding. Each point represents the average of two consecutive 24-h measurements; half standard deviations are shown.

Table 6. Postprandial changes in plasma triiodothyronine ($T_3$), thyroxine ($T_4$), insulin, and cortisol concentrations as measured on days −3, 64, and 88 in cows offered a low (L) or a high (H) plane of feeding. Number of growth hormone (GH) secretion peaks, duration and amplitude of peaks, and baseline GH concentrations are also shown

| | Plane of feeding | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | L | | | H | | | SEM[a] | Statistical |
| Item | d −3 | d 64 | d 88 | d −3 | d 64 | d 88 | (n = 6) | effects[b] |
| $T_3$, nmol/L | | | | | | | | |
| 0900 | .66 | .60 | 1.07 | .64 | .60 | 1.16 | | |
| 1100 | .80 | .79 | 1.13 | .94 | 1.03 | 1.30 | .076 | Day*** |
| 1500 | .80 | .72 | 1.08 | .88 | .84 | 1.35 | | |
| $T_4$, nmol/L | | | | | | | | |
| 0900 | 53.0 | 44.7 | 59.3 | 48.8 | 45.8 | 60.1 | | |
| 1100 | 53.9 | 54.4 | 58.8 | 53.1 | 59.2 | 69.5 | 2.46 | Day*** |
| 1500 | 58.9 | 48.4 | 67.2 | 60.3 | 51.8 | 64.0 | | |
| Insulin, μU/L | | | | | | | | |
| 0900 | 12.7 | 15.0 | 14.7 | 12.9 | 17.0 | 14.2 | | |
| 1100 | 11.3 | 13.9 | 14.9 | 14.2 | 16.2 | 13.6 | 1.90 | NS |
| 1500 | 11.3 | 13.8 | 14.3 | 12.0 | 13.5 | 16.4 | | |
| Cortisol, ng/mL | | | | | | | | |
| 0900 | 2.95 | 3.82 | 3.79 | 2.94 | 3.34 | 4.81 | | |
| 1100 | 2.12 | 4.17 | 4.84 | 2.37 | 6.65 | 6.88 | .859 | Day** |
| 1500 | 5.36 | 2.37 | 5.64 | 5.03 | 2.90 | 5.80 | | |
| GH | | | | | | | | |
| Average concentration, nmol/mL | — | — | 352.0 | — | — | 321.3 | 33.72 | NS |
| Baseline concentration, nmol/mL | — | — | 277.2 | — | — | 282.6 | 31.99 | NS |
| No. of peaks | — | — | 3.6 | — | — | 3.2 | .577 | NS |
| Duration of peaks, min | — | — | 68 | — | — | 46 | 12.2 | NS |
| Amplitude of peaks, nmol/mL | — | — | 542.4 | — | — | 495.0 | 52.35 | NS |

[a]SEM = standard error of treatment means (sampling hours were pooled).
[b]Day = day effect; ***$P < .001$; **$P < .01$; NS = nonsignificant.

responsible for discrepancies as high as 19%. The $ME_m$ values calculated from body energy changes were similar to those measured by Ferrell and Jenkins (1984) on Charolais crosses fed above maintenance, based on body composition measurements using $D_2O$ dilution. They were slightly lower than those calculated from BW changes in lactating Charolais cows fed at levels that were approximately equal to theoretical maintenance (Petit and Micol, 1981). By contrast, energy balance measurements using indirect calorimetry produced $ME_m$ values close to those measured for nonlactating dairy cows (105 kcal of ME·kg $BW^{-.75}$·$d^{-1}$; INRA, 1978). Baker et al. (1991) measured a fasting heat production of Charolais heifers of 109 kcal·kg $BW^{-.75}$·$d^{-1}$ after adjustment for zero physical activity, implying higher $ME_m$ than those calculated here. Such discrepancies are often noted and may be due to differences in physical activity (Webster, 1989).

Second, the calorimetry measurements pointed to very large day-to-day variations (up to 10%). In absolute terms, these differences are similar to those measured in lactating dairy cows in our laboratory; however, they seem larger when expressed in relative terms (4.55 vs 2%). Daily physical activity (e.g., time spent standing) was not measured in the present calorimetry experiment but could account for the observed variability (Baker et al., 1991). Indeed, J. M. Brockway (personal communication) measured high energy costs of standing in cattle, averaging up to 287 cal·kg $BW^{-.75}$·$d^{-1}$ (range 143 to 717 cal·kg $BW^{-.75}$·$d^{-1}$). Lower energy costs of standing had previously been obtained by other authors (range 134 to 282 cal·kg $BW^{-.75}$·$d^{-1}$; Vercoe, 1973; Toutain et al., 1977).

Increasingly, evidence suggests that maintenance energy requirements vary with the level of feeding. The range of variation can be as large as 40% (Johnson, 1984). The present experiment, however, showed that heat production responded within 10 d to changes in the planes of feeding but did not result in different calculated $ME_m$ when ME intake was close to or below theoretical maintenance. By contrast, a large bulk of studies conducted with ruminants showed that fasting heat production increased with intake whether above or below theoretical maintenance (Ortigues, 1991). Much of the variation in $ME_m$ with intake seemed to be related to changes in visceral organ mass and proportion relative to shrunk BW (Jenkins et al., 1986; Ferrell, 1988). Nevertheless, there is contradictory evidence on the modifications of digestive tissue

Table 7. Diet digestibility and partition of energy losses (kcal·kg $BW^{-.75}$·$d^{-1}$) measured in Charolais cows in respiration chambers 31 days after the switch in the plane of feeding (low [L] and high [H])

| | LH | | HL | |
|---|---|---|---|---|
| Item | Cow no. 81437 | Cow no. 82387 | Cow no. 80541 | Cow no. 79316 |
| Digestibility | | | | |
| Dry matter | .593 | .588 | .589 | .576 |
| Organic matter | .613 | .602 | .601 | .596 |
| Nitrogen | .584 | .585 | .571 | .551 |
| Energy | .577 | .564 | .560 | .555 |
| ADF | .659 | .639 | .634 | .658 |
| Gross energy intake | 291.89 | 289.25 | 207.52 | 208.62 |
| Energy losses | | | | |
| Feces | 123.42 | 126.08 | 91.36 | 92.90 |
| Urine | 13.40 | 12.89 | 12.50 | 7.53 |
| Methane | 18.37 | 21.21 | 15.94 | 12.88 |
| Heat production | 108.90 | 120.65 | 102.87 | 85.86 |
| ME:GE | .47 | .45 | .42 | .46 |

mass with intake in adult cattle. Weights of the gastrointestinal tract and liver as well as their proportions relative to slaughter weight were shown to be increased by intake in Angus and Hereford crossbred cows (Jenkins et al., 1986). No similar variations were noted in Holstein-Friesian (Doreau et al., 1985) or in Holstein, Limousin, and Charolais (Robelin et al., 1990) cows. It may, therefore, be possible that the relatively small changes in intake were insufficient to modify splanchnic tissue weights and proportions in the animals used in the present study. Changes in HP with intake occur relatively rapidly. Clapperton and Blaxter (1965) showed that 2 to 3 wk were sufficient for adult sheep to adjust their gut contents and thereby their gut sizes (Burrin et al., 1990) and their heat production after a change in the plane of feeding and that no further adjustment of metabolism occurred thereafter. In the present experiment, the large day-to-day variations in heat production prevented any more precise conclusion to be drawn relative to the longer-term adaptation of energy metabolism with time on feed. Feeding experiments with growing cattle as well as modeling studies had suggested longer adaptation phenomena with time (Ledger and Sayers, 1977; Turner and Taylor, 1983).

Physical activity has an energy cost that is included in the estimated $ME_m$ requirements. Animal behavior differed slightly between treatment groups but these differences were not sufficient to significantly alter $ME_m$. Indeed, it was calculated that the difference in physical activity would account for energy requirements that would be higher by 1.4 kcal·kg $BW^{-.75}$·$d^{-1}$ for the H cows, assuming that the energy costs of eating and ruminating averaged 645 cal·kg $BW^{-.75}$·$d^{-1}$ (Webster, 1978) and 81 cal·kg $BW^{-.75}$·$d^{-1}$ (Toutain et al., 1977), respectively, and that sleep reduced energy expenditures by 86 cal·kg $BW^{-.75}$·$d^{-1}$ (Toutain et al., 1977).

Blood metabolite concentrations confirmed the absence of large metabolic differences between animals fed at 75 or 113 kcal of ME·kg $BW^{-.75}$·$d^{-1}$. When energy supply is below requirements, body tissues are mobilized and plasma NEFA and betahydroxybutyrate concentrations can be increased (Russel and Wright, 1983). Such effects were mainly observed in the L treatment of the present experiment, but they were of small magnitude. No phenomenon of adaptation of blood metabolites was measured with time. Similarly, in an experiment with pregnant ewes suffering from cold stress after shearing, no long-term changes were noted in plasma glucose, NEFA, or betahydroxybutyrate concentrations compared with concentrations in unshorn ewes (Symonds et al., 1988).

In terms of hormonal responses to a reduction in energy intake relative to requirements, reduced plasma insulin, $T_3$, and $T_4$ and increased GH concentrations are usually observed in growing ruminants (Blum et al., 1985; Waghorn et al., 1987). A reduced molar insulin:GH ratio contributes to increasing the lipolytic rate and conserving body proteins (Waghorn et al., 1987). In the present experiment, in which feeding was reduced by approximately .40 × $ME_m$, no treatment differences in plasma hormone concentrations were detected.

## Implications

The present experiment contributed to the determination of the metabolizable energy requirements for maintenance of Charolais cows kept indoors (105 to 111 kcal of ME·kg $BW^{-.75}$·$d^{-1}$). These requirements

did not seem to respond to changes in intake of the order of one-third. However, very large day-to-day variation in heat production pointed out the importance of monitoring the behavior of cattle during respiratory exchange measurements.

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