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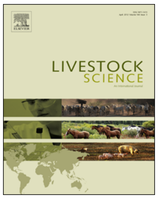

Changes in calculated residual energy in variable nutritional environments: An indirect approach to apprehend suckling beef cows' robustness

A. De La Torre [a,b,*], E. Recoules [a,b], F. Blanc [a,b], I. Ortigues-Marty [a,b], P. D'Hour [c], J. Agabriel [a,b]

[a] INRA, UMR1213 Herbivores, Saint-Genès-Champanelle 63122, France
[b] Clermont Université, VetAgro Sup, UMR1213 Herbivores, BP 10448, Clermont-Ferrand 63000, France
[c] INRA, UE1296, Unité Expérimentale des Monts d'Auvergne, Laqueuille 63820, France

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ABSTRACT

The major perturbation that beef cows have to face in extensive livestock systems is changes in feed resource availability. The ability of beef cows to face variable nutritional environments (robustness) involves adaptive processes that drive adjustments in the energy allocation toward life functions. This study proposes an indirect approach to quantify the modulation of energy allocation over a changing nutritional environment. The concept of residual energy (E_{resid}), defined as the net energy intake minus the energy secreted in milk and deposited in tissues, was used to investigate the variation in energy allocation priority for maintaining productive traits. In this study robustness was assessed by the difference in E_{resid} between cows experiencing either variable or non limiting nutritional trajectories and differing in body reserves at calving. Forty multiparous Charolais suckling cows, differing in their body condition at calving (moderate (M, $n=19$): $\mathrm{BCS_c}=2.0\pm0.04$ (scale 0–5)) vs fat (F, $n=18$): $\mathrm{BCS_c}=2.8\pm0.08$) were used. They were submitted to two energy levels during the first 120 days *post-partum* (P1): Control (MC ($n=9$) and FC ($n=9$)) vs Low (ML ($n=10$) and FL ($n=9$)). The average energy intake, expressed in net energy for lactation ($\mathrm{NE_L}$), was 90.7 and 54.7 MJ/d/cow for C and L cows, respectively. Subsequently (P2, 120–196 days *post-partum*) all the cows were turned out to a permanent pasture. BW, body condition and milk production were regularly measured in P1 and P2. Body lipid reserves were assessed at calving, end of P1 and end of P2 by measuring adipose cell diameter. The overall milk production was similar between groups of cows over the 2 phases of the changing nutritional trajectories highlighting the robustness of beef cows to achieve this function. During P1, L cows lost BW and body lipid reserves. During P2, BW and BCS gains were similar in FL and ML cows. At the end of P2, FL and ML cows weighed 20 and 10 kg less than FC and MC cows, respectively. Considering both experimental periods (P1+P2), E_{resid} was 23% lower in L than in C cows ($P<0.05$). This difference was observed regardless of $\mathrm{BCS_c}$, showing that thin beef cows withstood the change in nutritional trajectory after calving similarly to the fatter ones. E_{resid} changes reflect the ability of beef cows to preserve energy allocation toward life functions in changing nutritional environments and may be viewed as indirect criteria of robustness.

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[*] Corresponding author at: INRA, UMR1213, 63122 Saint-Genès-Champanelle, France.
E-mail address: anne.delatorre@clermont.inra.fr (A. De La Torre).

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1. Introduction

Concept of robustness is a major concern in extensive livestock production systems where animals have to cope with environmental perturbations. In its broadest definition, the robustness is a property that accounts for the ability of system to maintain its functions despite external/or internal perturbations (Kitano, 2004). At the animal level, robustness is viewed as its ability to maintain itself (i.e. survive and produce) in a broad variety of environments or to be able to face short and long-term perturbations (Knap, 2005; Strandberg, 2009). One of the major perturbations beef cows have to cope with in extensive livestock systems is changes in feed resources' availability and quality over the productive cycle. Various studies have shown that nutrition level may affect productivity traits in beef cows such as growth, milk production, reproductive performance and longevity (Blanc et al., 2006; Jenkins and Ferrell, 1994; Osoro and Wright, 1992). However, studies mainly conducted with dairy cows revealed that life functions (growth, reproduction (including pregnancy and lactation), health…) are not affected to the same extent when the female experiences undernutrition periods. In a constrained environment, trade-offs between life-functions may occur (Blanc et al., 2006; Friggens and Newbold, 2007) as adaptation to changes in nutrients availability involves modifications in nutrient partitioning. Such modifications in resource allocation will allow for varying priorities to the robustness of some of these life functions (Douhart, 2013; Friggens and Newbold, 2007; Friggens et al., 2013). Numerous studies have considered the question of energy allocation in high-producing dairy animals. Maintenance of milk yield is a good indicator of the priority given to the milk production function. Under constraining environments milk production may decrease but nutrient allocation for lactation remains a priority and may have consequences on fertility (Blanc et al., 2006; Friggens and Newbold, 2007; Martin and Sauvant, 2010). Less attention has been paid to the robustness of suckling beef cows that would take into account trade-offs between life functions and thus between production traits (Freetly et al., 2000; Johnson et al., 2003). Indeed, contrary to dairy cows, milk yield of beef cows is moderate (8–10 kg/cow/day in Charolais cows) and does not change much with underfeeding reflecting the priority given to maternal investment in calf viability (Houghton et al., 1990; Petit and Agabriel, 1993).

From a systemic point of view, the cow is considered as a dynamic system that takes up energy from the environment to maintain its functions over the productive cycle. It is well documented that energy partition changes with stage of lactation (Kirkland and Gordon, 2001) and that the various metabolic pathways, e.g. lipogenesis and lipolysis, are up or down-regulated at different stages of the productive cycle (Chilliard et al., 1998; Friggens and Newbold, 2007). The net result of such changes is that all life functions are not impacted in equal proportion when nutrient supply changes. Considering such a systemic approach, net energy fluxes can be summarized using the following equation (1) $\mathrm{EI} = E_l + E_y + E_r + E_{\mathrm{resid}}$, where EI represents the net energy intake, E_l the net energy allocated to milk yield, E_y the net energy retained by the foetus and the gravid uterus, and E_r the net energy mobilized ($E_r < 0$) or retained ($E_r > 0$) by tissues. When net energy intake is calculated from Feed Table values, the last term of this equation, E_{resid} refers to the difference between net energy intake and the theoretical energy allocated to milk production, tissue growth and reserves, so that E_{resid} accounts for energy not directly allocated to productive functions. More precisely E_{resid} and its variations, expressed in net energy for lactation, correspond to the energy for maintenance which covers fasting heat production, heat of voluntary activity and of thermal regulation and part of heat of fermentations, digestion, absorption and metabolism (Williams and Jenkinks, 2003), errors in measurements and estimations of intake ($\mathrm{NE_L}$ of milk) as well as adjustments of requirements and of partial efficiencies of utilization of diet metabolizable energy (kl, kf, kp). Individual components of E_{resid} are not easily measurable in practice. Consequently, we considered that E_{resid} reflects the adjustments in energy allocation which occur when the cow undergoes a changing nutritional trajectory and is proposed as a criteria to indirectly estimate robustness.

The objectives of this study were to investigate in beef cows (i) the difference in E_{resid} between cows experiencing a variable nutritional trajectory (energy restriction followed by refeeding) and cows experiencing a non limiting nutritional trajectory as a criteria of adjustment in energy allocation to functions other than milk production and tissue gain, and (ii) the influence of body condition at calving on E_{resid} changes.

2. Materials and methods

The experiment was carried out at the INRA experimental farm in Laqueuille (Auvergne, France) from January to July 2010. Animals were raised in conditions compatible with national legislation on animal care (Certificate of Authorization to Experiment on Living Animal no. 7740, Ministry of Agriculture and Fish Products, Paris, France) and was approved by the regional ethics committee (Approval no. A63.189.04).

2.1. Experimental design

Forty multiparous Charolais cows (5 ± 1.6 years and 802 ± 66 kg at calving) were involved. The experimental design was a 2 × 2 factorial combining two body condition scores at calving ($\mathrm{BCS_c}$, Fat (F) and Moderate (M) and two nutritional net energy levels (Control (C) and Low (L)). After calving and during the first 120 days post-partum (constraining period, P1), half of the cows experienced a nutritional restriction during the winter indoor period while the others were fed above requirements. Calving was grouped in early February. At turnout, all cows were reared at pasture in non-limiting conditions for a 76-day period (recovery period, P2, from May to end of July). Cow–calf pairs grazed the same permanent pasture, where continuous suckling was allowed. For reproduction a bull was introduced in the herd at turnout and removed after 2 months.

2.2. Constitution of initial body condition score

The two groups of cows of F or M body condition were created during a 4-month pre-experimental period (P0, from October to calving). Groups were balanced for initial BW (F: 836 ± 63 and M: 845 ± 44 kg) and expected calving date.

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Table 1
Composition of feedstuffs during the pre-experimental (P0), constraining (P1) and recovery (P2) periods.

	Hay (P0+P1)	Concentrate (P0+P1)	Grass (P2)
Dry matter (%)	87	87	17
Organic matter (g/kg DM)	897	838	932
Organic dry matter digestibility (%)	59[a]	70[b]	74[c]
Crude protein (g/kg DM)	98	210	170
Fill value[d] (kg DM)	1.20	–	1.13
Net energy for lactation (MJ/kg DM)	4.6	7.5	6.8

[a] Measured in castrated adult rams fed ad libitum according to standard INRA (2007) procedures.

[b] Calculated from chemical composition.

[c] Calculated from pepsin-cellulase in vitro digestibility.

[d] Fill value: reference unit of the ingestibility of feedstuffs as defined by Jarrige (1989) and INRA (2007).

Differences in body condition were obtained by supplying two levels of a common hay and commercial concentrate diet. Hay was good quality collected from permanent mountain pasture, first cut, at the beginning of the heading stage (Table 1). Amounts of hay and concentrate offered averaged per day and per cow: 10 and 4 kg DM for the F groups and 10 kg and 1 kg DM for the M groups, respectively. BCS was assessed every fortnight by two experienced assessors on a 0–5 scale (Agabriel et al., 1986). At the end of P0 (at calving), BW and BCS_c of F and M cows differed by about 100 kg of body weight and 0.8 point of body condition score (Tables 3 and 4).

2.3. Diets and rations during the constraining and recovery periods

Two weeks after parturition, F and M cows were randomly allocated to one of the two energy levels: C (120% of theoretical recommended requirements, INRA, 2007) or L (70% of theoretical recommended requirements). These two energy levels were maintained throughout the constraining period. Diets were composed of permanent pasture hay and a commercial concentrate (INRA Bufflo Vital, Groupe Altitude, 15000 Aurillac, France) in the following proportions: 70/30 for the C diet and 90/10 for the L diet. Chemical composition of hay and commercial concentrate are given in Table 1. Net energy allowances averaged 580 and 340 kJ/d/kg $BW^{0.75}$ for the F and M groups, respectively. Rations were balanced in nitrogen supply according to INRA recommended requirements (INRA, 2007).

During the recovery period, cow–calf pairs were all reared in a rotational pasture grazing system providing good quality and non-limiting grass. Pasture was representative of permanent pasture usually found in upland areas in the Auvergne region, with little or no fertilization (0 to 40 kg N/ha). Grass height measurements were made before and after pasture change using an electronic plate meter. Decisions to move from one plot to the next one depended on sward height (min value: 5 cm).

2.4. Measurements, chemical analyses and calculations

2.4.1. Feeds

During the constraining period, representative samples of offered hay and concentrate were taken twice weekly and pooled for chemical analyses. During the recovery period, representative grazed herbage was manually collected every week, dried in an oven (60 °C, 72 h). Samples were milled through a 0.85 mm mesh and analysed for DM, OM, nitrogen, cellulose as described in Ortigues et al. (1993), and in vitro digestibility using the pepsin-cellulase method (Aufrère et al., 2007). Separate feed samples were taken for DM determination (103 °C, 24 h). These analyses were used to estimate the nutritive value of offered diets and grazed pasture, and the fill value of grass) (INRA, 2007). The energy value of feeds and diets was expressed in NE_L according to INRA (2007).

2.4.2. Intake

During the constraining period, the amounts of feed offered and refused were weighed every day. During the recovery period, energy intake was individually estimated using the INRA Fill Unit system (Jarrige, 1989) as described by Faverdin et al. (2011). The Fill Unit system consists in separately predicting the intake capacity of each cow and the fill value of diets according to the references provided in the INRA (2007) tables. The Intake Capacity expressed in Fill Unit system was individually calculated as being equal to $3.2+(0.015\times BW_{calving})+(0.25\times \text{milk production (kg)})-[BCS\times BW_{calving}\times(BCS-2.5)]$, where $BW_{calving}$ corresponds to the body weight (kg) after calving, milk production measured over P2, and BCS measured by handling as described previously (0–5 scale). Herbage intake (kg DM/cow/d) was individually estimated by calculating the intake capacity/grass fill value ratio.

2.4.3. Diet digestibility

During the recovery period digestibility of rations was measured in all cows using the ytterbium oxide (Yb_2O_3) method (Delagarde et al., 2010). Each cow was orally dosed twice a day (at 0800 h and 1600 h) for 10 consecutive days with a capsule containing 1 g of Yb_2O_3 powder using a veterinary dosing gun. During the last 5 days of this dosing period, grab samples of faeces were collected twice a day. All morning and all evening faecal samples were pooled separately for each cow. They were analysed for DM and Yb_2O_3 content by the method of Ellis et al. (1982). Faecal dry matter output was calculated for each faecal sample by dividing the daily amount of Yb_2O_3 by its corresponding faecal concentration.

2.4.4. Milk production

Milk production was measured every two weeks by the weigh-suckle-weigh method (Le Neindre and Dubroeucq, 1973) over both the constraining and recovery periods. During the constraining period, calves were housed in a separate pen near their dams and were allowed to suckle twice a day (at 0800 h and at 1600 h). During the recovery period, calves were separated from their dams the evening prior to the measurement days. On each measurement day, calves were allowed to suckle twice a day (at 0800 h and at 1600 h). Calves were weighed before and after each suckling.

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Table 2
Dry matter intakes, dry matter digestibility and net energy for lactation (NE_L) intake per cow and per day: influence of body condition score at calving (BCS_c) and energy level supplied during the constraining period (P1).

	BCS_c[a]	Moderate		Fat	
	Energy level[b]	Control	Low	Control	Low
P1	Hay (kg DM/d)	10.7 ± 0.1	8.9 ± 0.4	11.3 ± 0.5	9.7 ± 0.4
	Concentrate (kg DM/d)	4.8 ± 0.1	1.0 ± 0.2	5.1 ± 0.3	1.3 ± 0.1
	Digestibility of DM (kg/kg)	0.61 ± 0.03	0.57 ± 0.02	0.60 ± 0.03	0.57 ± 0.04
	NE_L (MJ/cow/day)	87.7 ± 5.5	48.9 ± 2.6	90.7 ± 4.8	54.7 ± 1.7
P2	NE_L (MJ/cow/day)	78.4 ± 3.4	80.8 ± 4.0	78.8 ± 4.3	77.5 ± 3.9

P2 = recovery period.

[a] BCS_c = Body condition score at calving; Moderate: $BCS_c = 2.0 \pm 0.04$ and Fat: $BCS_c = 2.8 \pm 0.08$.

[b] Energy levels: energy level supplied during constraining period (P1, from 0 to 120 days post-partum); Control = 120% of theoretical requirements and Low = 70% theoretical requirements.

Table 3
Average milk yield (kg/d), calf birth weight (kg) and calf growth weights (kg/d) during the constraining (P1) and recovery (P2) periods: influence of body condition at calving (Moderate vs Fat) and post-partum energy level applied during P1 (from 0 to 120 days post-partum).

	BCS_c[a]	Moderate		Fat		SEM	*P* effects		
	Energy level[b]	Control	Low	Control	Low		BCS_c	Energy	BCS_c × Energy
Average milk yield (kg/d)	P1[c]	9.2	7.0	8.3	8.7	0.6	ns	ns	ns
	P2[d]	7.6	7.1	6.0	6.8	0.6	ns	ns	ns
Average calf birth weight (kg)	P1	48.0	52.0	48.0	52.0	3.2	ns	ns	ns
Average calves growth rates (kg/d)	P1	0.9	0.7	0.8	0.9	0.1	ns	ns	ns
	P2	0.9	0.8	0.9	1.0	0.1	ns	ns	ns

[a] BCSc = Body condition score at calving; Moderate: BCSc = 2.0 ± 0.04 and Fat: BCSc = 2.8 ± 0.08.

[b] Energy levels: energy level supplied during P1 (from 0 to 120 days post-partum); Control = 120% theoretical requirements and Low = 70% theoretical requirements.

[c] $n = 7$ measurements.

[d] $n = 6$ measurements.

Table 4
Body weight, adipose cell diameter (ACD), body condition score (BCS) and the percentage of lipids in empty body weight at calving, end of constraining period (P1) and end of recovery period (P2): influence of body condition at calving (Moderate vs Fat) and post-partum energy level applied during P1 (from 0 to 120 days post-partum).

	BCSc[1]	Moderate		Fat		SEM	*P* effects		
	Energy level[2]	Control	Low	Control	Low		BCS_c	Energy	BCS_c × Energy
Calving	BW[3]	760^{a}	753^{a}	846^{b}	852^{b}	17.6	*	ns	ns
	ACD[4]	54.9^{a}	52.9^{a}	79.2^{b}	80.6^{b}	3.1	***	ns	ns
	BCS[5]	2.0^{a}	1.9^{a}	2.8^{b}	2.8^{b}	0.1	***	ns	ns
	% Lipids in EBW[6]	10.7^{a}	10.7^{a}	14.2^{b}	14.4^{b}	0.4	***	ns	ns
End of P1	BW[3]	762^{ab}	720^{b}	835^{a}	810^{ab}	18.1	*	***	ns
	ACD[4]	61.7^{a}	45.2^{b}	84.7^{c}	71.4^{d}	2.4	***	***	ns
	BCS[5]	1.9^{a}	1.7^{a}	2.9^{b}	2.5^{b}	0.1	***	***	ns
	% lipids in EBW[6]	11.3^{a}	9.6^{b}	14.6^{c}	12.8^{d}	0.4	***	***	ns
End of P2	BW[3]	767	776	805	824	19.3	ns	ns	ns
	ACD[4]	67.2^{a}	56.3^{b}	86.4^{c}	70.6^{a}	3.1	***	***	ns
	BCS[5]	2.2^{ac}	2.0^{a}	2.8^{b}	2.5^{bc}	0.1	*	***	ns
	% lipids in EBW[6]	12.3^{ac}	11.0^{a}	14.8^{b}	13.4^{bc}	0.5	***	*	ns

^{abc}Values within a row with different superscripts differ significantly at $P < 0.05$.

[1] BCS_c = Body condition score at calving; Moderate: $BCS_c = 2.0 \pm 0.04$ and Fat: $BCS_c = 2.8 \pm 0.08$.

[2] Energy levels: energy level supplied during P1 (from 0 to 120 days post-partum); Control = 120% theoretical requirements and Low = 70% theoretical requirements.

[3] BW = body weight in kg.

[4] ACD: adipose cell diameter in μm.

[5] BCS: body condition score (0–5 scale).

[6] % lipids in EBW: percentage of lipids in empty body weight.

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As milking suckling beef cows is difficult in practice and that suckled milk composition is not well-known, we have considered that the content of energy of milk consumed by the calf was 3.2 MJ of NE_L/kg of milk, which corresponds to 42 g of fat/kg of milk and 33 g of protein/kg of milk (INRA, 2007) in both C and L energy level treatments.

2.4.5. *Body weight and body condition*

During the constraining period, cows were weighed twice a week at 1300 h with no prior feed withdrawal. During the recovery period, body weights were recorded once a week in the morning (0900 h). Body condition was assessed twice a month by the same two experienced assessors on a 0–5 scale (Agabriel et al., 1986).

2.4.6. *Adipose cell diameter and plasma NEFA concentrations*

Subcutaneous adipose tissue was collected by biopsy on the rump after local anaesthesia (4 mL of lidocaine/cow) at calving (start of the constraining period), turnout (end of the constraining period) and end of the recovery period. Adipose tissue samples were placed at 37 °C and fixed with osmium tetroxide as described by Robelin (1981). Adipocytes were dispersed in 8 M urea solution, and macroscopy was performed to determine the diameter of approximately 300 adipose cells with Optimas software (Optimas Corp., Bothell, WA).

During the constraining period, caudal vein blood samples were collected into evacuated EDTA tubes (Venosafe, TERUMO, EUROPE) once a week before diet distribution, and centrifuged immediately (4000g for 15 min at 20 °C). The harvested plasma was stored at −20 °C until assessment for non-esterified fatty acids (NEFA) by enzymatic colorimetry method (NEFA C Wako method).

2.4.7. *Estimation of body composition, energy retained in tissues and calculated E_{resid}*

EBW was calculated from BW according to the allometric equation proposed by Robelin and Daenicke (1980): $EBW = c_0 \times BW^{C1}$ where $c_0 = 0.8284$ and $c_1 = 0.8384$. These values for coefficients c_0 and c_1 correspond to large frame size beef cows (height at withers in the range 140–150 cm, Garcia and Agabriel, 2008). Total adipose tissue weight (TAD, % EBW) and empty body lipid weight (LIP, kg) were calculated from adipose cell diameter (ACD, μm) using equations proposed by Garcia and Agabriel (2008) based on a Charolais dissection: $TAD = 5.211 \times \exp^{(0.0114 \times ACD)}$ and $LIP = 1.134 \times TAD^{0.992}$. Empty body protein weight (PROT) was deduced from EBW and LIP by $PROT = (EBW - LIP) \times 0.20$, it being assumed that the composition of fat-free mass was 20% protein and 80% water (Hoch and Agabriel, 2004).

The energy retained in tissues (E_r) as fat and protein can be either mobilized ($E_r < 0$) or deposited ($E_r > 0$) in body reserves. E_r was expressed in the same unit as energy intake, namely NE_L. When cows mobilized body reserves, E_r was calculated for each relevant period by: $E_r = [((\text{LIP final} - \text{LIP initial}) \times 39.2\ \text{MJ}) + ((\text{PROT final} - \text{PROT initial}) \times 22.9\ \text{MJ})] \times 0.8$ assuming that body reserves are used for lactation with a partial efficiency of 0.8 (INRA, 2007). Inversely, when cows gained body reserves, E_r was calculated as $E_r = [((\text{LIP final} - \text{LIP initial}) \times 39.2\ \text{MJ}) \times 0.6)/0.6] + [((\text{PROT final} - \text{PROT initial}) \times 22.9\ \text{MJ} \times 0.6)/0.35]$ assuming that the efficiency of utilization of metabolizable energy for fat and protein deposition is 0.6 and 0.35, respectively and the efficiency of utilization of metabolizable energy for lactation is 0.6 (Geay, 1984; INRA, 2007).

E_{resid} (expressed in NE_L) corresponds to the energy intake minus the energy for milk and tissue growth ($E_r > 0$) or mobilization ($E_r < 0$), and was calculated from equation 1: $E_{resid} = EI - (E_l + E_y + E_r)$, where EI is the net energy intake (MJ/cow/d), E_l is the net energy secreted in milk, E_y the net energy retained by the foetus and the gravid uterus and E_r is the net energy retained or mobilized by tissues. For each cow, E_{resid} was calculated over both the constraining and recovery periods. The energy needed for conceptus growth was not taken into account in the E_{resid} calculation, as reproduction was late, beginning only mid-P2.

2.5. *Statistical analyses*

Data were analysed separately for the constraining and recovery periods. They were all analysed by ANOVA according a 2 × 2 factorial design with two main fixed effects: BCS_c and energy levels of diet, and their interaction plus one random effect: the animal using the appropriate MIXED procedure with a covariance structure of compound symmetry and a Satterthwaite degrees of freedom method (SAS, 2010).

More specifically this model was used for digestibility of diet, adipose cell diameter and all variables of body composition (percent of lipids in EBW, changes in EBW and in retained energy in fat and fat-free masses) and $E_{resid.}$ When serial measurements were performed within each experimental period (BW, Milk production, ADG of calves, body condition and plasma NEFA concentrations) a repeated measures procedure was added to the model. Treatment means were compared by the Tukey's test. Rates of change with time within each experimental period in BW and NEFA plasma concentrations were analysed by a linear mixed procedure, using BW at calving and NEFA concentration at calving as an intra-group covariable, respectively.

Because of a few missing data (see Section 3) all values were expressed as least square means (Lsmeans) with standard error of the mean (SEM). Groups were considered to differ when $P < 0.05$.

3. Results

Due to ill-health of their calves, three cows were removed from the experiment, leaving 37 cow–calf pairs. Hence, the four treatment groups studied over the nutritional challenge (P1+P2) were: Fat Control (FC, $n=9$), Fat Low (FL, $n=9$), Moderate Control (MC, $n=9$) and Moderate Low (ML, $n=10$).

3.1. *Diet composition and intake*

The net energy and fill values of dietary ingredients calculated from chemical composition results are reported in Table 1.

During the constraining period, the average energy intakes of C groups was 1.7 fold higher than that of L groups as

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planned (Table 2). DM digestibility was numerically higher for the C diet reflecting the higher proportion of concentrates as compared to the L diet. It did not differ according to BCS_c ($P=0.54$) supporting the hypothesis that the net energy value of diets did not differ with body condition.

During the recovery period, grass intake predictions based upon BW, BCS and milk yield did not suggest any differences between treatments (Table 2).

3.2. *Milk production and calf average daily gains*

Over both experimental periods (P1 + P2), the average milk production of groups ranged from 6.0 to 9.2 kg of milk/d (Table 3). Milk yield of MC cows was numerically the highest (9.2 kg of milk/d) but not statistically different from the other groups (Table 3). Peak of milk production was observed between weeks 4 and 6. Average calf birth weight was similar between groups and calf growth averaged 0.8 ± 0.09 kg/d during the constraining period and 1.1 ± 0.11 kg/d during the recovery period.

3.3. *Body weight dynamics*

Two weeks after parturition, BW of F and M cows differed by 93 kg ($P<0.05$, Table 4 and Fig. 1). During the constraining period, significant differences in BW were observed only between FC and ML groups, intermediate values were noted for the two other groups (Fig. 1). At the end of this period, the differences in BW between C and L groups reached 43 kg in M cows and 25 kg in F cows ($P<0.05$). Changes in BW with time over this period differed ($P<0.01$). The C energy level treatment led compared to weight gain ($+0.021 \pm 0.04$ kg/day) in M cows and compared to weight loss (-0.09 ± 0.03 kg/day) in F cows ($P<0.001$). The L energy level resulted in weight loss which was lower ($P<0.001$) in M cows (-0.28 ± 0.03 kg/day) than in F cows (-0.35 ± 0.04 kg/day). During the recovery period, BW recovery was significantly greater in the ML group ($+0.74 \pm 0.09$ kg/day over the period) than in the other groups (FC: -0.31 ± 0.09 kg/day, MC: $+0.06 \pm 0.08$ and FL: $+0.2 \pm 0.09$ kg/day, respectively). At the end of the experiment, the difference in BW observed at the start was numerically halved from 20 to 9 kg between F and M cows, respectively (Table 4, Fig. 1).

3.4. *Body lipid reserves dynamics*

At calving, BCS and adipose cell diameter measurements, as well as the amount of body lipids in EBW, confirmed expected differences in body lipid reserves between M and F cows ($P<0.001$, Table 4). BCS_c was significantly lower in M than in F cows (2.0 ± 0.04 and 2.8 ± 0.08, Table 4). Adipose cell diameters were 32% lower in M than in F cows (53.4 ± 1.7 vs 78.1 ± 1.7, $P<0.001$), and body lipids calculated in EBW were 25% lower in M cows (10.7 ± 0.3% vs 14.3 ± 0.3%, $P<0.001$). At the end of P1, body lipid reserves of cows differed between BCS_c (M vs F) and energy level treatments (L vs C) ($P<0.001$, Table 4). The M cows showed lower ACD, BCS and percent of lipid in EBW than F cows ($P<0.001$). L energy level resulted in a decrease of 26% of ACD in M and 15% in F cows ($P<0.001$) respectively during P1. The combined effects of BCS_c and *post partum* energy level resulted in a decrease in the proportion of lipids in EBW of 15% in M cows and 12% in F cows at the end of P1. At the end of P2, ACD of L cows was significantly lower than that of C cows whatever the BCS_c. BCS and estimation of percentage of lipids in EBW did not differ between the two energy levels within the M and F groups (Table 4). Only the cows belonging to the most contrasting BCS_c and energy level treatment groups (ML vs FC) presented significant differences in body lipid reserves (Table 4). Over the recovery period, the recovery of body lipid reserves was proportionately highest in ML cows (ACD: +24.5%, $P<0.05$; % lipids in EBW: +14.6%, $P<0.01$) (Table 4).

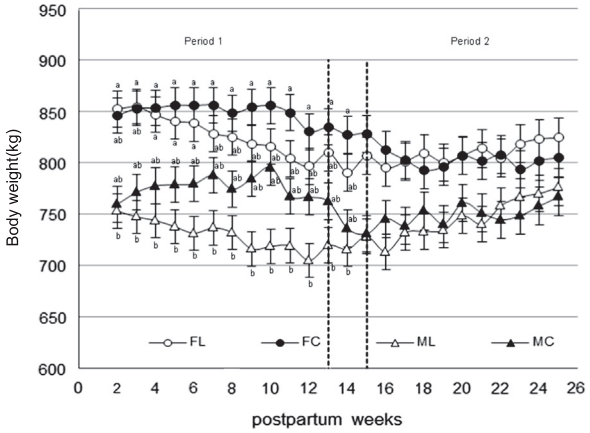

Fig. 1. Time course of mean body weight during constraining (P1) and recovery periods (P2) according to the body condition at calving (Moderate, M, $BCS_c=2.0 \pm 0.04$ vs Fat, F, $BCS_c=2.8 \pm 0.08$, $P<0.0001$) and the *post partum* energy level applied during P1 from 0 to 120 days *post partum* (Control = 120% theoretical requirements and Low = 70% theoretical requirements).

Variations of plasma NEFA concentrations throughout the constraining period are depicted in Fig. 2. At parturition, mean NEFA concentrations did not differ significantly between F and M cows (0.31 ± 0.04 vs 0.23 ± 0.05 mmol/L). The L energy level treatment resulted in an increase of plasma NEFA concentrations for the M and F groups, with peak values reached during the first month of lactation (0.47 ± 0.09 and 0.45 ± 0.07 mmol/L, respectively). NEFA concentrations in L groups decreased thereafter, with a high variability between cows. In both C groups (FC and MC), NEFA concentrations remained at a low and similar level during the constraining period (0.13 ± 0.027 and 0.14 ± 0.027 mmol/L in FC and MC groups, respectively).

3.5. *Changes in body composition and energy allocation*

Changes in body composition and estimates of E_r and E_{resid} during both experimental periods are reported in Table 5. During the constraining period, variations in EBW, fat and protein masses differed only according to the energy level treatment ($P<0.01$). Variations in EBW during this period were higher in L than in C cows whatever the BCS_c (-33.5 vs $+2.5$ kg in ML and MC respectively and -42.5 vs -11.4 kg in FL and FC respectively, Table 5). Such variations were also observed for fat and protein masses. The C cows showed a slight decrease in protein mass (MC: -0.2 ± 1.96 and FC: -2.5 ± 1.96 kg) and a low gain of fat mass (MC: 3.4 ± 2.59 and FC: 1.2 ± 2.59 kg) (Table 5).

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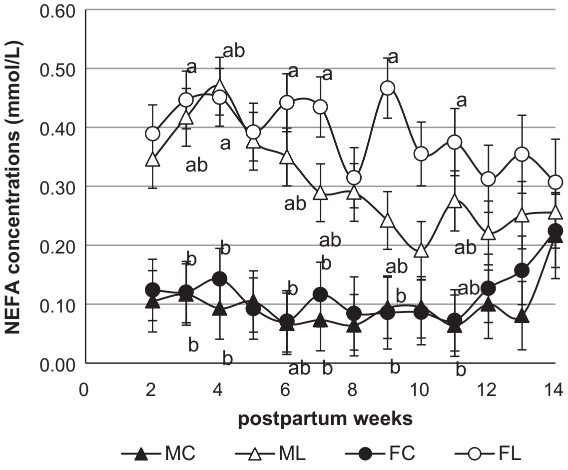

Fig. 2. Time course of plasma concentrations of non-esterified fatty acid (mmol/L) over P1 according to body condition at calving (Moderate, M, $BCS_c=2.0\pm0.04$ vs Fat, F, $BCS_c=2.8\pm0.08$, $P<0.0001$) and the *post partum* energy level applied during P1 from 0 to 120 days *post partum* (Control = 120% theoretical requirements and Low = 70% theoretical requirements).

As expected, during the constraining period EI was 1.45 and 1.3 times higher in MC and FC cows than in ML and FL cows, respectively. Expressed per metabolic BW, these intakes were close to planned values (0.60 vs 0.42 $MJ/d/kg^{0.75}$ in the M group and 0.68 vs 0.51 $MJ/d/kg^{0.75}$ in the F group). Body composition changes led to positive or negative variations in net energy retained in tissues (E_r). E_{resid} was affected both by BCS_c and the post-partum energy level treatment during the constraining period ($P<0.001$). The L energy level decreased E_{resid} compared with the C level by 25% and 27% in M and F cows, respectively (MC: 0.35 vs ML: 0.26 and FC: 0.47 vs FL: 0.34 $MJ/d/kg\ BW^{0.75}$, $P<0.001$). During the recovery period, EBW, body composition changes and E_r were affected by both BCS_c and energy level treatment ($P<0.01$). During the recovery period, EBW decreased in FC cows (-29.8 kg) in contrast to the three other groups, where EBW variations ranged from $+4.7$ to $+56.5$ kg (Table 5). The decrease in EBW in FC cows was linked with a decrease in both fat (-3.3 kg) and protein masses (-5.3 kg). In the three other groups (FL, MC and ML), a significant reconstitution of both fat and protein masses was observed during the recovery period (Table 5), and resulted in positive values of E_r. During the recovery period, E_{resid} was lowest in ML cows (0.36 ± 0.08 MJ of $NE_L/d/kg\ BW^{0.75}$) and highest in FC cows (0.49 ± 0.07 MJ of $NE_L/d/kg\ BW^{0.75}$). MC and FL cows showed intermediate values (0.41 ± 0.08 and 0.43 ± 0.05 MJ of $NE_L/d/kg\ BW^{0.75}$). This E_{resid} ranking of groups ($ML<MC=FL<FC$, $P<0.05$) was also observed over the overall experiment (P1 + P2), with values ranging from 0.32 to 0.49 $MJ/d/kg\ BW^{0.75}$ (data not shown).

4. Discussion

According to the concept of reaction norm (Bryant et al., 2006), robustness in cows is defined as the capacity to maintain function and resilience when facing environmental disturbances (Strandberg, 2009). Such a capacity relies on adaptive abilities of animals that may involve trade-off between life functions when the environment becomes limiting (Blanc et al., 2006, 2013; Friggens and Newbold, 2007). Maintaining milk production in suckling beef cows despite feed restriction reflects prioritization for this function and robustness. This study used an indirect approach to evaluate the modulation of energy allocation in lactating mature beef cows. The difference of residual energy between the non limiting and the changing nutritional trajectories (ΔE_{resid}) calculated over the entire experiment reflects changes in energy allocation to life functions. This criterion was evaluated by comparing groups following different trajectories because ΔE_{resid} cannot be calculated for each individual cow.

The choice was made to express E_{resid} as a net energy value in line with the INRA feed evaluation system. Interpretation of absolute values of E_{resid} depends on it; nevertheless, it is possible to compare the relative values between groups according to the nutritional trajectory of cows and their body condition at calving.

The dietary energy intake over the constraining period was calculated for the two feeding treatments. No differences in diet digestibility were observed between groups of cows, which suggests that variations in E_{resid} are not due to differences in digestibility. During the recovery period, EI was estimated for each cow according to the fill unit system applied at grass as proposed Faverdin et al. (2011). As cows were managed together on the same plots, errors in estimations of EI were assumed to be equal between groups of cows.

In this trial, the milk production did not differ significantly between groups. Few data are available concerning milk composition in beef cows. In dairy cows, the composition of milk and especially the protein content vary with the level of energy intake (Coulon and Remond, 1991). Variations in protein content averaged 0.08 g per kg of milk/MJ of ME of diet. By contrast, variations in milk fat content are independent of variations in milk production and protein content (Coulon and Remond, 1991). Milk fat content is affected by numerous factors such as the proportion of concentrate in diet, its composition and the feed distribution. However, when the proportions of concentrate in diet increased from 0 to 40%, variations in fat content were relatively small increasing by 0.04 g/kg/MJ of ME which only tends to compensate the decrease in milk energy content due to the decrease in protein content (Journet and Chilliard, 1985). In our experimental conditions, it is not possible to determine the milk composition. During the first month of the constraining period, L cows mobilized body fat (Fig. 2) which may increase milk fat content, nevertheless the milk yield production being moderate and to simplify, we assumed that milk composition was constant whatever the BCS_c and energy level supplied. The energy secreted in milk was then assumed to be similar between groups. This result suggests the priority of energy allocation in favour of the preservation of milk production when the energy provided by the environment is limited. If validated by direct measurements in future studies, this would confirm the priority of the lactation function (maternal investment) in suckling beef cows. Such a priority would imply that the energy allocation among life functions other than lactation has been modified.

Amounts and variations between C and L treatments in calculated E_{resid} have been observed between groups of cows and ranged from 12 to 27% according to body condition at

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Table 5

Empty body weight changes, fat and protein mass (kg) changes, energy intake (EI), energy in milk production (E_l), energy in body tissues (E_r) and residual energy (E_{resid}) during constraining (P1) and recovery (P2) periods: influence of body condition at calving (Moderate vs Fat) and post-partum energy level applied during P1 (from 0 to 120 days post-partum). All energy variables are expressed in NE_L.

	BCS_c[1]	Moderate		Fat		SEM	*P* effects		
	Energy level[2]	Control	Low	Control	Low		BCS_c	Energy	$BCS_c \times$ Energy
over P1	EBW change (kg)[3]	2.5^{a}	-33.5^{ab}	-11.4^{ab}	-42.5^{b}	11.3	ns	**	ns
	Fat mass change (kg)	3.4^{a}	-10.2^{b}	1.2^{a}	-15.6^{b}	2.6	ns	***	ns
	Protein mass change (kg)	−0.2	−4.7	−2.5	−5.4	2.0	ns	ns	ns
	EI (MJ/d)[4]	73.7^{a}	50.7^{b}	88.0^{c}	65.7^{d}	1.2	***	***	ns
	E_l (MJ/d)[5]	29.2	22.2	26.6	27.2	1.9	ns	ns	ns
	E_r (MJ/d)[6]	1.5^{a}	-3.4^{b}	0.4^{a}	-4.9^{b}	1.0	ns	***	ns
	E_{resid} (MJ/d)[7]	43.0^{a}	31.8^{b}	60.9^{c}	43.4^{a}	1.7	***	***	ns
	E_{resid} (MJ/d/kg BW ^{0,75})[8]	0.35^{a}	0.26^{b}	0.47^{c}	0.34^{a}	0.02	***	***	ns
over P2	EBW change (kg)[3]	4.7^{a}	56.5^{b}	-29.8^{ab}	14.6^{ab}	13.7	**	***	Ns
	Fat mass change (kg)	7.1^{ab}	14.1^{a}	-3.3^{b}	5.6^{ab}	3.8	**	**	ns
	Protein mass change (kg)	-0.5^{a}	8.5^{b}	-5.3^{a}	1.8^{ab}	2.4	*	***	ns
	EI (MJ/d)[4]	78.8	77.5	74.4	80.8	1.3	ns	ns	ns
	E_l (MJ/d)[5]	24.3	22.3	18.6	21.7	1.9	ns	ns	ns
	E_r (MJ/d)[6]	4.1^{a}	11.6^{ab}	-2.2^{b}	4.3^{ab}	2.3	**	**	ns
	E_{resid} (MJ/d)[7]	50.4^{ab}	43.5^{a}	62.1^{b}	54.8^{ab}	3.0	**	*	ns
	E_{resid} (MJ/d/kg BW ^{0,75})[8]	0.41^{ab}	0.36^{a}	0.49^{b}	0.43^{ab}	0.03	**	*	ns

[abc] Values within a row with different superscripts differ significantly at $P < 0.05$.

[1] BCS_c = Body condition score at calving; Moderate: $BCS_c = 2.0 \pm 0.04$ and Fat: $BCS_c = 2.8 \pm 0.08$.

[2] Energy level: energy level supplied during P1 (from 0 to 120 days post-partum); Control = 120% theoretical requirements and Low = 70% theoretical requirements.

[3] EBW: body weight.

[4] EI: energy intake (measured over P1 and estimated over P2) expressed in megajoules per day of net energy for lactation.

[5] E_l: energy for milk production expressed in megajoules per day of net energy for lactation.

[6] E_r: energy retained in tissues expressed in megajoules per day of net energy for lactation.

[7] E_{resid}: energy residual corresponding to the energy intake minus the energy for milk and tissue growth expressed in megajoules per day of net energy for lactation.

[8] E_{resid}: energy residual corresponding to the energy intake minus the energy for milk and tissue growth expressed in megajoules per day and per kg of body metabolic weight of net energy for lactation.

calving and the period. Changes in body composition and energy expenditures could be involved in this response to the nutritional challenge as proposed by Williams and Jenkinks (2003) in their model of energy utilization in mature cattle. At the end of the constraining period, E_{resid} in the low energy feeding level cows was lower than in control energy level cows (close to −25%) regardless of BCS_c. Such variations in E_{resid} could be partly explained by variations in heat production losses and in maintenance requirements linked with body composition changes. Indeed, a similar decrease in heat production (measured in respiratory chambers) due to a low feeding level was previously observed in mature non-pregnant non-lactating Charolais (Ortigues et al., 1993) or composite cows (Freetly and Nienaber, 1998). In these two studies, a non-linear weight loss pattern occurred within the first 14 days after the feeding level change and no further adaptation of energy metabolism with time was reported (Ortigues et al., 1993). A similar dynamic pattern of body weight change was observed in the present study for L cows. BW changes are associated with variations in adipose reserves. The fat loss in L groups was confirmed by both the decrease in ACD and the increase in plasma concentrations of NEFA within the first 28 days after the beginning of feed restriction as previously noticed by Agenas et al. (2006). Variations over time in the amounts of body adipose tissue as indicated by NEFA concentrations followed a similar pattern to body weight, with a rapid decrease early after the start of feed restriction followed by a slower decrease as feed restriction was prolonged.

During the recovery period, amounts of E_{resid} were higher than those calculated over the constraining period in both L and C feeding levels. Nevertheless, a 12% difference between the two nutritional trajectories remained whatever the BCS_c. These observations are certainly in part linked to an increase in intake and a process observed in recovery growth called rebound (Hoch et al., 2003; Hornick et al., 2000). When the nutritional constraint is removed, a lag is observed before the gradual increase in the energy metabolism that will enable the underfed cows to recover their weight and body condition (Agabriel and Petit, 1987; Freetly et al., 2000). Although varying according to many factors, this delay in energy metabolism recovery occurred within the first month of the recovery period (Freetly and Nienaber, 1998). During this period, body weight gain changes were almost linear. At the end of this latter, underfed cows had recovered a large part of their initial body weight and body condition.

Considering both experimental periods (P1 + P2, 196 days), a low feeding level followed by a recovery period at pasture resulted in a decrease of more than 20% of E_{resid} in both moderate and fat cows, without affecting milk production, final body weight or body condition. These results suggest that changing nutritional trajectories (underfeeding/refeeding) resulted in differences in energy allocation between functions and modulated the available nutrient partitioning and use in response to environmental pressure (Friggens and Newbold, 2007). From a practical point of view, a robust cow keeping its milk production constant when feed allowances are restricted will have a lower E_{resid}. In this respect, E_{resid} could be a useful indicator of robustness.

In our study, no interaction between initial body reserves and energy level of the diet was observed. Lean cows exhibited similar E_{resid} changes than fatter cows when they were subjected to an underfeeding/refeeding trajectory, suggesting that there was no difference in prioritization of energy allocation. This could be different with thinner cows or with cows of higher milk potential. Various authors previously reported the importance of body adipose reserves to buffer differences between energy supply and needs which enable animals to cope with constraining nutritional environments (Petit and Agabriel, 1993; Blanc et al., 2006). Under our experimental conditions, we can conclude that the ability of suckling cows to cope with a nutritional challenge occurring after calving is similar between fatter and leaner cows, and depends on the adaptive abilities of cows to modulate the energy allocation between functions.

5. Conclusions

This study illustrates the ability of suckling Charolais cows to maintain milk production when experiencing variable nutritional trajectories. Within changing nutritional trajectories, the robustness of Charolais cows relies on changes in energy resource allocation between life functions as weight and body composition vary. Our results show that robustness for milk production is weakly sensitive to body condition, because lean cows exhibited similar abilities to fat ones to cope with a nutritional challenge.

Long-term nutritional changes give an opportunity to measure variations in calculated E_{resid}. E_{resid} changes reflect safeguarding of energy allocation to life functions and could be considered as an indirect criterion of robustness.

These findings require further investigations especially to validate the relevance of E_{resid} as a trait of robustness in a changing nutritional environment. It is a major issue, as ruminant livestock production will have to face more changing nutritional environments in the future.

Conflict of interest

None of the authors have any conflicts of interest regarding this manuscript.

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