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Exploration of robustness indicators using adaptive responses to short-term feed restriction in suckling primiparous beef cows

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ABSTRACT

Animal robustness is a complex trait of importance for livestock production systems and genetic selection. Phenotyping is essential for evaluation of the adaptation of different genotypes to changing environments. This study tested an experimental framework to induce marked deviations in the adaptive responses of suckling beef cows and to identify relevant indicators of responses to characterise individual differences in the robustness of cows. The production and metabolic responses of primiparous suckling Charolais cows to two periods of feed restriction (**FR**, 50% of their net energy requirements) of different durations were monitored. After calving, 13 cows (aged 39 ± 2 months, BW of 680 ± 42 kg at calving) had *ad libitum* access to a diet composed of hay and supplemented with concentrate to meet their energy and protein requirements. Starting at 54 ± 6 days postcalving, the cows underwent two periods of FR: 4 days of FR (FR4), which was followed by 17 days of *ad libitum* intake to study the recovery from FR4, and 10 days of FR (FR10), which was followed by 18 days of *ad libitum* intake to study the recovery from FR10. The milk yield (**MY**), BW, body condition score and plasma non-esterified fatty acid (**NEFA**), β-hydroxybutyrate, glucose and urea concentrations were measured before, during and after each FR. Among all measured variables, the MY and NEFA concentrations showed the most significant changes in response to FR. A functional data analysis approach was applied to the MY and NEFA data to model the adaptive responses and extract quantifiable indicators of deviation and recovery. Linear correlations ($P < 0.03–0.07$) between FR4 and FR10 were found for some indicators describing MY and NEFA levels before and after FR. The overall repeatability of MY and NEFA responses between both FR accounted for 46% based on quartile analysis performed on average responses. Moreover, the variance in both the MY and NEFA variables did not differ significantly between FR4 and FR10, despite a trend for higher variances in FR10. Altogether, (1) the calculated variables derived from the functional data analysis of the time patterns of the MY and NEFA accounted for the differences in the cow responses to FR, and (2) the animal responses appeared to show concordance between FR4 and FR10. In conclusion, short-term FR is a relevant framework for studying productive and metabolic adaptive responses in suckling cows and allows the identification of potential robustness indicators.

Implications

Animal robustness corresponds to the ability to maintain performance and survival in changing environments. It relies on multiple components that are difficult to quantify for ranking individuals. This study showed that short-term feed restriction at 50% of net energy requirements for lactation is a relevant experimental framework for detecting the between-cow variability in temporal adaptive patterns of productive and metabolic indicators. Variables that describe the intensity and duration of temporal changes in milk yield and plasma non-esterified fatty acid concentration appear to be relevant for ranking animals according to their responses and to distinguish between less and more robust animals.

Introduction

The frequency and intensity of extreme climatic events are expected to increase, and these may result in highly variable environmental conditions. Such changes have direct (e.g., production, health and animal welfare) and indirect (e.g., availability of forage resources) impacts on animals (Rojas-Downing et al., 2017). Ruminants managed in pasture-based systems are particularly exposed

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(Rust, 2019) because conditions in these systems are generally more variable and uncertain than in indoor systems (Delaby et al., 2018).

Suckling beef cows must be robust, i.e. able to cope with perturbations and maintain productive and functional traits selected by breeding programmes in a broad variety of environments (Knap, 2005; Strandberg, 2009). The robustness of cows has to be phenotyped, and the underlying traits need to be defined before animals can be ranked based on their ability to face perturbations. When animals experience a perturbation, their adaptive response may involve changes in physiological, metabolic, behavioural and/or productive traits (Strandberg, 2009; Friggens et al., 2017). The amplitude and length of the deviations observed during a perturbation account for the animal's ability to resist, whereas resilience corresponds to the ability to recover quickly to the preperturbed state. Such resistance and resilience traits could be used to rank animals based on their individual responses (Ollion et al., 2016; Friggens et al., 2016). Several studies have focused on the characterisation of animal robustness based on an analysis of adaptive trajectories (Berry et al., 2013; Sadoul et al., 2015a; Macé et al., 2019); however, a standardised procedure for ranking individuals based on their robustness is still lacking. The definition of such a procedure requires a standard experimental framework and relevant indicators of robustness that could be used to select animals according to breeding strategies and the environmental conditions in which they are raised.

Experimental frameworks have been applied to dairy cows (Bjerre-Harpøth et al., 2012; Bedere et al., 2017; Billa et al., 2020) and goats (Friggens et al., 2016) to characterise the responses of the animals to nutritional challenges and to quantify changes in productive, functional or metabolic traits and their variability. Short-term nutritional challenges have been used in several recent studies [e.g., short feed restriction (**FR**) with durations ranging from 2 to 6 days, Bjerre-Harpøth et al., 2012; Friggens et al., 2016, Billa et al., 2020] and induce marked responses, which can be studied over time at different levels of organisation (e.g., biological functions, whole animal, groups of animals). Such experimental FR models are therefore commonly used to induce nutrient deficits at different stages of lactation in order to assess the production and metabolic responses (Bjerre-Harpøth et al., 2012), and the effects on various biological functions (Abdelatty et al, 2017; Pires et al., 2016). In lactating cows, short-term FR leads to an intense mobilisation of body reserves to buffer the shortfall of nutrients and support milk production (Bjerre-Harpøth et al., 2012; Billa et al., 2020). Concomitantly, FR may induce metabolic and hormonal changes, which also reflect the nutritional status and tissue responsiveness, and their deviations can be monitored at the individual level (Chilliard et al., 1998; Gross et al., 2011, Bjerre-Harpøth et al., 2012). Therefore, a description of the dynamic nature of the adaptive responses of animals, i.e., trajectories, appears promising (Codrea et al., 2011; Sadoul et al., 2015b; Poppe et al., 2020).

The effects of short-term FR on productive and metabolic responses have been investigated in dairy cows (Bjerre-Harpøth et al., 2012; Abdelatty et al., 2017). In suckling beef cows, few studies have analysed the effects of FR on productive traits and, all focused on long-term FR, e.g. more than 90 days (D'hour et al., 1995; Freetly et al., 2006, De La Torre et al., 2015). Such a low number of studies are probably due the difficulty to measure milk yield in suckling beef cows by quantification of the milk drunk by the calf (Le Neindre and Dubroeucq, 1973, Beal et al., 1990, Sepchat et al., 2017). Moreover, as milk production in suckling beef cows corresponds approximately to one-fifth of dairy cows, suckling beef cows may be able to mobilise body reserves to buffer FR. Given the context of climate change and the variability of forage resources, it is relevant to assess the robustness based on the ability of suckling cows to maintain milk production when they experience perturbations. We proposed to test whether a short-term FR framework is relevant to assess the robustness of milk production in suckling beef cows, and as a model to reveal adaptive differences between individuals. A short-term FR not exceeding 50% of the net energy requirements (**NE**) was chosen based on literature from dairy cows (Leduc et al., 2021; Billa et al., 2020) because it was shown to induce mensurable metabolic and production responses, while complying with animal health and ethical considerations. Our hypothesis was that FR would lead to quantifiable adaptive responses in suckling beef cows. Two objectives were defined: (1) to test whether a short-term FR could be a suitable experimental framework for inducing quantifiable adaptive responses in suckling beef cows and (2) to identify relevant productive and metabolic indicators of the robustness of measured variables. An exploratory methodological approach using functional data analysis (**FDA**) was applied to time-series data to identify potential indicators.

Material and methods

The experiment was performed at the INRAE Low Mountain Ruminant Farming Systems Facility in Laqueuille (HerbiPole, INRAE, 2018, https://doi.org/10.15454/1.5572318050509348E12) in compliance with national legislation on animal care.

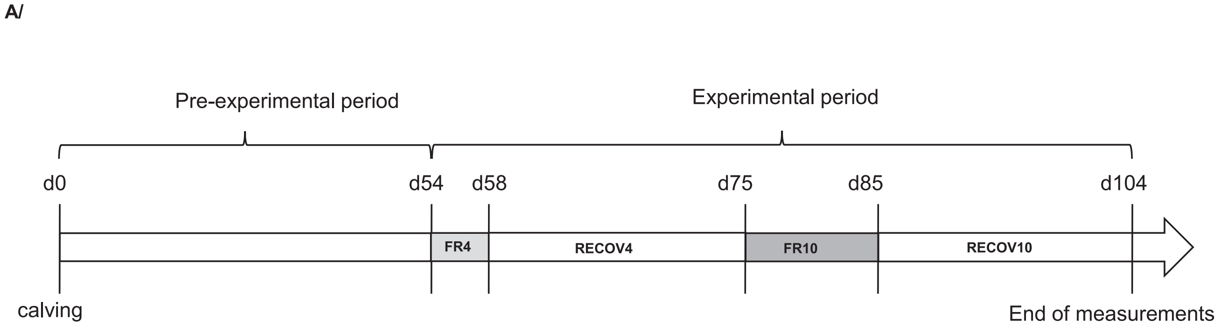
Experimental design

All the animals were subjected to the same FR treatments applied over time. After a pre-experimental period of 54 days, which started on the day of calving (Day 0), the cows were subjected to an experimental period of 50 days (from Day 54 to Day 104). During this period, the animals experienced two periods of FR with time being the experimental factor, and each FR was followed by a recovery period. The experimental unit was the animal because the treatments were applied and the measurements were performed at the individual level. The experimental design is shown in Fig. 1A, and the measurements and their frequencies are presented in Fig. 1B.

Animals and diets

Thirteen suckling primiparous Charolais cows (39 ± 2 months and 680 ± 42 kg at calving) were used in this experimental framework that intended to be a proof of concept. They were born and raised in INRAE facilities under controlled conditions and had never been exposed to experimental underfeeding. These animals derived from artificial insemination using semen from bulls were evaluated and indexed at the national level, and were therefore representative to Charolais breed. The calving was grouped in late February (27/02/2018 ± 5.6 days), and the cows were housed in free stalls equipped with feed troughs and automatic gates for individual feeding. Water and salt blocks were available for *ad libitum* intake.

The beginning of the experimental period was set at week 8 of lactation, which is after the peak of lactation, in order to limit potential confounding effects between the physiological negative energy balance which can occur in early lactation and the negative energy balance induced by the experimental short-term FR, (Sepchat et al., 2017). During the pre-experimental period (from calving to 54 days postpartum), the cows were fed individually and allowed *ad libitum* intake of hay from permanent grasslands (10% refusals) that was supplemented with a concentrate (INRA Bufflo Vital, Groupe Altitude, Centraliment, France) to meet their predicted NE and metabolisable protein requirements (INRA,



B/

	Pre-experimental period			Experimental period																				
				FR4				RECOV4																
	0-49	50	51	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
BW	x	x	x			x	x				x			x				x			x	x		
BCS	x	x				x					x											x		
MY	x	x		x	x	x	x	x	x	x	x		x		x			x		x		x		
Blood	x	x	x	x	x	x	x	x	x	x	x	x	x		x			x		x		x		

	Experimental period																										
	FR10											RECOV10															
	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	104
BW			x	x					x						x	x			x					x	x	x	x
BCS			x						x						x				x						x		
MY	x	x	x	x	x				x		x	x	x	x	x		x		x			x		x		x	x
Blood	x	x	x	x	x			x		x	x	x	x	x	x		x		x			x		x		x	x

Fig. 1. Schematic representation of the sequence of treatments applied to suckling primiparous Charolais cows (A) and measurements and sampling timeline (B). The experimental period included two periods of feed restriction (FR4: short-term feed restriction for 4 days; and FR10: short-term feed restriction for 10 days) in which the feed allowance was reduced to meet 50% of the net energy requirements for lactation calculated during the last week of the pre-experimental period and two recovery periods (RECOV4 and RECOV10) with *ad libitum* intake. *Abbreviations:* BCS = body condition score; MY = milk yield.

2007). The chemical composition and nutritive values of the diets are presented in Table 1. During the experimental period, the cows were subjected to a 4-day FR period (FR4, Days 54–58), which was followed by a 17-day recovery period with *ad libitum* intake of hay supplemented with concentrate (**RECOV4**, Days 58–75), and a 10-day FR period (FR10, Days 75–85), which was followed by a 19-day recovery period with *ad libitum* intake of hay supplemented with concentrate (**RECOV10**, Days 85–104) (Fig. 1A). The feed allowance during the restriction periods was calculated to meet 50% of the NE requirements for lactation based on BW, body condition score (**BCS**) and MY data collected during the last week of the pre-experimental period and according to INRA (2007).

Measurements and sampling

Intake

During both the pre-experimental and experimental periods, the amounts of feed offered and refused and their DM content (60 °C, 72 h) were recorded individually in the experimental facility to take into account potential differences in bales of hay. The total DM intake (**DMI**) was computed for each animal as the daily DM offered minus the DM refused. The concentrate ratio in the diet averaged 16% during the experiment.

Table 1
Chemical composition and nutritive value of feeds comprising the diet of suckling primiparous Charolais cows.

	Hay	Concentrate
Chemical composition, as measured (g/kg DM)		
CP	105	203
NDF	627	–
ADF	352	–
Starch	–	285
Feed value[1] (/kg DM)		
NEL (MJ/kg DM)	4.8	6.9
MP (g PDI/kg DM)	70	134

Abbreviations: NEL = the net energy of lactation; MP = metabolisable protein.
[1] Calculated according to INRA (2007).

During FR4 and FR10, no refusals were observed, and daily samples of the offered hay were collected and pooled per FR. During the *ad libitum* pre-experimental period, subsamples of the offered and refused hay were collected 4 days per week and pooled. During the recovery periods (RECOV4 and RECOV10), the offered hay and refusals were sampled daily and pooled individually per period and stored at room temperature until chemical analyses. The DM (103 °C for 24 h), ash (550 °C for 6 h) and chemical composition in the pooled samples were analysed. The contents of neutral and acid detergent fibre in subsamples previously dried at 60 °C for 72 h and ground through a 1-mm screen were analysed (Van Soest et al., 1991).

BW and body condition score

The BW at calving was calculated as the mean of two consecutive weightings measured at 1300 h on Days 4 and 5 postpartum. Afterwards, the cows were weighed once a week at 1300 h without prior feed withdrawal. During the FR periods, additional weightings were performed on Days 56 and 57 (in FR4) and Days 77, 78, 83 (in FR10; Fig. 1B). During the recovery periods, the cows were weighed on Days 61, 64, 68, 71 and 72 (RECOV4) and Days 89, 90, 93, 98, 99, 100 and 104 (RECOV10; Fig. 1B). The body condition was assessed weekly during the entire experiment by the same two experienced scorers on a scale of 0–5 (Agabriel et al., 1986). Each BCS corresponds to the average of the scores given by the two scorers (Fig. 1B).

Milk production

Milk production was measured using the weight-suckle-weight method (Le Neindre and Dubroeucq, 1973). The calves were housed in a separate pen near their dams to enable visual and olfactory contact. For each cow, the daily milk production was estimated as the sum of the milk drunk by the calf in the evening and in the following morning (suckling times, 1600 h and 0800 h).

During the pre-experimental period, the production of milk was measured once a week from Days 0 to 49 and on two consecutive days (Days 49 and 50) to determine the milk production before FR4 (Fig. 1B). During the experimental period, the production of milk was measured on Days 55, 56, 57, and 58 (in FR4); 59, 60, 61, 63, 65, 68, 70, 72 and 75 (in RECOV 4); 76, 77, 78, 79, 83, 85 and 86 (in FR10); and 87, 88, 89, 91, 93, 96, 98, 100 and 104 (in RECOV 10; Fig. 1B).

Plasma metabolites

During the pre-experimental period, blood was sampled on Days 50, 51 and 54, and during the experimental period, blood samples were obtained on Days 55, 56, 57 and 58 (in FR4); 59, 60, 61, 62, 63, 65, 68, 70, 72, 73 and 75 (in RECOV4); 76, 77, 78, 79, 82, 84, 85 and 86 (in FR10); and 87, 88, 89, 91, 93, 96, 98, 100 and 104 (in RECOV 10, Fig. 1B). The blood samples were collected from coccygeal vein before morning feeding using evacuated tubes containing ethylenediaminetetraacetic acid (1.95 mg/ml, TERUMO Europe NV, Leuven, Belgium) and immediately centrifuged at 1 500*g* for 20 min at room temperature. Plasma was stored at −20 °C until analysis of non-esterified fatty acids (**NEFA**, acyl-CoA synthase method, WAKO, Sobioda, France), glucose (glucose oxidase method, Thermo Electron, SAS France), urea (glutamate dehydrogenase method, Thermo Electron, SAS France), and β-hydroxybutyrate (**BHB**, D-beta-hydroxybutyrate dehydrogenase method, Thermo Electron, SAS France) using an automatic analyser (ARENA 20XT, Thermo Fischer Scientific, Cergy-Pontoise, France), which are metabolites useful to assess nutritional status and body reserve mobilisation (Russel and Wright, 1983; Richards et al., 1989, Agenas et al., 2006). The intra- and interassay CV were 1.6 and 3.3% for NEFAs, 2.3 and 3.8% for glucose, 6.8 and 8.1% for urea, and 2.3 and 3.6% for BHB.

Smoothing method for the phenotyping of adaptive trajectories

Because the MY and plasma NEFA concentrations were significantly affected by FR, a smoothing method considering the time patterns of these two biological variables was used. Individual profiles of the MY and plasma NEFA concentrations in response to FR were obtained from daily data using FDA, which is a smoothing approach previously described by Ramsay et al. (2020). This approach was implemented using the statistical software R© version 3.5.2 (R Development Core Team, 2020). Detailed algorithms for differential smoothing of time series from animals exposed to controlled FR were described in Barreto-Mendes et al., 2022. The quality of the fit was assessed visually by adjusting the roughness coefficient (λ) value. A higher λ value indicates that finer details of the curve are captured. Each cow was considered under its own control.

Briefly, the daily MY and plasma NEFA concentrations were converted into continuous functions. For each cow and variable, two smoothed functions were obtained: a reference function and an adaptive function. The reference function allows unbiased comparisons of individual responses between both FR. Hence, considering the milk production function for example, the individual slope of lactation curve is taken into account at the individual level. The reference function ($MY_{reference}$ or $NEFA_{reference}$) was defined as the expected response in the absence of any FR. The $MY_{reference}$ function was obtained by applying the FDA algorithm to MY data measured outside the FR and RECOV periods. The value of λ was the same for all the cows and set to 100 000. The $NEFA_{reference}$ function was assumed to be a straight horizontal line because the NEFA concentrations remain lower than 0.2 mmol·L^{-1} if cows are not underfed (Guedon et al., 1999; Adewuyi et al., 2005). A $NEFA_{reference}$ function was defined for both FR4 and FR10 by calculating the average plasma NEFA concentration at Days −3 and 0 (FR4) and Days 18 and 21 (FR10). The adaptive functions for each cow and variable [$MY = f_{MY}(t)$ or $NEFA = f_{NEFA}(t)$] included both the pre-experimental and experimental periods. The value of λ for the adaptive functions was the same for all the cows and was set to 1 000 for the MY and 10 for NEFA.

Once the reference and adaptive functions for the MY and NEFA were determined, their respective first derivatives were calculated. The functions and their first derivatives were used to calculate new variables for describing the MY and plasma NEFA profiles obtained during the deviation and recovery phases of FR. These calculated variables described the MY and plasma NEFA concentrations before [reference level point (**Pref**) and pretrough inflexion point (**Ipre**)], during (trough value, **T**) and after [post-trough value (**Ppost**) and post-trough inflexion point (**Ipost**)] FR and their changes [rate of response, rate of recovery, amplitude, area under the curve, A1 (during the deviation phase) and A2 (during the recovery phase)]. All calculated variables are defined in Table 2 and illustrated in Supplementary Fig. S1.

Statistical analyses

The statistical analyses were performed using SAS software (version 9.4; SAS Institute INC, Cary, NC, USA). The daily DMI, MY, BCS, BW and plasma metabolite data were averaged within animals and periods to perform comparisons among the periods (pre-experimental period, FR4, RECOV4, FR10 and RECOV10). The models included the fixed effect of the period and the random effect of cows. Time differences were tested using *posthoc* Tukey's test. The daily MY and plasma NEFA concentrations were analysed as repeated measures by mixed models that included day as a fixed effect, cow as a random effect, and Kenward-Roger adjustments for the calculation of denominator degrees of freedom. The choice of variance–covariance structures (compound symmetry, autoregressive, heterogeneous autoregressive, and spatial power) was based on Akaike's criterion obtained from the analyses. The residuals were checked for normality. The daily plasma NEFA concentrations were log-transformed, and statistical *P*-values were obtained based on the transformed dataset, whereas the least square mean (**LSM**) and SEM values are reported for non-transformed data.

Individual variables resulting from the FDA analyses and describing the deviation and recovery profiles obtained for the MY and NEFA data were calculated within each FR period. Two cows had missing MY data during FR4, and one cow had missing MY data during FR10. The means and SDs per FR were compared by paired Wilcoxon's test. The individual variability in each calculated variable was quantified by the CV. The homogeneity of variances observed during FR4 and FR10 was tested with Levene's test. The relationships between FR4 and FR10 for each variable describing the deviation and recovery profiles for the MY and plasma NEFA concentrations were explored by Spearman rank correlations using R software (https://www.r-project.org). The repeatability of average MY and NEFA responses between FR4 and FR10 was assessed by the proportion of animals ranked in similar group between the two duration of FR based on a quartile analysis. The significance level was predefined as $P \leq 0.05$, and $0.05 < P \leq 0.10$ indicated trends towards significance.

Results

Effects of feed restriction on DM intake, BW, body condition score and milk yield

Significant period effects were observed on the DMI, BW and MY ($P < 0.001$; Table 3, Fig. 2). The DMI during the pre-experimental and recovery periods averaged 13.80 kg/d (Table 3). Based on the design, the DMI was almost halved during FR4 and FR10 in comparison to the *ad libitum* intake periods ($P < 0.001$). The cows lost 25 (FR4) and 28 (FR10) kg of BW on average, which

Table 2
Definition of variables representing the deviation and recovery profiles of the milk yield and plasma NEFA concentrations in suckling primiparous Charolais cows subjected to 4 days (FR4) or 10 days of feed restriction (FR10).

Item	For the milk yield	For the plasma NEFA concentration
Variables of the response profile		
P_{ref}	Reference value corresponding to the MY at Days 54 (FR4) and 75 (FR10) estimated by the smoothed reference curve representing an undisturbed response; expressed in kg·day^{-1}	Reference concentration defined as the average concentration at Days 51 and 54 (FR4) and Days 74 and 75 (FR10); expressed in mmol·L^{-1}
I_{pre}	Pre-trough inflexion point corresponding to the minimum value of the first derivative; expressed in kg·day^{-1}	Pre-trough inflexion point that corresponds to the maximum value of the first derivative; expressed in mmol·L^{-1}
T	Minimum value of the MY (kg·day^{-1}) measured at the maximum of the deviation	Maximum concentration (mmol·L^{-1}) measured at the highest level of the deviation
Amplitude	Amount of maximum deviation calculated for each FR as the difference between the T value and the reference value estimated by the reference curve; expressed in kg·day^{-1}	Amount of maximum deviation calculated for each FR as the difference between the T value and the reference value estimated by the reference line; expressed in mmol·L^{-1}
Relative amplitude	Ratio of the amplitude of the deviation to the pre-FR level; expressed in percent	Ratio of the amplitude of the deviation to the pre-FR level; expressed in percent
Rate of increase or decrease*	Minimum value of the first derivative; expressed in kg·day^{-2}	Maximum value of the first derivative; expressed in mmol·L^{-2}
Relative rate of increase or decrease*	Ratio of the rate of increase to the amplitude of the deviation; expressed in percent	Ratio of the rate of decrease to the amplitude of the deviation; expressed in percent
A1*	Area between the smoothed reference trajectory and the smoothed adaptive trajectory from Days 54 to 58 (FR4) and Days 75 to 85 (FR10); expressed in kg	Area between the reference line and the smoothed adaptive trajectory from Days 54 to 58 (FR4) and Days 75 to 85 (FR10); expressed in mmol·L^{-1}·day
Variables of the recovery profile		
P_{post}	Located in the post-trough period where the first derivative crosses the reference curve; expressed in kg·day^{-1}	Located in the post-trough period where the first derivative crosses the reference curve; expressed in mmol·L^{-1}
I_{post}	Post-trough inflexion point corresponding to the maximum value of the first derivative; expressed in kg·d^{-1}	Post-trough inflexion point corresponding to the maximum value of the first derivative; expressed in mmol·L^{-1}
Rate of increase or decrease*	Maximum value of the first derivative; expressed in kg·d^{-2}	Minimum value of the first derivative; expressed in mmol·L^{-2}
Relative rate of increase or decrease*	Ratio of the rate of decrease to the amplitude of the deviation; expressed in percent	Ratio of the rate of increase to the amplitude of deviation; expressed in percent
A2*	Area between the smoothed reference trajectory and the smoothed adaptive trajectory from Days 58 to 61 (RECOV4) and Days 85 to 87 (RECOV10); expressed in kg	Area between the smoothed reference line and the smoothed adaptive trajectory from Days 58 to 61 ((RECOV4) and Days 85 to 87 (RECOV10); expressed in mmol·L^{-1}·day

Abbreviations: MY = milk yield; NEFA = non-esterified fatty acids; P_{ref} = reference value; I_{pre} = pre-trough inflexion point; T = trough; A1 = area between the smoothed reference trajectory and the smoothed adaptive trajectory during the deviation phase; P_{post} = post-trough value, I_{post}: post-trough inflexion point; and A2 = area between the smoothed reference trajectory and the smoothed adaptive trajectory during the first three days of the recovery phase.

* Indicates variables that describe the dynamics of the milk yield and plasma NEFA concentrations.

corresponded to a significant loss of 3.6 and 4% of BW in comparison to the pre-FR conditions ($P < 0.001$). The cows fully recovered their BW (+22 kg) during RECOV4 but showed only partial recovery (+10 kg) during RECOV10. No significant changes in the BCS were observed during the whole experiment. The MY averaged 6.6 kg/d over the first 50 days (Fig. 2). Feed restriction resulted in a significant decrease in MY, from 12 (FR4) to 15% (FR10), in comparison to the pre-FR period. The milk loss observed during FR4 fully recovered after 2 days, whereas incomplete recovery was observed during RECOV10 ($P < 0.001$, Fig. 2).

Effects of feed restrictions on plasma metabolite concentrations

The plasma metabolite concentrations are presented in Fig. 3 and Supplementary Table S1. The plasma NEFA concentrations measured during FR4 and FR10 were 2.5- and 3.4-fold higher,

Table 3
Changes in the DM intake (DMI), BW, body condition score (BCS) and milk yield (MY) of suckling primiparous Charolais cows (n = 13) during the pre-experimental and experimental periods.

	Pre-experimental period[1] (n = 55 d)	Experimental period[2]				SEM	*P*-value
		FR4 (n = 4 d)	RECOV4 (n = 10 d)	FR10 (n = 17 d)	RECOV10 (n = 18 d)		
DMI of hay (kg/d)	10.67^{a}	6.06^{b}	11.67^{c}	6.17^{b}	11.28^{c}	0.29	0.0001
DMI of concentrate (kg/d)	3.15^{a}	1.17^{b}	2.32^{c}	1.18^{b}	2.34^{c}	0.17	0.0001
DMI (kg/d)	13.82^{a}	7.24^{b}	13.98^{a}	7.35^{b}	13.63^{a}	0.4	0.0001
BW (kg)	686^{a}	661^{bc}	683^{a}	655^{c}	665^{b}	9.31	0.0001
BCS (scale 0–5)	1.86	1.91	1.89	1.89	1.87	0.08	0.9014
MY (kg/d)	6.57^{a}	5.81^{b}	5.59^{b}	4.77^{c}	4.40^{d}	0.31	0.0001

^{a,b,c,d}The period LSMEANS (least square means) not sharing a common superscript are different ($P < 0.05$).

Abbreviations: DMI = DM intake; BCS = body condition score; MY = milk yield.

[2] The experimental period included two periods of feed restriction (FR4: short-term feed restriction for 4 days; and FR10: short-term feed restriction for 10 days) in which the feed allowance was reduced to meet 50% of the net energy requirements for lactation calculated from BW, BCS and MY data collected during the last week of the pre-experimental period (FR4) and two recovery periods (RECOV4 and RECOV10) with *ad libitum* intake.

[1] During the pre-experimental period, suckling cows were *ad libitum* fed hay supplemented with a concentrate to meet their predicted and metabolisable protein requirements (INRA, 2007).

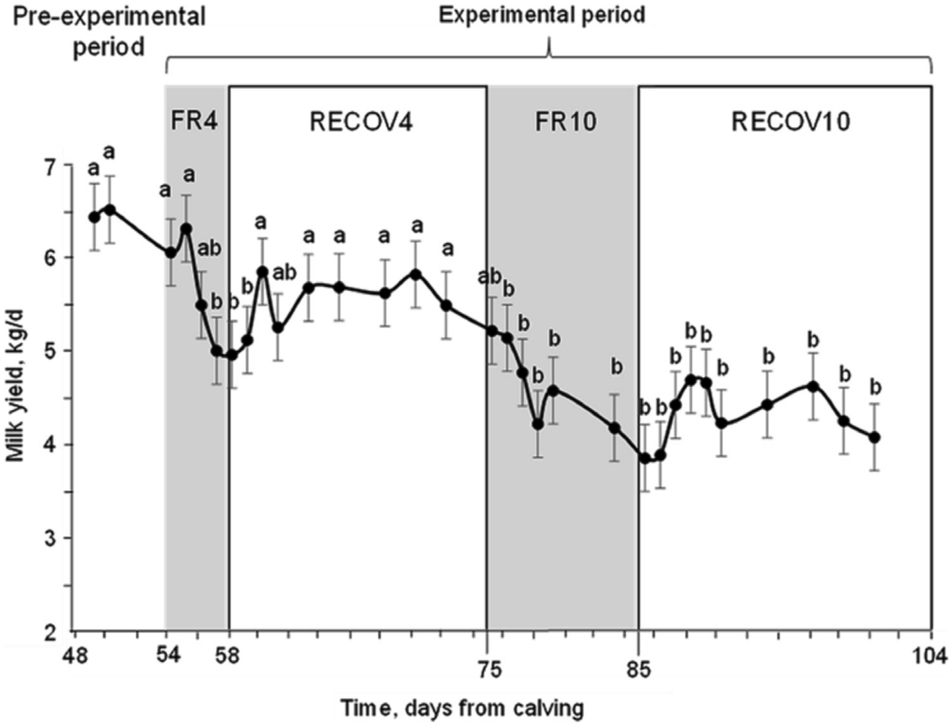


Fig. 2. Changes in the milk yield (kg/d) of suckling primiparous Charolais cows during the pre-experimental and experimental periods. Cows were *ad libitum* fed hay supplemented with concentrate during the pre-experimental period. The experimental period included two periods of feed restriction (FR4: short-term feed restriction for 4 days; and FR10: short-term feed restriction for 10 days) in which the feed intake was limited to 50% of the net energy for lactation requirements and two recovery periods (RECOV4 and RECOV10) with *ad libitum* intake. The differences between days are indicated with different letters ($P < 0.05$).

respectively, than those measured in cows fed *ad libitum* (Fig. 3A, $P < 0.05$). An increase in the plasma NEFA concentrations was observed on the first day of FR4 and thereafter, and a 2-fold increase was observed on the second day of FR10. The plasma NEFA concentrations returned to their pre-restriction level one day after FR4 and 2 days after FR10 (Fig. 3A). The average plasma concentrations of BHB (Fig. 3B) and glucose (Fig. 3C) were 0.271 and 0.450 g/L, respectively, and remained unchanged during FR4 and FR10. The plasma concentrations of BHB measured during RECOV10 differed significantly from those measured in the other periods ($P < 0.001$). The plasma urea concentrations averaged 0.236 g/L throughout the study period, with the exception of those measured during RECOV4, when the concentrations were 1.4 times lower than those measured during other periods ($P < 0.05$, Fig. 3D).

Profile analyses of the milk yield and plasma non-esterified fatty acids

The MY variables measured during the FR and recovery phases are presented in Table 4 and Supplementary Fig. S1A. In the present study, the $\mathrm{MY}_{\mathrm{reference}}$ averaged 6.53 kg/d before FR4 and 5.58 kg/d before FR10. The amplitude of the milk loss was less than 1 kg/d and did not differ between FR4 and FR10 ($P = 0.11$).

During the recovery periods, the rate of increase in the MY did not differ between FR4 and FR10, regardless of whether the variables are expressed as absolute (0.11 vs. 0.13 kg/d for FR4 and FR10, respectively; $P = 0.28$) or relative values (13.5 vs. 14.9% for FR4 and FR10, respectively; $P = 0.85$). The MY at Pref, Ipre, T, Ipost and Ppost were significantly or tended to be correlated between the FR periods (Table 4, $0.07 < P < 0.02$). Variables accounting for the changes in the MY during deviations (amplitude, relative amplitude, rate of milk loss, relative rate of milk loss, area under the curve) and recoveries (rate of milk recovery, area under the curve) were not significantly correlated between FR4 and FR10 (Table 4). Based on a quartile analysis performed on the average MY response during both FR, the proportion of animals re-ranked by one or more groups between FR4 and FR10 accounted for 54%. The variance of all the variables calculated from deviation-recovery profiles did not differ between FR4 and FR10 with the exception of A1 (Table 4, $P = 0.02$). However, the CV for variables accounting for the relative changes in the MY (ranging from 28 to 74%) was 2.3–3.7 times greater than that for variables accounting for the MY levels (ranging from 17 to 22%).

The NEFA variables measured during the FR and recovery phases are presented in Table 5 and Supplementary Fig. S1B. The plasma NEFA concentrations measured before FR (Pref) were low and did not differ between the FR periods ($P = 0.59$, Table 5). The plasma NEFA levels increased 2.6–3.5 times during FR relative to the pre-FR concentrations. The amplitude of the increase was significantly higher in FR10 than in FR4 ($P = 0.01$). Nevertheless, when expressed as a proportion of the deviation, no difference was observed between the FR periods ($P = 0.27$). After FR, the rate of recovery of the plasma NEFA levels did not differ between FR periods ($P = 0.34$). The plasma concentrations of NEFA measured before (Pref) or after (Ppost) FR were correlated between FR4 and FR10, regardless of whether these are expressed as absolute or relative amplitudes (Table 5). No significant correlations between FR4 and FR10 were observed for any other variables describing the deviation and recovery profiles of plasma NEFA. The repeatability of average NEFA response between both FR was of 46% based on a quartile analysis. The CV of all the variables ranged from 21 to 106% for both FR periods and did not show differences between FR4 and FR10, with the exception of A1 ($P < 0.001$).

Discussion

Suckling beef cows are considered to be more able to face FR than dairy cows mainly due to their low MY (~1 800 kg of milk production per lactation corresponding to ~25–30% of the theoret-

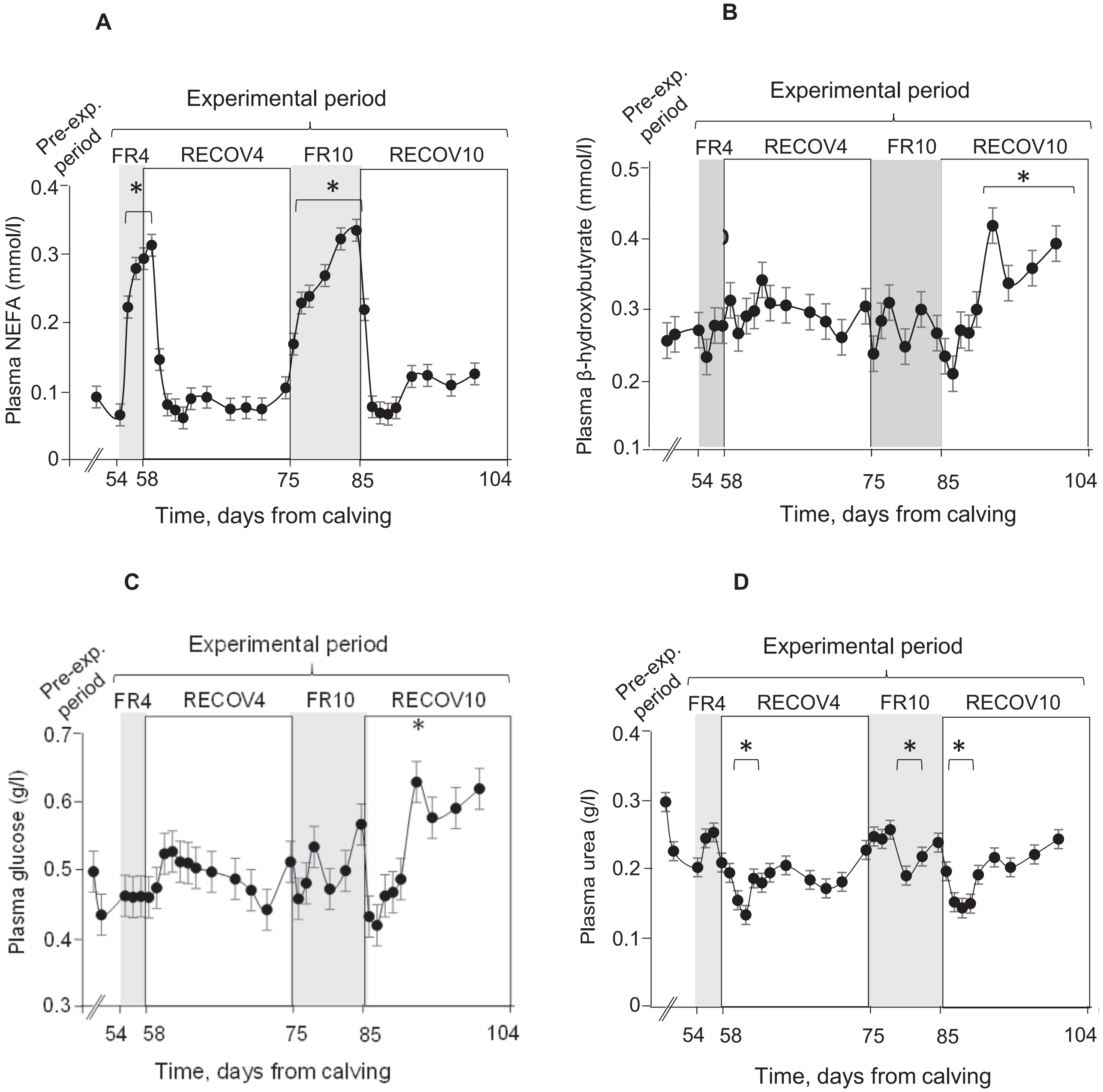


Fig. 3. Concentrations of plasma non-esterified fatty acids (NEFA, A), β-OH butyrate (B), glucose (C) and urea (D) in suckling primiparous Charolais cows during the pre-experimental period (pre-exp., Days −6 to 0), periods of feed restriction (FR4, Days 0–4; and FR10, Days 21–31) and recovery periods (RECOV4, Days 5–20; and RECOV10, Days 32–48). Cows were *ad libitum* fed hay supplemented with concentrate during the pre-experimental period. The experimental period included two periods of feed restriction (FR4: short-term feed restriction for 4 days; and FR10: short-term feed restriction for 10 days) in which the feed intake was limited to 50% of the NE for lactation requirements and two recovery periods (RECOV4 and RECOV10) with *ad libitum* intake. The data are given as the Least Square Means ± SEM. Differences between periods are indicated with an asterisk (*; $P < 0.05$).

ical NE requirements in mid-lactation, Sepchat et al., 2017). However, the results of our study revealed that a 4-day period of FR at 50% of the NE requirements for lactation is a relevant experimental framework for phenotyping the robustness of suckling beef cows through quantification of their adaptive trajectory deviations. A short-term FR led to significant changes in both the MY and plasma NEFA concentrations in suckling beef cows, and did not cause welfare concerns. Increasing the duration of FR to 10 days did not affect the pattern or amplitude of the cow responses. Complete recovery (i.e., recovery to the pre-restriction levels) of the MY and plasma NEFA concentrations was observed 2 days after FR4, revealing the resilience and existence of efficient adaptive processes of suckling beef cows to FR. The use of the FDA approach with MY and NEFA time-series data to capture the individual dynamics of adaptive responses provided relevant indicators of deviations and recoveries, and these indicators may enable us to rank cows according to their responses to FR and thus their respective robustness.

Relevance of the experimental framework

The experimental framework of short-term FR implemented in this study proved relevant to induce significant productive and metabolic responses in Charolais suckling beef cows that have a relatively low MY, and were representative of the breed (Sepchat et al., 2017). A 4-day period of FR (50% of the NE requirements for lactation) induced significant quantitative decreases in the MY and BW and concomitant increases in the plasma NEFA

Table 4
Milk yield variables of suckling primiparous Charolais cows measured during the deviation and recovery phases after 4 days (FR4) or 10 days of feed restriction (FR10).

	Feed restriction	Mean	SD	CV (%)	*P*-value Wilcoxon's test	Spearman rank correlation (r)	*P*-value Spearman rank correlations	*P*-value Levene's test
Variables of the deviation phase								
Pref (kg·day^{-1})	FR4	6.53	1.15	17.6	0.002	0.60	0.073	0.708
	FR10	5.58	1.16	20.2				
Ipre (kg·day^{-1})	FR4	6.13	1.26	20.6	0.002	0.70	0.031	0.742
	FR10	5.05	1.02	20.2				
Rate of milk loss (kg·day^{-2})	FR4	−0.18	0.09	47.0	0.193	0.29	0.427	0.935
	FR10	−0.21	0.08	39.2				
Relative rate of milk loss (%)	FR4	−23.5	10.4	44.1	0.344	0.19	0.113	0.457
	FR10	−25.0	7.0	28.1				
T (kg·day^{-1})	FR4	5.59	1.17	21.0	0.002	0.87	0.003	0.923
	FR10	4.26	0.91	21.4				
Amplitude (kg·day^{-1})	FR4	0.80	0.36	44.5	0.105	0.49	0.154	0.497
	FR10	0.89	0.47	52.5				
Relative amplitude (%)	FR4	13.25	8.64	65.2	0.020	0.58	0.088	0.384
	FR10	15.51	6.22	40.1				
A1 (kg)	FR4	2.47	1.51	61.1	0.006	0.20	0.584	0.023
	FR10	6.37	4.38	68.8				
Variables of the recovery phase								
Ppost (kg·d^{-1})	FR4	6.12	1.02	16.7	0.002	0.62	0.060	0.779
	FR10	4.83	1.05	21.8				
Ipost (kg·day^{-1})	FR4	5.90	1.09	18.5	0.002	0.72	0.024	0.984
	FR10	4.61	0.97	20.9				
Rate of milk recovery (kg·day^{-2})	FR4	0.11	0.07	66.1	0.275	0.09	0.811	0.702
	FR10	0.13	0.08	66.2				
Relative rate of milk recovery (%)	FR4	13.53	5.69	42.0	0.846	−0.64	0.054	0.361
	FR10	14.86	11.01	74.1				
A2 (kg)	FR4	2.24	0.94	42.1	0.432	0.61	0.066	0.967
	FR10	1.67	1.04	62.4				

Abbreviations: Pref = reference value; Ipre = pre-trough inflexion point; T = trough; A1 = area between the smoothed reference trajectory and the smoothed adaptive trajectory during the deviation phase; Ppost = post-trough value, Ipost = post-trough inflexion point; and A2 = area between the smoothed reference trajectory and the smoothed adaptive trajectory during the first three days of the recovery phase.

Table 5
Variables of the plasma non-esterified fatty acid concentration of suckling primiparous Charolais cows measured during the deviation and recovery phases after 4 days (FR4) or 10 days of feed restriction (FR10).

	Feed restriction	Mean	SD	CV (%)	*P*-value Wilcoxon's test	Spearman rank correlation (*r*)	*P*-value Spearman rank correlations	*P*-value Levene's test
Variables of the deviation phase								
Pref (mmol·L^{-1})	FR4	0.08	0.04	53.65	0.588	0.57	0.047	0.332
	FR10	0.07	0.03	34.72				
Ipre (mmol·L^{-1})	FR4	0.15	0.04	25.96	0.006	0.27	0.373	0.135
	FR10	0.22	0.08	34.90				
Rate of increase (mmol·L^{-2})	FR4	0.07	0.05	30.16	0.002	0.42	0.157	0.661
	FR10	0.05	0.02	35.33				
Relative rate of increase (%)	FR4	113.1	60.6	53.62	0.013	0.56	0.05	0.253
	FR10	68.93	38.7	56.08				
T (mmol·L^{-1})	FR4	0.26	0.06	22.23	0.010	0.45	0.125	0.172
	FR10	0.33	0.10	29.05				
Amplitude (mmol·L^{-1})	FR4	0.19	0.06	33.12	0.010	0.54	0.064	0.247
	FR10	0.26	0.09	35.28				
Relative amplitude (%)	FR4	319.2	182.4	57.13	0.273	0.55	0.055	0.755
	FR10	374.1	204.0	53.74				
A1 (mmol·L^{-1}·day)	FR4	0.61	0.20	33.01	0.001	0.52	0.071	0.0003
	FR10	1.79	0.88	49.25				
Variables of the recovery phase								
Ppost (mmol·L^{-1})	FR4	0.08	0.04	51.27	0.168	0.65	0.020	0.404
	FR10	0.08	0.03	30.94				
Ipost (mmol·L^{-1})	FR4	0.17	0.05	29.02	0.305	0.39	0.196	0.710
	FR10	0.19	0.06	33.73				
Rate of recovery (mmol·L^{-2})	FR4	−0.06	0.01	20.60	0.340	0.39	0.196	0.178
	FR10	−0.06	0.02	31.00				
Relative rate of recovery (%)	FR4	−93.37	39.7	42.55	0.635	0.35	0.239	0.397
	FR10	−87.52	30.2	34.53				
A2 (mmol·L^{-1}·day)	FR4	0.27	0.17	64.43	0.048	0.29	0.344	0.956
	FR10	0.15	0.16	106.25				

Abbreviations: Pref = reference value; Ipre = pre-trough inflexion point; T = trough; A1 = area between the smoothed reference trajectory and the smoothed adaptive trajectory during the deviation phase; Ppost = post-trough value, Ipost = post-trough inflexion point; and A2 = area between the smoothed reference trajectory and the smoothed adaptive trajectory during the first three days of the recovery phase.

concentrations. In contrast, other key variables of beef cow performance (e.g., BCS) and metabolic status (e.g., plasma concentrations of glucose, urea, and BHB) were not significantly affected. The intensity of body reserve mobilisation during FR is certainly not enough to induce significant changes in these physiological variables. In dairy cows, mobilisation of body reserves is associated with increased plasma NEFA, with eventual changes in BHB, urea and glucose concentrations (Bjerre-Harpøth et al., 2012; Chilliard et al., 1998; Billa et al., 2020). But the intensity of metabolic changes depends on multiple factors, including lactation stage, severity of FR, body fatness, type of diet and genetics (Leduc et al., 2021). For instance, changes in plasma glucose and BHB are observed in early lactation (Bjerre-Harpøth et al., 2012). Nonetheless, plasma metabolite concentrations do not necessarily reflect changes in nutrient supply or demand because of key roles of the liver in nutrient metabolism and tight homeorhetic regulations (Loncke et al., 2015, 2020). The duration and severity of the FR applied in this study were chosen from previous dairy cow studies reporting significant effects of intense FR on production and metabolic responses (Billa et al., 2020). To our knowledge, this study provides the first assessment of the changes to short-term FR in suckling beef cows; only the responses to longer and less intense FR have been reported thus far (De La Torre et al., 2015). The results obtained with suckling charolais primiparous cows are also expected for multiparous, or other suckler cow genotypes. Nonetheless, differences in magnitude are likely, as multiparous cows have higher milk production than primiparous (+20%, Sepchat et al., 2017; INRAE, 2017), and may calve with higher body condition scores as the growth function is less significant. The magnitude of responses to the FR will depend on the nature, the duration and the intensity of the restriction relative to the level of production (Chilliard et al., 1998) and to other cumulative effects (e.g. lactation stage).

Among the variables significantly affected by FR, the BW changes measured during the entire experiment did not discriminate the responses of cows to short-term FR. In mature cows, changes in BW reflect both short-term changes in digestive contents and medium- to long-term changes in body reserves (mobilisation or accretion). These two components are sensitive to variations in the DMI (Faverdin et al., 2017). A decrease in the DMI of 1 kilogram corresponds to a 4–6 kg decrease in BW (INRA, 2018). Here, the DMI decreased by 6.6 kg on average during FR, and this decrease may induce a loss of BW of up to 39 kg. Under our experimental conditions, the significant changes in BW (at most 28 kg) may be explained by short-term changes in the DMI and digestive contents. This finding is in accordance with the lack of changes in the BCS between the *ad libitum* intake and FR periods because BCS measurements usually reflect medium- to long-term mobilisation or accretion of body reserves. In this study, the relatively low production level and the lactation stage of the cows did not induce measurable changes in body reserves assessed by the BCS.

The MY and plasma NEFA concentrations were the two most relevant variables accounting for the adaptive responses of suckling beef cows to short-term FR and are thus the only variables able to discriminate individual differences in the way cows cope with FR, which allows the ranking of cows based on their robustness of lactation function. In this study, the observed decreases in the MY (12–15%) and the concomitant increases in the plasma NEFA concentrations (159–246%) in response to FR were close to the changes reported in both primiparous (Recoules et al., 2013, De La Torre et al., 2016) and multiparous (De La Torre et al., 2015) beef cows subjected to FR (70% of the NE requirements for lactation) during a 100-day postcalving period. These changes in the MY and plasma NEFA concentrations were nevertheless lower than those reported for dairy cows subjected to short-term FR, which included a 30–35% decrease in the MY (Pires et al., 2016, Billa et al., 2020) and a 300–630% increase in the plasma NEFA concentrations (Billa et al., 2020). Similar to dairy cows, lactation function tends to remain a priority in underfed suckling beef cows (De La Torre et al., 2015), and the differences observed between beef and dairy breeds may be partially explained by the higher energy imbalance in dairy cows than in suckling beef cows due to their higher MY. The MY of these latter, in addition to being low, is difficult to measure and subject to greater bias and uncertainty than that in dairy cows (Beal et al., 1990; De La Torre and Agabriel, 2017). Novel phenotyping methods based on continuous measurement of the calf weight open new possibilities for easier and more reliable measurements of the MY in suckling beef cows (Sepchat et al., 2017).

Prolonging the FR duration from 4 to 10 days did not increase deviations in the MY or NEFA concentrations. The MY recovered from FR4 and reached the pre-restriction levels within 2 days but failed to recover after FR10. The relatively advanced stage of lactation, the low MY and a possible shift in the calves' choice towards a greater consumption of solid feed in response to a prolonged period of MY loss may explain the incomplete recovery of the MY after 10 days of FR. Nonetheless, the time needed to recover to the initial MY levels was concordant with the results from previous studies on dairy cows, which showed that a period of 3 days (Bjerre-Harpøth et al., 2012) to 2 weeks (Billa et al., 2020) is needed for recovery depending on the intensity and duration of the FR.

In our study, a rapid return of the circulating NEFA levels to the initial values was observed within the first two days following the end of the FR period, regardless of the FR duration. These results are consistent with the literature (Gross et al., 2011; Billa et al., 2020), even if the responses vary depending on the duration of FR, the diet energy density (Ferraretto et al., 2014), and the stage of lactation (Bjerre-Harpøth et al., 2012).

Relevance of calculated variables for the phenotyping of animal responses

To explore adaptive responses and identify candidate traits for the phenotyping of robustness, a smoothing approach, termed FDA (Ramsay et al., 2018), was separately performed using the MY and plasma NEFA concentrations. This approach allowed us to calculate variables that characterise the deviation and recovery phases in response to FR. The variables were grouped into two categories: (i) to describe the absolute values of the MY or plasma NEFA concentrations (Pref, Ipre, T, Ipost, Ppost) and (ii) to describe the dynamics (rates and amplitude) of the changes.

Overall, under our experimental conditions, prolonging the FR duration from 4 to 10 days did not modulate the direction of the changes observed in response to FR. More specifically, the deviation phase was always characterised by a decrease in the MY and an increase in the plasma NEFA concentrations in all cows. During the recovery phase, a return to conditions close to those prevailing before FR was observed. Variables describing MY and plasma NEFA concentrations before (Ppre, Ipre) and after FR (Ppost, Ipost), the relative amplitude of the deviation presented correlations between FR4 and FR10 that were moderate to significant ($P < 0.003–0.09$). The repeatability of average MY and plasma NEFA responses accounts for 46% based on a quartile analysis. This suggests that the *ad libitum* intake during the recovery period between FR4 and FR10 may have possibly prevented the occurrence of cumulative effects from the two successive FR periods. In contrast, no significant correlation with FR duration was observed for variables that describe the dynamics of the MY and plasma NEFA concentrations, which suggests individual diversity in the temporal responses of cows to FR.

Our results show that FDA is a promising tool for exploring the individual variability in the MY and plasma NEFA concentrations of suckling beef cows. This method allowed us to rank cows based on variables describing the shape of deviation-recovery phases. These variables represent the ability of cows to resist and recover from a perturbation (Sadoul et al., 2015a). The analysis of the MY and NEFA traits showed a negative correlation between the amplitudes of the milk and plasma NEFA changes in response to FR10 ($r = -0.70$, $P = 0.015$) but not to FR4. This outcome illustrates the ability of suckling beef cows to mobilise body reserves to serve as a buffer to feed shortages and to support milk production when the duration of FR increases. Nevertheless, FDA remains a first step for providing generic variables from deviation/recovery phases. Different multivariate analyses have been proposed for studying adaptive capacity (Moyes et al., 2013; Sadoul et al., 2015a). For instance, a clustering procedure linked to a piecewise mixed model has been used to characterise types of responses and rank goats subjected to 2 days of FR based on multiple traits related to their robustness (Friggens et al., 2016). Unfortunately, the limited numbers of data points and animals in this study precluded us from testing this approach.

Conclusion

In mid-lactation suckling Charolais primiparous cows, short-term FR for 4 or 10 days (50% of NE requirements) resulted in significant productive and metabolic changes. Even the shortest FR (4 days) appeared relevant to investigating the adaptive responses of suckling beef cows. Such an experimental framework could provide the opportunity to (i) rank animals according to their responses to FR and recovery and (ii) test the cumulative effects of short-term FR on adaptive capacity. Among the changes induced by FR, a decrease in the MY and a concomitant increase in the plasma NEFA concentrations appear to be the two most relevant variables for exploring adaptive capacity in response to short-term FR. The application of FDA independently to the MY and plasma NEFA data resulted in new variables that could better describe the individual dynamic responses during and after FR. The FDA approach is appropriate for exploring the individual variability of dynamic responses and allows the ranking of cows according to their capacity to resist and recover from FR. Further research with a larger number of animals is needed to investigate the most appropriate dynamic variables and to test their relevance as indicators of animal robustness.

Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.animal.2022.100556.

Ethics statement

The experimental protocol was approved by the Ethics Committee of the Auvergne-Rhône-Alpes region and the French Ministry of Higher Education, Research and Innovation (APAFIS #16859-2015043014541577v6).

Software and data repository resources

None of the data were deposited in an official repository. The data that support the study findings are available from the corresponding author upon reasonable request.

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Declaration of interest

None.

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References

Abdelatty, A.M., Iwaniuk, M.E., Garcia, M., Moyes, K.M., Teter, B.B., Demonte, P., Kadegowda, A.K.G., Tony, M.A., Mohamad, F.F., Erdman, R.A., 2017. Effect of short-term feed restriction on temporal changes in milk components and mammary lipogenic gene expression in mid-lactation Holstein dairy cows. Journal of Dairy Science 100, 4000–4013. https://doi.org/10.3168/jds.2016-11130.

Adewuyi, A.A., Gruys, E., van Eerdenburg, F.J., 2005. Non esterified fatty acids (NEFA) in dairy cattle. A review. Veterinary Quaterly 27, 117–126. https://doi.org/10.1080/01652176.2005.9695192.

Agabriel, J., Giraud, J.-M., Petit, M., 1986. Détermination et utilisation de la note d'état d'engraissement en élevage allaitant. Bulletin Technique CRZV Theix INRA 66, 43–50.

Agenas, S., Heath, M.F., Nixon, R.M., Wilkinson, J.M., Phillipds, C.J.C., 2006. Indicators of undernutrition in cattle. Animal Welfare 15, 149–160.

Barreto-Mendes, L., De La Torre, A., Ortigues-Marty, I., Cassar-Malek, I., Pires, J.A.A., Blanc, F., 2022. How to approach the resilience of livestock exposed to environmental challenges? Quantification of individual response and recovery by means of differential calculus. Animal Open Science 1, 1–8. https://doi.org/10.1016/j.anopes.2022.100008.

Beal, W.E., Notter, D.R., Akers, R.M., 1990. Techniques for estimation of milk yield in beef cows and relationships of milk yield to calf weight gain and postpartum reproduction. Journal of Animal Science 68, 937–943. https://doi.org/10.2527/1990.684937x.

Bedere, N., Disenhaus, C., Ducrocq, V., Leurent-Colette, S., Delaby, L., 2017. Ability of dairy cows to ensure pregnancy according to breed and genetic merit for production traits under contrasted pasture-based systems. Journal of Dairy Science 100, 2812–2827. https://doi.org/10.3168/jds.2016-11588.

Berry, D., McParland, S., Bastin, C., Wall, E., Gengler, N., Soyeurt, H., 2013. Phenotyping of robustness and milk quality. Advances in Animal Biosciences 4, 600–605. https://doi.org/10.1017/S2040470013000150.

Billa, P.A., Faulconnier, Y., Larsen, T., Leroux, C., Pires, J.A.A., 2020. Milk metabolites as noninvasive indicators of nutritional status of mid-lactation Holstein and Montbéliarde cows. Journal of Dairy Science 103, 3133–3146. https://doi.org/10.3168/jds.2019-17466.

Bjerre-Harpøth, V., Friggens, N.C., Thorup, V.M., Larsen, T., Damgaard, B.M., Ingvartsen, K.L., Moyes, K.M., 2012. Metabolic and production profiles of dairy cows in response to decreased nutrient density to increase physiological imbalance at different stage of lactation. Journal of Dairy Science 95, 2362–2380. https://doi.org/10.3168/jds.2011-4419.

Chilliard, Y., Bocquier, F., Doreau, M., 1998. Digestive and metabolic adaptations of ruminants to undernutrition, and consequences on reproduction. Reproduction Nutrition Development 38, 131–152.

Codrea, M.C., Hojsgaard, S., Friggens, N.C., 2011. Differential smoothing of time-series measurements to identify disturbances in performance and quantify animal response characteristics: An example using milk yield profiles in dairy cows. Journal of Animal Science 89, 3089–3098. https://doi.org/10.2527/jas.2010-3753.

Delaby, L., Buckley, F., McHugh, N., Blanc, F., 2018. Robust animals for grass-based production systems. Book of abstracts of the 27th General Meeting of the European Grassland Federation (EGF), 17-21 June 2018, Cork, Ireland. pp. 389–400.

De La Torre, A., Recoules, E., Blanc, F., Ortigues Marty, I., D'hour, P., Agabriel, J., 2015. Changes in calculated residual energy in variable nutritional environments: An indirect approach to apprehend suckling beef cows' robustness. Livestock Production Science 176, 75–84. https://doi.org/10.1016/j.livsci.2015.03.008.

De La Torre, A., Blanc, F., D'hour, P., Agabriel, J., 2016. Salers cows are more efficient than Charolais cows to face changing nutritional environments. Book of abstracts of the Steps to sustainable livestock International Conference, 12–15 January 2016, Bristol, UK, p. 19.

De La Torre, A., Agabriel, J., 2017. Prendre en compte l'efficience alimentaire des vaches allaitantes dans les recommandations alimentaires à travers la quantification de leurs dépenses non productives. INRAE Productions Animales 30, 153–164. https://doi.org/10.20870/productions-animales.2017.30.2.2241.

D'hour, P., Petit, M., Pradel, P., Garel, JP., 1995. Evolution du poids et de la production laitière au pâturage de vaches allaitantes Salers et Limousines dans deux milieux. Book of abstracts of the 2nd Rencontres Recherches Ruminants, 13–14 December 1995, Paris, France, pp. 105–108.

Faverdin, P., Charrier, A., Fischer, A., 2017. Prediction of dry matter intake of lactating dairy cows with daily live weight and milk production measurements. Book of abstracts of the 8th European Conference on Precision Livestock Farming (ECPLF), 12–14 September 2017, Nantes, France, pp. 35-44.

Ferraretto, L.F., Gencoglu, H., Hackbart, K.S., Nascimento, A.B., Dalla Costa, F., Bender, R.W., Guenther, J.N., Shaver, R.D., Wilbank, M.C., 2014. Effect of feed restriction on reproductive and metabolic hormones in dairy cows. Journal of Dairy Science 97, 754–763. https://doi.org/10.3168/jds.2013-6925.

Freetly, H., Nienaber, J.A., Brown-Brandl, T., 2006. Partitioning energy during lactation of primiparous beef cows. Journal of Animal Science 84, 2157–2162. https://doi.org/10.2527/jas.2005-534.

Friggens, N.C., Duvaux-Ponter, C., Etienne, M.P., Mary-Huard, T., Schmidely, P., 2016. Characterizing individual differences in animal responses to a nutritional challenge: toward improved robustness measures. Journal of Dairy Science 99, 2704–2718. https://doi.org/10.3168/jds.2015-10162.

Friggens, N.C., Blanc, F., Berry, D.P., Puillet, L., 2017. Review: Deciphering animal robustness. A synthesis to facilitate its use in livestock breeding and management. Animal 11, 2237–2251. https://doi.org/10.1017/S175173111700088X.

Guedon, L., Saumande, J., Desbals, B., 1999. Relationships between calf birth weight, prepartum concentrations of plasma energy metabolites and resumption of ovulation postpartum in Limousine suckled beef cows. Theriogenology 52, 779–789. https://doi.org/10.1016/S0093-691X(99)00171-5.

Gross, J., van Dorland, H.A., Bruckmaier, R.M., Schwarz, F.J., 2011. Performance and metabolic profile in dairy cows during lactational and deliberately induced negative energy balance with subsequent realimentation. Journal of Dairy Science 94, 1820–1830. https://doi.org/10.3168/jds.2010-3707.

Inra, 2007. Alimentation des bovins, ovins et caprins: Besoins des animaux, valeurs des aliments. Editions Quae, Versailles, France.

INRA, 2018. INRA feeding system for Ruminants. Wageningen Academic Publishers, Wageningen, The Netherlands. https://doi.org/10.3920/978-90-8686-292-4.

Knap, P.W., 2005. Breeding robust pigs. Australian Journal of Experimental Agriculture 45, 763–773.

Leduc, A., Souchet, S., Gelé, M., Le Provost, F., Boutinaud, M., 2021. Effect of feed restriction on dairy milk production: a review. Journal of Animal Science 99, 1–12. https://doi.org/10.1093/jas/skab167.

Le Neindre, P., Dubroeucq, H., 1973. Observations sur l'estimation de la production laitière des vaches allaitantes par la pesée du veau avant et après tétée. Annales de Zootechnie 22, 413–422.

Levene, H., 1960. Robust Tests for Equality of Variances. In: Olkin, I. (Ed.), Contributions to Probability and Statistics. Stanford University Press, Palo Alto, CA, USA, pp. 278–292.

Loncke, C., Noziere, P., Bahloul, L., Vernet, J., Lapierre, H., Sauvant, D., Ortigues-Marty, I., 2015. Empirical prediction of net splanchnic release of ketogenic nutrients, acetate, butyrate and beta-hydroxybutyrate in ruminants: a meta-analysis. Animal 9, 449–463. https://doi.org/10.1017/s1751731114002638.

Loncke, C., Nozière, P., Vernet, J., Lapierre, H., Bahloul, L., Al-Jammas, M., Sauvant, D., Ortigues-Marty, I., 2020. Net hepatic release of glucose from precursor supply in ruminants: a meta-analysis. Animal 14, 1422–1437. https://doi.org/10.1017/S1751731119003410.

Macé, T., González-García, E., Carrière, F., Douls, S., Foulquié, D., Robert-Granié, C., Hazard, D., 2019. Intra-flock variability in the body reserve dynamics of meat sheep by analyzing BW and body condition score variations over multiple production cycles. Animal 13, 1986–1998. https://doi.org/10.1017/S175173111800352X.

Moyes, K.M., Larsen, T., Ingvartsen, K.L., 2013. Generation of an index for physiological imbalance and its use as a predictor of primary disease in dairy cows during early lactation. Journal of Dairy Science 96, 2161–2170. https://doi.org/10.3168/jds.2012-5646.

Ollion, E., Ingrand, S., Delaby, L., Trommenschlager, J.-M., Colette-Leurent, S., Blanc, F., 2016. Assessing the diversity of trade-offs between life functions in early lactation dairy cows. Livestock Science 183, 98–107. https://doi.org/10.1016/j.livsci.2015.11.016.

Pires, J.A.A., Stumpf, L.F., Soutullo, I.D., Pescara, J.B., Stocks, S.E., Grummer, R.R., 2016. Effects of abomasal infusion of nicotinic acid on responses to glucose and β-agonist challenges in underfed lactating cows. Journal of Dairy Science 99, 2297–2307.

Poppe, M., Veerkamp, R.F., van Pelt, M.L., Mulder, H.A., 2020. Exploration of variance, autocorrelation, and skewness of deviations from lactation curves as resilience indicators for breeding. Journal of Dairy Science 103, 1667–1684. https://doi.org/10.3168/jds.2019-17290.

R Development Core Team, 2020. R: A language and environment for statistical computing (https://www.R-project.org/). R Foundation for Statistical Computing, Vienna, Austria.

Ramsay, J.O., Graves, S., Hooker, G., 2020. Package FDA. V5.1.9. Retrieved 25 August 2021 from https://www.functionaldata.org.

Ramsay, J.O., Wickham, H., Graves, S., Hooker. G., 2018. Functional Data Analysis, R package version 2.4.8. Retrieved 15 January 2020 from https://CRAN.R-project.org/package=fda.

Recoules, E., De La Torre, A., Agabriel, J., Egal, D., Blanc, F., 2013. Subcutaneous body lipids affect cyclicity and estrus behavior in primiparous Charolais cows. Animal Reproduction Science 140, 115–123. https://doi.org/10.1016/j.anireprosci.2013.06.017.

Richards, M.W., Wettemann, R.P., Schoenemann, H.M., 1989. Nutritional anoestrus in beef cows: concentrations of glucose and nonesterified faaty acids in plasma and insulin in serum. Journal of Animal Science 67, 2354–2362. https://doi.org/10.2527/jas1989.6792354x.

Russel, A.J.F., Wright, I.A., 1983. The use of blood metabolites in the determination of energy status in beef cows. Animal Production Science 37, 335–343.

Rust, J.M., 2019. The impact of climate change on extensive and intensive livestock production systems. Animals Frontiers 9, 20–25. https://doi.org/10.1093/af/vfy028.

Rojas-Downing, M.M., Pouyan Nejadhashemi, A., Harrigan, T., Woznicki, S.A., 2017. Climate change and livestock: Impacts, adaptation, and mitigation. Climate Risk Management 16, 145–163. https://doi.org/10.1016/j.crm.2017.02.001.

Sadoul, B., Martin, O., Prunet, P., Friggens, N.C., 2015a. On the use of a simple physical system analogy to study robustness features in animal sciences. PLoS ONE 10, 1–14. https://doi.org/10.1371/journal.pone.0137333.

Sadoul, B., Leguen, I., Colson, V., Friggens, N.C., Prunet, P., 2015b. A multivariate analysis using physiology and behavior to characterize robustness in two isogenic lines of rainbow trout exposed to a confinement stress. Physiology and Behavior 140, 139–147. https://doi.org/10.1016/j.physbeh.2014.12.006.

Sepchat, B., D'hour, P., Agabriel, J., 2017. Production laitière des vaches allaitantes: caractérisation et étude des principaux facteurs de variation. INRAE Productions Animales 30, 139–152. https://doi.org/10.20870/productions-animales.2017.30.2.2240.

Strandberg E., 2009. The role of environmental sensitivity and plasticity in breeding for robustness: lessons from evolutionary genetics. In Breeding for robustness in cattle (Klopčič, M., Reents, R., Philipsson, J., Kuipers, A.). Wageningen Academic Publishers, Wageningen, The Netherlands, pp. 17–34.

Van Soest, P., Robertson, J.B., Lewis, B.A., 1991. Methods for dietary fiber, neutral detergent fiber, and non-starch polysaccharides in relation to animal production. Journal of Dairy Science 74, 3583–3597.