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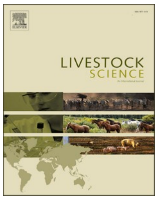

Influence of feed restriction and subsequent recovery on lactating Charolais cows

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HIGHLIGHTS

- Dietary restriction affects milk production and body reserves at the same intensity.
- Recovery is quicker for milk production and reproduction than for body weight and condition.
- A long-term full recovery is observed for the dams but not for the calves.

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ABSTRACT

One of the potential consequences of global climate change is that forage resources may become more limited at certain times of the year. In this study, 340 primiparous Charolais cows from two experimental farms participated in a feed restriction challenge in order to better understand how lactating beef cattle can adapt to this limitation. Therefore, half of the animals were fed 3 forage units (FU) less than their expected needs (around 30% reduction) from 10 days after calving until they were turned out on grass in April (average duration of 85 days). All animals were then kept together until mid-July (recovery period, average duration of 89 days). Regular measurements were taken of dam weight, body condition score (BCS), and calf weight; three estimates were made of dam milk production during lactation; and the date of each cow's resumption of cyclicity was recorded. On one of the farms, the experiment was extended for two more lactations, for a total of 592 lactations among all the animals examined. The effects of dietary restriction were analyzed using generalized linear models of the phenotyped traits. We found that winter feed restriction in early-lactation Charolais cows affected all traits, with generally similar impacts on the mobilization of body reserves and limitation of milk production. At the end of the winter period, diet-restricted dams were an average of 55 kg lighter than their unrestricted counterparts (corresponding to 0.66 standard deviations, s.d.) and had BCS values that were 0.81 points lower (0.55 s.d.). Similarly, calves from restricted dams were also lighter (20 kg difference, corresponding to 0.68 s.d.), reflecting the reduced milk production of their mothers (-1.7 L at 90 days in milk, corresponding to 0.77 s.d.). On average, feed-restricted primiparous cows resumed cyclicity almost an entire cycle later than their control counterparts (difference of 17 days, corresponding to 0.48 s.d.). For cow traits, the differences between groups remained significant but decreased in magnitude as spring went on, especially for milk production; by the start of the next

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Abbreviations: ADDBCSrec, Average daily difference in body condition score during the spring (recovery) period; ADDBCSrest, Average daily difference in body condition score during the winter (restriction) period; ADDWrec, Average daily difference in body weight during the spring (recovery) period; ADDWrest, Average daily difference in body weight during the winter (restriction) period; ADGrec, Average daily gain in calf weight during the spring period; ADGrest, Average daily gain in calf weight during the winter period; BCS, Body condition score; BCSi, Initial BCS (at the start of the winter period); BCSrec, BCS at the end of the spring (recovery) period; BCSrest, BCS at the end of the winter (restriction) period; BWi, Initial body weight; BWrec, Body weight at the end of the spring period; BWrest, Body weight at the end of the winter period; CW150, Calf weight at 150 days; CWi, Initial calf weight; CWrec, Calf weight at the end of the spring period; CWrest, Calf weight at the end of the winter period; INRAE, French National Research Institute for Agriculture, Food, and the Environment; FU, Forage unit; L1, first lactation; L2, second lactation; L3, third lactation; Milk1, milk production at the first milk assessment; Milk2, milk production at the second milk assessment; Milk3, milk production at the third milk assessment; Res_cycl, resumption of cyclicity.

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calving period, the effects of restriction were no longer visible. For calves, however, the differences in weight between groups remained steady, suggesting that the feed restriction occurred too early in their lives for them to be able to experience compensatory growth at refeeding.

Introduction

Feed restriction is regularly and deliberately used on commercial cattle farms to prepare females for calving (Roche, 2007), to facilitate dry off (Tucker et al., 2009), or to achieve compensatory growth in young animals (Galyean et al., 1999; Pereira et al., 2020). However, feed restriction may also occur involuntarily due to limitations in forage resources, a situation that is likely to become more frequent in the context of climate change (Giridhar and Samireddypalle, 2015; Rust, 2019).

The effects of feed restriction have been observed at the molecular level (e.g. Chouzouris et al., 2018; Keogh et al., 2015), at the behavioral level (e.g., Tucker et al., 2009; Schütz et al., 2013), and on individual performance (e.g., D'Hour et al., 1995; de la Torre et al., 2010). An animal's response to feed restriction and its potential for future recovery depend on its breed and the duration and severity of restriction. These responses include reduction of body weight and changes in body composition (Hornick et al., 2000; Taylor et al., 2018), growth (Trubenbach et al., 2019), decrease in milk production and composition changes (Agenäs et al., 2003; Gabbi et al., 2016; Roche, 2007), negative effect on reproductive performance or gestation (Matthews et al., 2015; Taylor et al., 2018; Noya et al., 2019), and improvement of feed efficiency (Fischer et al., 2020). However, the relative influence of restriction on different parameters of production has rarely been studied. Likewise, little is known about the influence of several months of restriction—i.e. what could be expected with involuntary seasonal restriction—on early lactation in beef cows.

A cow's adaptive capacity in a feed restriction context has been defined as its ability to mobilize body reserves without impairing its subsequent productive and reproductive performances (Blanc et al., 2010). Different profiles of adaptive responses may exist. For example, D'Hour et al. (1995) found that Salers dams prioritized the maintenance of milk production over that of their own body reserves, while the opposite was observed in Limousine cows. A similar study was performed in Charolais cattle, but it examined only 28 individuals (de la Torre et al., 2010), hindering our ability to make generalizations on the adaptive response of this breed. To address this, we designed an experiment with 340 Charolais cows (592 lactations) to investigate the influence of winter feed restriction followed by a period of recovery and to determine the response profiles and adaptive capacity of these cows.

Materials and methods

Ethics statement

Throughout the course of the experiment, all animals were handled with care in line with INRAE's ethics policy and in compliance with the guidelines on animal research issued by the French Ministry of Agriculture (https://www.legifrance.gouv.fr/eli/decret/2013/2/1/2013–118/jo/texte).

Experimental animals

The experiment was performed at two experimental farms belonging to the French National Research Institute for Agriculture, Food, and the Environment (INRAE, formerly INRA): Le Pin (Farm 1, 198 females) and Bourges (Farm 2, 142 females). The females were purebred Charolais cows that calved for the first time between 2014 and 2018. At Farm 1, whenever possible, the cows were retained and studied for their second ($n = 161$) and third ($n = 91$) lactations. Overall, data were obtained for a total of 592 lactations. The calving season was November to February, with primiparous females calving first. In the event of twins, only one calf was raised by the dam. Adoption was possible if the adopting dam had herself calved fewer than 10 days before. During the winter, the cows were kept indoors in pens of 10 to 20 individuals on straw litter.

Feed management and challenge

Ten days after calving, the females were assigned randomly to one of two diet groups (HIGH and LOW). Two periods were defined: winter, corresponding to the restriction period, and spring, corresponding to the recovery period. The winter period lasted from ten days after calving to the start of the spring period, which was initiated as soon as grazing conditions were favorable, generally in mid-April depending on the weather. During the winter period, similarly to what was applied in de la Torre et al. (2010), the HIGH group was fed 2 FU (forage units, 1 FU = 7.12 MJ (INRA, 2018)) more than its theoretical needs, while the LOW group was fed 3 FU less than its theoretical needs. The HIGH group was fed high-quality grass silage plus 1 kg of commercial pellets while the LOW group had access to low-quality grass silage, 0.5 kg canola, 200 g mineral and vitamin supplementation, and enough straw to fill the intake capacity; there was thus no difference between the groups in terms of intake volume as both diets were matching intake capacity. Both diets were designed to be equivalent in terms of protein per FU, meaning that protein intake was likewise restricted in the LOW group. Estimates of each individual's theoretical needs were based on recommendations from the INRAE nutrition system (INRA, 2018) and were updated every year. For example, a primiparous cow weighing 700 kg and producing 7 kg of milk daily was estimated to have maintenance needs of 5.6 FU, milk production needs of 3.2 FU, and growth needs of 0.7 FU. On average, cows in the LOW group were fed 6.5 FU while those in the HIGH group received 11.5 FU. Restriction thus consisted of a reduction of around 30% in energy intake compared to theoretical needs and around 45% compared to the HIGH group. Some information about average individual daily intake for each diet group, estimated from quantities distributed by pen and number of animals in it, are provided in Table 1.

The spring period lasted from the first day on grass (generally mid-April) until mid-July. During this period, both HIGH and LOW groups were kept together with ad libitum access to high-quality pastures.

On average, the winter period lasted 85 days (s.d. 28 days, minimum duration of 40 days) and the spring period 89 days (s.d. 11 days, minimum duration of 60 days). Cows who were tracked for more than one lactation were kept in the same diet group during successive lactations.

Phenotypes

Multiple phenotypes were recorded during both the restriction and recovery periods. The weights of cows and calves, as well as each cow's body condition score (BCS, with a 0.5 increment, on a scale of 0 to 5; Agabriel et al., 1986) were recorded twice at both the start and end of

Table 1
Average individual estimated daily intake (and standard deviation) of dry matter (DMI), crude fiber (CF), crude protein (CP) for each of the two diet groups during the winter period.

Trait	Mean of HIGH group (S.D.)	Mean of LOW group (S.D.)
DMI (kg)	14.0 (1.3)	9.7 (0.8)
CF (g/kg of DM)	237.4 (18.9)	286.0 (20.6)
CP (g/kg of DM)	111.8 (23.4)	76.2 (11.0)

each period, and again every two weeks within each period. For BCS, scores were assigned by two trained technicians on each farm and the average score was used.

The milk production of each dam was measured indirectly three times during lactation, using calf weight before and after suckling following the method implemented by Le Niendre et al. (1975), confirmed by Sepchat et al. (2017). For this, the calf was separated from its dam the evening before measurement. The next morning, the calf was weighed, reunited with its dam for suckling, and weighed again immediately afterwards before being separated once again. A second suckling event was recorded in the same way in the evening and then the calf and dam were returned to their pen together. Milk production was estimated by adding together the morning and evening weight gains of the calf. The first series of measurements was recorded midway through the winter period (on average, 35 days after the start of the winter period, s.d. 10 days), the second series at the end of the winter period (on average, 80 days after the start, s.d. 24 days), and the third midway through the spring period (on average, 133 days after the start of winter, or 48 days from the start of spring, s.d. 30 days). The choice of three points of milking during the lactation was made as a balance between the information given on the lactation curve and workforces available on farms.

Starting from 30 days after calving, trained technicians collected a blood sample from each dam every 10 days and sent it to the INRAE PRC Unit (Nouzilly, France) for the determination of progesterone levels. Determination was performed by ELISA quantification and a concentration above 1.5 ng/mL was considered as positive (Canépa et al., 2008). Two successive positive samples were deemed to indicate the resumption of cyclicity. Animals were sampled until cyclicity resumed.

analyses

A total of 20 traits were defined. For dam weight, we quantified initial body weight at the start of restriction (BWi); body weight at the end of the winter period, i.e. the end of restriction (BWrest); body weight at the end of the spring period, i.e. the end of recovery (BWrec); the average daily difference during the winter period (ADDWrest); and the average daily difference during the spring period (ADDWrec). The five BCS traits corresponded exactly to the weight traits: BCSi, BCSrest, BCSrec, ADDBCSrest, and ADDBCSrec. For calf weight, we considered weight at the start of restriction (CWi), at the end of restriction (CWrest), and at the end of the recovery period (CWrec); the average daily gain during restriction (ADGrest) and during recovery (ADGrec); and the weight at 150 days of age estimated by regression (CW150). The three assessments of milk production were designated Milk1, Milk2, and Milk3, and resumption of cyclicity (in days after calving) was recorded as Res_cycl.

Tests for significant effects were conducted for each trait with the following linear model using Proc GLM in SAS/STAT® software (SAS institute Inc., 2008):

$$y = Xb + e$$

where y is the vector of observations for the considered trait, b is the vector containing the appropriate fixed effects for that trait, X is the incidence matrix assigning observations to effects and e is the residual. Tested fixed effects were contemporary group (farm-year), parity (number of lactations), diet, duration of restriction and/or recovery period, as well as calf sex, age of calf, whether the calf was from a single or twin calving for calf traits. For milk-related traits, the effect of lactation stage was also tested by grouping all cows within the same 10-day milk interval. All interactions were included into each model.

Based on the results of the linear models for each trait, the average value for each diet and for each lactation group (corrected for all other effects) was estimated. In addition, to more easily compare the effect of restriction on the different traits, the estimated difference between the HIGH and LOW groups was standardized by dividing it by the standard deviation of the HIGH group.

In order to determine whether dietary restriction influenced the correlations among traits, the same linear model (but without diet as a fixed effect) was applied to the 20 traits. Two-tailed Pearson's correlations were then calculated separately on the residuals from the HIGH and LOW groups using R software (R Development Core Team, 2005).

Results

Modeling and significant effects

For each of the 20 traits considered, the significant effects and the coefficients of determination (R^2 values) of the respective models are presented in Table 2. The average R^2 was 0.49, with values ranging from 0.22 for BCSi to 0.70 for ADDWrec. The strongest values were found relative to cow body weight changes and calf weight. It is interesting to note that diet had no significant effect on any of the variables measured before restriction (BWi, BCSi, and CWi), but affected all other traits.

Effects on traits related to cow body weight

The average values of all traits associated with cow body weight in the two diet groups, corrected for all other effects, are presented in Table 3. Although both groups began the challenge at a similar average weight, at the end of the winter period, the difference in weight between HIGH and LOW group cows reached 55 kg, declining to 30 kg by the end of the spring period. When expressed in standard deviation to enable comparison, this difference was even greater with respect to other traits that directly represented weight gains or losses (e.g., ADDWrest).

Body weight also increased with the number of lactations, with the average values for the first, second, and third lactations (corrected by all other effects including diet) being 654 kg, 702 kg, and 740 kg at the start of winter; 652 kg, 680 kg, and 724 kg at the end of winter; and 675 kg, 730 kg, and 769 kg at the end of spring, respectively. For ADDWrest, there was a significant interaction between diet and parity: within the HIGH group, ADDWrest was negative, although very small in magnitude, for L2 (0.26 kg/day, −0.04 kg/day, and 0.29 kg/day for L1, L2, and L3 respectively), while ADDWrest was always negative in the LOW group, with decreasing values for subsequent lactations (−0.36 kg/day, −0.56 kg/day, and −0.61 kg/day for L1, L2, and L3 respectively).

Effects on traits related to body condition

The average values of all traits related to body condition score in the two diet groups, corrected for all other effects, are presented in Table 4. With the exception of BCSi, which was measured before the start of the winter period, diet had an effect on all traits, with restricted females displaying lower BCS or BCS-related performance. BCS was also influenced by parity, with primiparous females having the highest scores at the start of the challenge and second-lactation females the lowest (2.53 for L1, 2.35 for L2, and 2.49 for L3). For two traits, BCSrec and ADDBCSrec, we found a significant diet-by-parity interaction. For BCSrec, this was linked to the difference between L2 and L1 or L3, which was even greater in HIGH versus LOW cows. For ADDBCSrec, the interaction reflected the performance of L3 females, in which the diet effect was less marked than for the other lactation groups.

Effects on traits related to calf weight

The average values of all traits related to calf weight in the two diet groups, corrected for all other effects, are presented in Table 5. While calves in both groups started at the same weight, the dietary restriction of the dams in the LOW group had a clear effect on the growth of their calves, with a weight difference that persisted even through the spring period (at around 20 kg). Calf weight and growth were also affected by the parity of their dams, with calves from multiparous cows performing

Table 2

Significance of the tested effects and R^2 values from linear models of the 24 traits considered.

Trait	Contemporary group	Parity	Diet	Restriction duration	Recovery duration	Lactation stage	Sex of the calf	Age of the calf	Singleton or Twin	Diet x parity	Diet x contemporary group	Contemporary group x parity	R^2
BWi	***	***	NS							NS	NS	***	0.35
BWrest	***	***	***	NS						NS	***	***	0.40
BWrec	***	***	**	NS	*					NS	NS	**	0.33
ADDWrest	***	***	***	**						*	***	***	0.60
ADDWrec	***	***	***	NS	**					NS	***	***	0.70
BCSi	***	*	NS							NS	NS	***	0.22
BCSrest	***	***	***	NS						***	***	NS	0.49
BCSrec	***	**	***	NS	***					*	**	***	0.32
ADDBCSrest	***	*	***	NS						NS	***	NS	0.37
ADDBCSrec	***	***	***	NS	***					**	***	***	0.40
CWi	***	***	NS				***	***	***	NS	NS	NS	0.46
CWrest	***	***	***	NS			***	**	**	NS	***	*	0.68
CWrec	***	***	***	NS	NS		***	***	**	NS	***	NS	0.65
ADGrest	***	**	***	**			*	NS	*	NS	**	NS	0.42
ADGrec	***	***	**	NS	**		***	NS	NS	NS	***	NS	0.56
CW150	***	***	***	NS	NS		***	NS	**	NS	***	*	0.48
Milk1	***	*	***			*	NS		NS	NS	**	**	0.42
Milk2	***	*	***			NS	NS		NS	NS	**	*	0.57
Milk3	***	NS	*			**	NS		NS	NS	NS	NS	0.43
Res_cycl	***	***	*	***						*	NS	*	0.53

With **ADDBCSrec**: Average daily difference in body condition score during the spring (recovery) period, **ADDBCSrest**: Average daily difference in body condition score during the winter (restriction) period, **ADDWrec**: Average daily difference in body weight during the spring (recovery) period, **ADDWrest**: Average daily difference in body weight during the winter (restriction) period, **ADGrec**: Average daily gain in calf weight during the spring period, **ADGrest**: Average daily gain in calf weight during the winter period, **BCSi**: Initial body condition score (at the start of the winter period), **BCSrec**: Body condition score at the end of the spring (recovery) period, **BCSrest**: Body condition score at the end of the winter (restriction) period, **BWi**: Initial body weight, **BWrec**: Body weight at the end of the spring period, **BWrest**: Body weight at the end of the winter period, **CW150**: Calf weight at 150 days, **CWi**: Initial calf weight, **CWrec**: Calf weight at the end of the spring period, **CWrest**: Calf weight at the end of the winter period, **Milk1**: milk production at the first milk assessment, **Milk2**: milk production at the second milk assessment, **Milk3**: milk production at the third milk assessment, and **Res_cycl**: resumption of cyclicity.

Table 3

Corrected means of traits related to dam weight in the HIGH and LOW groups and the difference between groups expressed as standard deviations of the HIGH group.

Trait	Mean of HIGH group	Mean of LOW group	Difference expressed as standard deviation
BWi (kg)	699	698	0.01
BWrest (kg)	712	657	0.66
BWrec (kg)	740	710	0.40
ADDWrest (kg/day)	0.16	−0.49	1.16
ADDWrec (kg/day)	0.25	0.55	−0.67

With **ADDWrec**: Average daily difference in body weight during the spring (recovery) period, **ADDWrest**: Average daily difference in body weight during the winter (restriction) period, **BWi**: Initial body weight, **BWrec**: Body weight at the end of the spring period, and **BWrest**: Body weight at the end of the winter period.

better than those from primiparous cows. No interaction was observed between diet and parity with respect to calf weight.

Effects on milk production traits

The average values of milk production traits in the two diet groups, corrected for all other effects, are presented in Table 6. Cows in the HIGH group always produced more milk than those in the LOW group but the difference decreased drastically in the spring period. Indeed, milk production in the LOW group was higher mid-recovery than at the end of the winter period, while milk yields in the HIGH group continued to decline according to the typical lactation curve. Multiparous cows produced more milk than primiparous females, with a maximum during L2. No interaction with diet was observed.

Table 4

Corrected means of traits related to dam body condition score in the HIGH and LOW groups and the difference between groups expressed as standard deviations of the HIGH group.

Trait	Mean of HIGH group	Mean of LOW group	Difference expressed as standard deviation
BCSi	2.45	2.45	0
BCSrest	2.66	2.11	0.81
BCSrec	2.81	2.57	0.41
ADDBCSrest (*1000)	3.7	−5.4	0.99
ADDBCSrec (*1000)	2.2	5.9	−0.55

With **ADDBCSrec**: Average daily difference in body condition score during the spring (recovery) period, **ADDBCSrest**: Average daily difference in body condition score during the winter (restriction) period, **BCSi**: Initial body condition score (at the start of the winter period), **BCSrec**: Body condition score at the end of the spring (recovery) period, and **BCSrest**: Body condition score at the end of the winter (restriction) period.

Effects on the resumption of cyclicity

A significant interaction was observed between diet and parity with respect to the resumption of cyclicity; these results are presented in Table 7. A difference between diet groups was observed only among primiparous females. The fact that the diet effect (without interaction) is significant in the model is due to the large proportion of primiparous females in the experiment and was not explored further.

Correlations between traits in the two diet groups

Pearson correlations between the 20 selected traits are presented separately for the two diet groups in Fig. 1. Although the profile of correlations between traits was largely the same for both diet groups

Table 5

Corrected means of traits related to calf weight in the HIGH and LOW groups and the difference between groups expressed as standard deviations of the HIGH group.

Trait	Mean of HIGH group	Mean of LOW group	Difference expressed as standard deviation
CWi (kg)	53.6	52.9	0.08
CWrest (kg)	137.0	117.0	0.68
CWrec (kg)	239.5	216.5	0.56
ADGrest (kg/day)	0.99	0.79	1.00
ADGrec (kg/day)	1.18	1.15	0.14
CW150 (kg)	200.4	179.6	0.72

With **ADGrec**: Average daily gain in calf weight during the spring period, **ADGrest**: Average daily gain in calf weight during the winter period, **CW150**: Calf weight at 150 days, **CWi**: Initial calf weight, **CWrec**: Calf weight at the end of the spring period, and **CWrest**: Calf weight at the end of the winter period.

Table 6

Corrected means of traits related to milk production in the HIGH and LOW groups and the difference between groups expressed as standard deviations of the HIGH group.

Trait	Mean of HIGH group	Mean of LOW group	Difference expressed as standard deviation
Milk1 (L)	7.9	6.6	0.62
Milk2 (L)	7.4	5.7	0.77
Milk3 (L)	6.8	6.3	0.18

With **Milk1**: milk production at the first milk assessment, **Milk2**: milk production at the second milk assessment, **Milk3**: milk production at the third milk assessment, and **Res_cycl**: resumption of cyclicity.

Table 7

Corrected means for the resumption of cyclicity in the HIGH and LOW groups as a function of parity (lactation 1, 2, or 3).

Diet group	Cyclicity resumption (days) in lactation 1	Cyclicity resumption (days) in lactation 2	Cyclicity resumption (days) in lactation 3
HIGH	105	80	66
LOW	122	83	64

(the average difference being 0.10 between the groups), some slight differences were observed at the cow level, such as a negative correlation between cow weight variables and ADDWrec in the HIGH group only, or in contrast, a negative correlation between BWi and ADDWrest in the LOW group only. The relationship between body weight and BCS was also less marked in LOW-group females. There was almost no difference between the correlations for the two groups regarding calf-weight traits.

Discussion

I this study, a large experimental design was implemented to offers additional information in the still scarce field of feed restriction on lactating beef cattle. The strength of the experiment is the high number of individuals, which allows accurate analyses of the considered phenotypes. However, this also brings intrinsic limits, as the animals have to be raised over several years and on two different farms. These conditions imply the use of different aliments across years and locations, with slight changes in the feed chemical composition despite the diets being formulated to remain as constant as possible. All these environmental differences are absorbed in the model by the contemporary group effect and therefore are not affecting the results presented here. However, it can explain why the contemporary group x diet interaction is often significant and this could be the subject of an additional study.

Influence of restriction

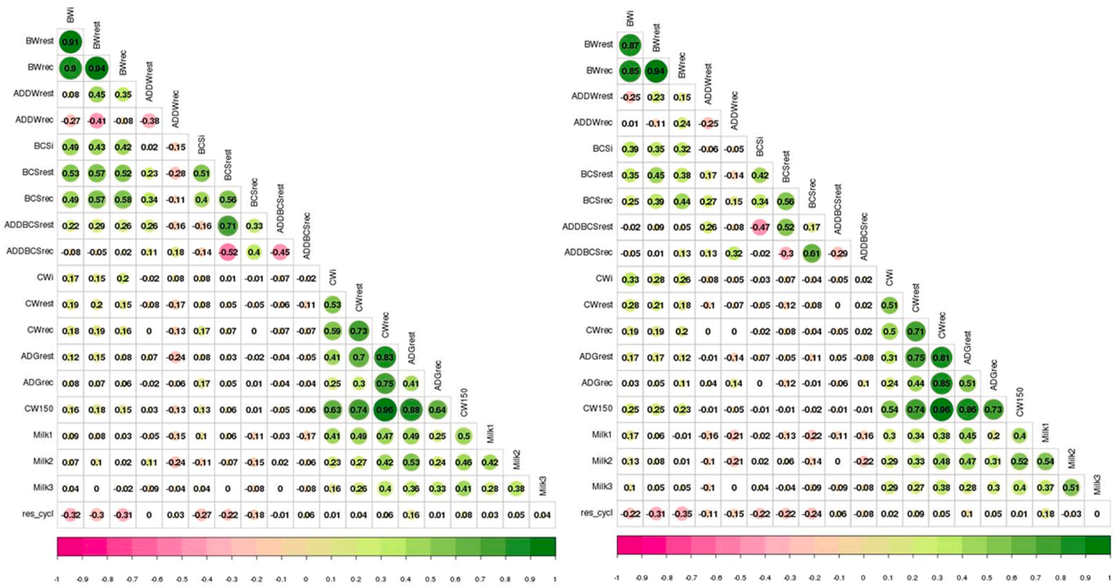
Dietary restriction had a demonstrable effect on all observed traits; it was associated with reductions in weight, BCS, milk production, and calf growth, and a delay to the resumption of cyclicity. These results are consistent with those of previous studies examining winter restriction in early-lactation beef cattle (de la Torre et al., 2010; D'Hour et al., 1995). In general, restriction generates a negative energy balance, to which females try to adapt by reducing production and mobilizing body reserves (Fruscalso et al., 2013). It is fully expected that lactating cows may lose weight under these conditions (Gross et al., 2011). An early study in the Charolais breed found that a mobilization of body reserves up to 80 kg constituted 75% lipid mobilization and 25% protein (Petit and Agabriel, 1993). The decline in BCS observed here could be evidence of a similar pattern in this study, as BCS evaluates subcutaneous fat, which is a good indicator of general lipid reserves (Petit and Agabriel, 1993). Another possible factor that contributes to weight loss and has often been reported in the literature in the context of feed restriction (e.g., de la Torre et al., 2010) is that a reduction in feed intake lowers the weight of digestive content, resulting in a lighter body weight. This effect was probably limited here because, although the LOW diet was formulated to be energy-restrictive, both diets were designed to match the intake capacity of the dams.

An earlier study of lactating beef females reported that, even though all females lost weight in response to restriction, the loss was greater in primiparous females (D'Hour et al., 1995); other authors hypothesized that primiparous cows might be more sensitive to restriction because of their unfinished growth, which acts as an additional energy sink (Freetly et al., 2006). Here, no difference in response was observed between primiparous and multiparous females in term of body weight. This was consistent with the results of de la Torre et al. (2010), who also studied Charolais cows. Those authors suggested that, in their case, this result might have been due to their use of primiparous dams who were already heavy (768 kg on average), with a good body shape that was very close to adult conformation. This was not true, though, of the primiparous females used in our study, which on average weighed 654 kg at the start of the experiment. It is possible that this result reflects the normal response to feed restriction in this breed, with no difference between lactations. However, our results may also have been influenced by the fact that the additional energy needs of primiparous females for growth were taken into account in our calculations of diet formulation.

Reductions in milk production due to feed limitation have been reported in all dairy cows regardless of lactation stage, from post-calving (Roche, 2007) to dry off (Tucker et al., 2009), with the intensity of the response varying among breeds (D'Hour et al., 1995; Gabbi et al., 2016). Such a reduction can also be accompanied by changes in milk composition (Roche, 2007). Here, it was not possible to obtain any information on milk composition as the females were not milked.

Most studies that monitor body weight in response to dietary restriction are performed on growing animals, and thus typically report slower growth rather than weight loss (i.e., Roberts et al., 2007; Keogh et al., 2015). This is similar to what we observed regarding calf growth, with the exception that the restriction in this study only affected calves indirectly through the reduced milk production of their dams. This reduction in milk availability may have also encouraged calves to try a solid diet slightly earlier than usual.

Regarding the resumption of cyclicity, a link between feed restriction and reproductive abilities has been reported in several previous studies. For example, Matthews et al. (2015) found that after 18 days of severe feed restriction (animals received 0.4 of their energy needs for maintenance), 9 of 28 beef heifers experienced abrupt anestrus. Butler (2003) reported delayed ovarian activity in dairy cows experiencing a negative



	BWi	BWrest	BWrec	ADDWrest	ADDWrec	BCSi	BCSrest	BCSrec	ADDBCSrest	ADDBCSrec	CWi	CWrest	CWrec	ADGrest	ADGrec	CW150	Milk1	Milk2	Milk3
BWrest	0.91																		
BWrec	0.9	0.94																	
ADDWrest	0.08	0.45	0.35																
ADDWrec	-0.27	-0.41	-0.08	-0.38															
BCSi	0.49	0.43	0.42	0.02	-0.15														
BCSrest	0.53	0.57	0.52	0.23	-0.28	0.51													
BCSrec	0.49	0.57	0.58	0.34	-0.11	0.4	0.56												
ADDBCSrest	0.22	0.29	0.26	0.26	-0.16	-0.16	0.71	0.33											
ADDBCSrec	-0.08	-0.05	0.02	0.11	0.18	-0.14	-0.52	0.4	-0.45										
CWi	0.17	0.15	0.2	-0.02	0.08	0.08	0.01	-0.01	-0.07	-0.02									
CWrest	0.19	0.2	0.15	-0.08	-0.17	0.08	0.05	-0.05	-0.06	-0.11	0.53								
CWrec	0.18	0.19	0.16	0	-0.13	0.17	0.07	0	-0.07	-0.07	0.59	0.73							
ADGrest	0.12	0.15	0.08	0.07	-0.24	0.08	0.03	-0.02	-0.04	-0.05	0.41	0.7	0.83						
ADGrec	0.08	0.07	0.06	-0.02	-0.06	0.17	0.05	0.01	-0.04	-0.04	0.25	0.3	0.75	0.41					
CW150	0.16	0.18	0.15	0.03	-0.13	0.13	0.06	0.01	-0.05	-0.06	0.63	0.74	0.96	0.88	0.64				
Milk1	0.09	0.08	0.03	-0.05	-0.15	0.1	0.06	-0.11	-0.03	-0.17	0.41	0.49	0.47	0.49	0.25	0.5			
Milk2	0.07	0.1	0.02	0.11	-0.24	-0.11	-0.07	-0.15	0.02	-0.06	0.23	0.27	0.42	0.53	0.24	0.46	0.42		
Milk3	0.04	0	-0.02	-0.09	-0.04	0.04	0	-0.08	0	-0.08	0.16	0.26	0.4	0.36	0.33	0.41	0.28	0.38	
res_cycl	-0.32	-0.3	-0.31	0	0.03	-0.27	-0.22	-0.18	-0.01	0.06	0.01	0.04	0.06	0.16	0.01	0.08	0.03	0.05	0.04

	BWi	BWrest	BWrec	ADDWrest	ADDWrec	BCSi	BCSrest	BCSrec	ADDBCSrest	ADDBCSrec	CWi	CWrest	CWrec	ADGrest	ADGrec	CW150	Milk1	Milk2	Milk3
BWrest	0.87																		
BWrec	0.85	0.94																	
ADDWrest	-0.25	0.23	0.15																
ADDWrec	0.01	-0.11	0.24	-0.25															
BCSi	0.39	0.35	0.32	-0.06	-0.05														
BCSrest	0.35	0.45	0.38	0.17	-0.14	0.42													
BCSrec	0.25	0.39	0.44	0.27	0.15	0.34	0.56												
ADDBCSrest	-0.02	0.09	0.05	0.26	-0.08	-0.47	0.52	0.17											
ADDBCSrec	-0.05	0.01	0.13	0.13	0.32	-0.02	-0.3	0.61	-0.29										
CWi	0.33	0.28	0.26	-0.08	-0.05	-0.03	-0.07	-0.04	-0.05	0.02									
CWrest	0.28	0.21	0.18	-0.1	-0.07	-0.05	-0.12	-0.08	0	0.02	0.51								
CWrec	0.19	0.19	0.2	0	0	-0.02	-0.08	-0.04	-0.05	0.02	0.5	0.71							
ADGrest	0.17	0.17	0.12	-0.01	-0.14	-0.07	-0.05	-0.11	0.05	-0.08	0.31	0.75	0.81						
ADGrec	0.03	0.05	0.11	0.04	0.14	0	-0.12	-0.01	-0.06	0.1	0.24	0.44	0.85	0.51					
CW150	0.25	0.25	0.23	-0.01	-0.05	-0.01	-0.01	-0.02	-0.01	-0.01	0.54	0.74	0.96	0.86	0.73				
Milk1	0.17	0.06	-0.01	-0.16	-0.21	-0.02	-0.13	-0.22	-0.11	-0.16	0.3	0.34	0.38	0.45	0.2	0.4			
Milk2	0.13	0.08	0.01	-0.1	-0.21	0.02	0.06	-0.14	0	-0.22	0.29	0.33	0.48	0.47	0.31	0.52	0.54		
Milk3	0.1	0.05	0.05	-0.1	0	0.04	-0.04	-0.09	-0.09	-0.08	0.29	0.27	0.38	0.28	0.3	0.4	0.37	0.51	
res_cycl	-0.22	-0.31	-0.35	-0.11	-0.15	-0.22	-0.22	-0.24	0.06	-0.08	0.02	0.09	0.05	0.1	0.05	0.01	0.18	-0.03	0

Fig. 1. Comparison of the set of correlations among traits for the HIGH (left) and LOW (right) groups.

energy balance (which is often the case now during early lactation in dairy cows). According to Ferreira et al. (2000), monitoring postpartum body weight was of primary importance in ensuring that females had sufficient reserves to enable the manifestation of estrus. They also found that a 15% weight loss after a restriction did not affect the reproduction of Girolando cows. In our study, detrimental effects on reproduction were only observed in primiparous females, but this may have been due to the design of the experiment. Due to constraints on space and labor, it was not possible for all females to calve at precisely the same moment; primiparous females calved earlier in the season so they would have more time to cycle and reproduce in time for the next year. Consequently, these females experienced a longer winter period than their multiparous counterparts, which meant the restriction period for the LOW group was longer. This may have been one reason why the diet effect was different between primiparous and multiparous cows. Furthermore, primiparous females in the HIGH group resumed cyclicity during the winter period, while multiparous females in both diet groups did so at the onset of the spring period. A return to abundant feed and exposure to natural light in the spring are both known to have a positive effect on ovarian activity (e.g., Yavas and Walton, 2000; Adjorlolo et al., 2019) and here, all females that had not cycled at the end of the winter period did so soon after being turned out on grass (within a matter of a few days). This radical change in housing and diet probably had a strong effect on the multiparous females in both groups but only on LOW-group primiparous females, which contributed to the diet x parity interaction observed.

Level of recovery from the restriction

It is important to note that the differences between the LOW and HIGH groups in all traits diminished over the course of the recovery period, suggesting that recovery did indeed occur. However, even at the end of the recovery period, weight and BCS in the LOW group remained lower than in the HIGH group, so this recovery was only partial. According to Blanc et al. (2010), this type of profile can be defined as flexible. The fact that no difference was observed in these traits between LOW and HIGH multiparous females at the start of their second or third challenges indicates that the cows were eventually able to fully recover, and that their response might in fact be elastic. Based on this, it is clear that the recovery period monitored during this experiment (until mid-July) was too short to observe a full recovery and the time required to achieve true recovery under these conditions remains uncertain (between 3 and 8 months).

The reduction in differences observed between the LOW and HIGH groups during the recovery period indicates that the LOW group performed better during recovery than the non-restricted females. This increase in performance over normal levels is referred to as the “adaptive response of compensation” or “rebound” (Blanc et al., 2006). Only a few days are necessary for digestive and metabolic adaptations to become effective in response to an improvement in nutritional conditions (Hoch et al., 2005). In the present case, cows in the LOW group started to rebuild their body reserves and increased both their weight and BCS. In terms of milk production, the rebound effect took the form of an increase in production, causing a second peak in the lactation curve. This unusual curve shape has previously been observed in situations of increased feed availability, such as during a rainy season (Atti, 1998; Koonawootrittriron et al., 2001). The most frequent type of adaptive response described in the literature is the compensatory growth observed after the refeeding of growing animals (Pereira et al., 2020; Mullins et al., 2021). This phenomenon has been reported extensively and is now commonly used in the management of growing beef cattle. When applied correctly, restriction followed by a refeeding period produces animals of the same weight and body composition as if they had been fed ad libitum throughout, but with a smaller total amount of feed intake (Fitzsimmons et al., 2017). During our study, though, no compensatory growth was observed in calves: the average daily weight gain of calves in both groups during the spring period was almost the same, and the differences in weight at the end of winter remained steady until the end of the spring period. For these traits, it was not possible to verify if full recovery was achieved at a later stage because this information was not available. This is however unlikely, as compensatory growth usually begins rapidly after the start of refeeding (Pereira et al., 2020), which was not the case here, probably because of the young age of the calves. Indeed, the potential for compensatory growth has been found to be dependent on age (among other factors), and calves restricted before weaning display only low levels of compensation (Berge, 1991). Although the economic impact of the restriction on the cows themselves would be limited, as they completely recover before their next calving, the absence of compensatory growth for the calf would be economically detrimental for the farmer, especially considering that selling young calves (of 10 to 12 months of age) has nowadays a large influence on farmers’ revenue (Veysset et al., 2019).

Variations between traits in the correlation set

Through the different correlations between traits in the LOW and HIGH groups, it was possible to detect the influence of restriction on various biological processes. For example, the negative correlation between BWi and ADDWrest in the LOW group was a direct reflection of the fact that, in a situation of feed restriction, greater mobilization is possible with larger body reserves. It is also known that when feed is not limited, lipid accretion and the rebuilding of reserves will be more rapid in thin animals (Petit and Agabriel, 1993), which may explain the negative correlation between cow weight variables and ADDWrec in the HIGH group. When body reserves are low, they logically represent a smaller proportion of body weight, and this was expressed by the weaker correlations between weight and BCS in the LOW group. Finally, the correlation between cyclicity resumption and loss of weight/BCS in LOW animals was indicative of the influence of nutritional status on ovarian activity (Butler, 2003; Diskin et al., 2003). Typically, reproduction is delayed until a female's nutritional status improves and the investment required for gestation no longer competes with maintenance of her own bodily functions (Friggens, 2003).

Prioritization among biological functions

As shown above, all traits were affected by dietary restriction, but the magnitude of the restriction effect was not the same in all cases. By dividing the difference between diet groups by the standard deviation of the HIGH group, we were able to express these differences on the same scale and thus compare them directly. At the end of the winter period, the difference between the two groups was in the same range (between 0.66 and 0.80) for all four types of traits (dam weight, BCS, milk, and calf weight). In general, the ability to mobilize and rebuild body reserves has been found to depend on breed or age (Blanc et al., 2006). During the restriction period, our lactating Charolais females were able to respond through considerable mobilization of their body reserves, but this was not sufficient to preserve normal milk production. In this, the Charolais breed seems to be intermediate between the Salers breed, which prioritizes milk production through extreme mobilization and reduced growth (in primiparous females), and the Limousin breed, which prioritizes the maintenance of body reserves and development over milk production (D'Hour et al., 1995). During the spring period, the trade-off clearly shifted in favor of milk production, with the difference between the two groups reduced to 0.18 s.d. mid-spring compared to 0.4 s.d. for weight and BCS at the end of spring. It was slightly more difficult to compare the resumption of cyclicity because a difference at a given time (at the end of the winter period for example) could not be expressed for that trait. All we can say is that there was a difference of 0.46 s.d. between LOW and HIGH first-lactation females and that all females who had not yet resumed cyclicity did so within a few days of being turned out on grass. However, the effect of this trait seemed to differ slightly from the others as it demonstrated a bimodal response rather than a continuous one. It may be, then, that the resumption of cyclicity depends on a threshold based on nutritional status rather than truly competing with other life functions for scarce energy resources.

Conclusion

Here, we report that winter feed restriction in early-lactation Charolais cows affected all traits measured and generated a response that was balanced between the mobilization of body reserves and the limitation of milk production. This experiment was performed on a large number of females to investigate broad patterns and overall effects, but it might be interesting in the future to study the variation in individual responses to restriction and recovery and the potential genetic factors responsible.

CRediT authorship contribution statement

Pauline Martin: Formal analysis, Investigation, Writing – original draft, Data curation. **Aurélie Vinet:** Data curation, Writing – review & editing. **Lucie Allart:** Data curation, Writing – review & editing. **Frédéric Launay:** Resources. **Dominique Dozias:** Resources. **David Maupetit:** Resources. **Gilles Renand:** Conceptualization, Methodology, Data curation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors have no conflicts of interest to declare.

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