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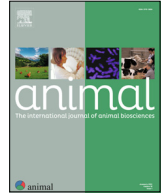
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## Combined mechanistic and genetic modelling to benchmark body reserve traits as proxies of dairy cows' lifetime efficiency in grass-based production systems



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### ABSTRACT

Improving lifetime lactation efficiency of dairy cows by selection is difficult due to the complexity of this trait and the existence of genotype-by-environment interactions. This study aimed at assessing the relevance of traits derived from body reserves as lifetime efficiency indicators under contrasting nutritional environments. Given the absence of large-scale datasets covering a panel of feeding regimes, phenotypes were simulated for populations of 20 000 dairy cows using a mechanistic bioenergetic model. Ten phenotypes were computed for third-lactation cows. Analysed phenotypes comprised total milk production, lactation efficiency, BW at calving (**BWcalv**), DM intake (**DMI**) and interval between first insemination and conception. Five traits described levels and changes of body reserves at different periods during lactation. Lifetime lactation efficiency was computed for all cows (**Life\_Eff**). Three nutritional environments were defined considering a grass-based production system with seasonal calving: a high non-limiting scenario (**HS**) mimicking *ad libitum* access to feed and two limiting environments with moderate (**MS**) and low (**LS**) feed offer. Variance components were estimated for all traits within and between environments using REML. Heritabilities estimated for milk production, lactation efficiency, BWcalv and DMI were moderate in the different environments ( $0.27\text{--}0.35 \pm 0.04$ ). The heritability of body reserve levels and dynamics were moderate in the HS and MS scenarios ( $0.23\text{--}0.30 \pm 0.03$ ) and lower in the LS scenario ( $0.14\text{--}0.25 \pm 0.03$ ). The heritability of Life\_Eff was low in the HS environment ( $0.07 \pm 0.01$ ) and slightly increased in the limiting environments. All genetic correlations estimated between environments were moderate to high ( $\geq 0.66 \pm 0.07$ ), suggesting low to moderate genotype-by-environment interactions. Estimated genetic correlations were moderate between Life\_Eff and body reserve levels (from 0.39 to  $0.51 \pm 0.08$ ) and moderate but negative between Life\_Eff and change in body reserves traits ( $-0.27$  to  $-0.37 \pm 0.09$ ) in the HS environment. The genetic correlations between Life\_Eff and body reserve levels increased to higher values in the limiting environments. In contrast, genetic correlations between Life\_Eff and the changes in body reserves were closer to zero. In conclusion, this study showed that body reserve levels were relevant proxies of lifetime irrespective of the environment. In contrast, changes in body reserves that reflected energy mobilisation in early lactation were less informative about lifetime efficiency in environments with severe feed restrictions.

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### Implications

Increasing lifetime efficiency of dairy cows by selection can improve the sustainability of dairy production at the farm and industry level. However, this trait is difficult to record on a large-scale. The availability of proxies that are easy to record and less

affected by the environment could therefore be valuable to increase selection efficiency. Based on simulated data, this study showed that body reserve levels in early lactation were consistently correlated with lifetime efficiency across nutritional environments. Changes in body reserves were good indicators of short-term efficiency. However, the magnitude of genetic correlations with lifetime efficiency depended on the nutritional environment.

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## Introduction

Given its economic importance in dairy production, feed efficiency is increasingly included in breeding goals to better control genetic gain on both milk yield and feed intake (Brito et al., 2020). The timescale considered to measure feed efficiency is expected to influence selection decisions. Short-term measures of efficiency (at the lactation level) will favour cows with high energy allocation to lactation whereas lifetime efficiency will favour cows able to maintain productive life, at least sufficiently long to dilute the costs of unproductive periods. Thus, selecting for lifetime efficiency is appealing because it will increase lactation efficiency at the animal but also at the herd and production system levels (Martin et al., 2021). To increase lifetime efficiency by genetic selection, it is important to consider traits relating to efficiency and fitness in the breeding goal. Due to the scarcity of feed intake data recorded in practical breeding schemes and the low heritability of fitness-related traits, proxy traits can be included in multi-trait genetic evaluations to increase the accuracy of estimated breeding values on both aptitudes. For example, body condition score (BCS), that is a measure of body reserve level at a given time point, is currently considered in genetic evaluations of many countries (Battagin et al., 2012). Indeed, the ability to maintain sufficient BCS in early lactation is critical to ensure reproduction success and extend productive life (Roche et al., 2009a). On the other hand, change in body reserves in early lactation is an indicator of energy balance. It is genetically correlated with higher lactation efficiency but also poorer fertility performance (Roche et al., 2009a), both aptitudes being needed for achieving high lifetime efficiency. This trait is not yet currently included in genetic evaluations of dairy cattle but automated phenotyping of BCS based on image analysis could make it possible to have phenotypes on a large scale (Spoliansky et al., 2016). Both levels and change in BCS are life-history traits that influenced by the genetics of cows and the nutritional environment (Berry et al., 2003b). In this study, we hypothesised that cows with high lifetime lactation efficiency would exhibit different body reserve profiles during lactation under contrasting nutritional environments. This means that indicator traits derived from body reserve levels and changes in a non-limiting environment may not be relevant in a nutritional environment with more severe energy restriction. To our knowledge, little research has addressed this issue given the scarcity of datasets available with both body reserve and feed intake records under-contrasted nutritional environments.

To overcome this issue, we capitalised on the mechanistic bioenergetic model of a dairy cow developed by Puillet et al. (2021) to simulate performance datasets of a population of related cows. This mechanistic model is based on the energy allocation framework applied to livestock (Beilharz et al., 1993; Rauw, 2009). In the model, acquisition and allocation equations are viewed as “meta-mechanisms” (Tardieu et al., 2020) that aggregate underlying processes bound to the dynamic interplay between life functions. Therefore, it is possible to represent variation in lifetime trajectories of various phenotypes by defining different combination of acquisition and allocation parameters (AAPs). Further, the model explicitly allows trade-offs to occur between productive and non-productive life functions, both because of energy partitioning (e.g. energy partitioned between milk production and body reserves) and also because of the milk production and BCS feedback on the probability of conception (e.g. lower conception probability for high milk production level). Thereby, it is possible to evaluate the correlations between efficiency measured over different timescales. The development of such mechanistic simulation model was shown to be relevant to cast light on how genetically driven energy acquisition and allocation traits could generate

genotype-by-environment (GxE) interactions on lifetime efficiency of dairy cows in case of nutritional constraints (Puillet et al., 2021). Although such models rely on a series of assumptions (for a review see (Douhard et al., 2021)), it makes a good starting point to explore scenarios in which the nutritional constraint only is varied. The objective of this study was to evaluate the magnitude of GxE interactions that affect lifetime efficiency and its underlying components, including body reserve levels and changes during lactation, along a gradient of nutritional constraint.

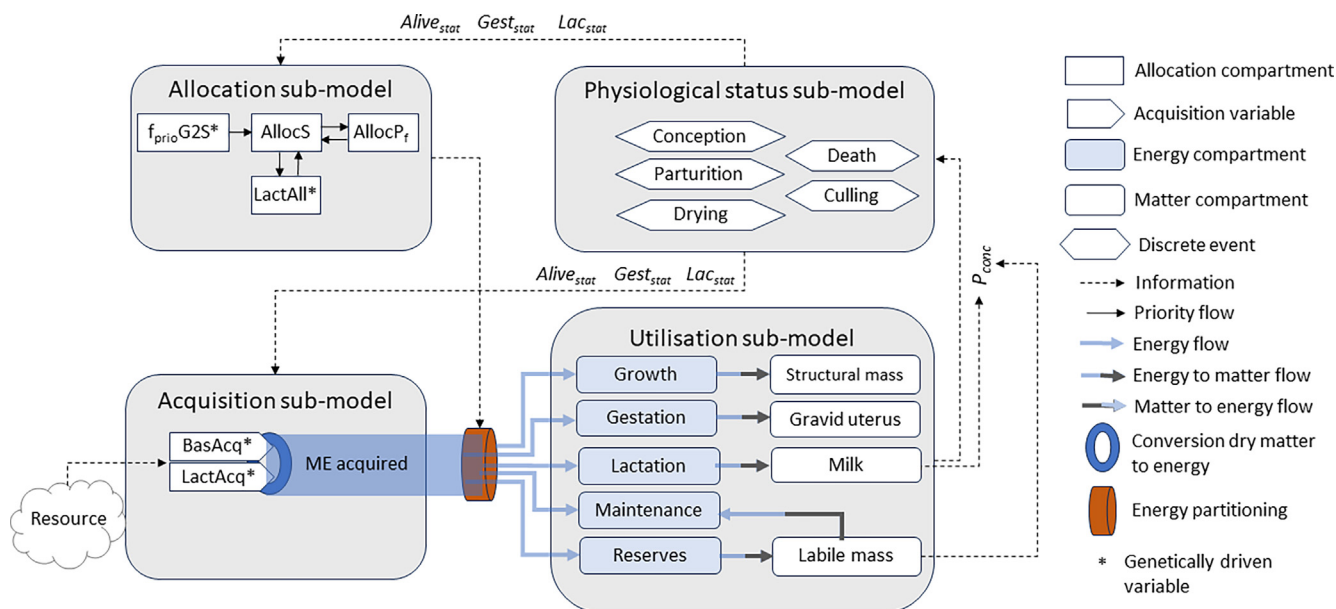
## Material and methods

### Mechanistic dairy cow model

We used the mechanistic model implemented in the AQAL stochastic simulation tool developed by (Puillet et al., 2016; 2021). This bioenergetic model simulates dynamic energy flows in a dairy cow from intake to allocation to the main energy sinks (maintenance, lactation, growth, gestation, body reserves). The phenotypic trajectories of milk production, DM intake (DMI) and body mass components, including body reserves, are then simulated over the lifetime of cows. This includes the timing and success of reproduction events as well (Puillet et al., 2016). Variability in phenotypic trajectories was simulated by tuning four energy acquisition and allocation variables that represented the main inter-individual sources of variance for energy acquisition and allocation (Fig. 1). They were also assumed to be genetically driven as described in the following section. The acquisition parameters relate to the maximal DMI in a non-constraining environment for a non-lactating female (basal acquisition, **BasAcq**, in kg of DM/d), and the maximal increase in DMI during lactation (lactation acquisition, **LactAcq**, in kg of DM/d). The first energy allocation parameter ( $f_{\text{prioG2S}}$ , dimensionless) is the rate of transfer from allocation to growth (i.e. building structural mass) toward allocation to survival (i.e. covering maintenance costs and building body reserves). This parameter drives the longitudinal change in energy allocation to growth over the female lifetime. A high value implies a fast decrease in allocation to growth as the female ages, i.e. a lower structural mass and higher body reserves. The second energy allocation parameter drives the allocation to lactation and corresponds to the magnitude of the shift from allocation to survival toward allocation to lactation at parturition (**LactAll**, dimensionless), i.e. the female's investment into milk production in terms of proportion of energy intake. The mean values of BasAcq, LactAcq,  $f_{\text{prioG2S}}$  and LactAll were determined by cross-validation using real data and were set to 7.00 kg DM/d, 10.25 kg DM/d, 0.0035 and 0.56, respectively, as in Puillet et al. (2021). Further details concerning the model and its implementation can be found in Puillet et al. (2016 and 2021).

### Genetic determinism of acquisition and allocation parameters

The four AAPs were under genetic control, meaning that part of the phenotypic variance around the mean values was explained by additive genetic effects. The genetic parameters assumed for acquisition and allocation of input traits were determined based on a sensitivity analysis to generate simulated datasets with realistic genetic parameters for milk production and feed efficiency traits (Bouquet et al., 2022a). Heritability was set to 0.35 for the four AAPs and the phenotypic CV to 0.10. A genetic module enabled the simulation of a population of 20 000 cows with a simple half-sib pedigree structure. It was simulated by mating at random 200 unrelated sires and 20 000 unrelated dams to generate a single generation of 200 half-sib families of 100 cows. The true breeding value (TBV) of cow  $i$  for AAP  $j$  was calculated as:



**Fig. 1.** Conceptual representation of the variables in the bioenergetic model of a dairy cow and their inter-connections (adapted from Fig. 1 in Puillet et al., 2016). LactAll: allocation to lactation;  $f_{prioG2S}^*$ : change in allocation priority from growth to survival; AllocP<sub>f</sub>: allocation to gestation (future progeny); AllocS: allocation to soma; BasAcq: basal acquisition; LactAcq: lactation acquisition; ME: feed metabolisable energy;  $P_{conc}$ : probability of conception;  $Alive_{stat}$ : Boolean for alive status;  $Gest_{stat}$ : Boolean for gestating status;  $Lac_{stat}$ : Boolean for lactating status.

$$TBV_{i,j} = 0.5 * (TBV_{s,j} + TBV_{d,j}) + MS_{i,j}$$

where  $TBV_{s,j}$  and  $TBV_{d,j}$  are the TBV of the unrelated sire  $s$  and dam  $d$  for trait  $j$ , sampled from independent normal distributions for each AAP with genetic variance  $\sigma_{g,j}^2$ , and  $MS_{i,j}$  is the Mendelian sampling term of cow  $i$  for AAP  $j$  that was drawn independently from a normal distribution with variance equal to  $0.5 * \sigma_{g,j}^2$ . Based on these TBV, a phenotypic value  $y_{i,j}$  was sampled for AAP  $j$  of individual  $i$  as:

$$y_{i,j} = \mu_j + TBV_{i,j} + e_{i,j}$$

with  $\mu$  the mean value of AAP trait  $j$ , and  $e_{i,j}$  a residual term sampled from a normal distribution with residual variances determined to achieve the desired level of heritability. The phenotypic values sampled for AAPs described the energy acquisition and allocation strategy of the cow, influencing thereby individual responses to nutritional challenges. They were used as input variables to simulate lifetime phenotypic trajectories of each individual cow using equations in the energy utilisation sub-model (Puillet et al., 2016) and environmental information as described in the next section.

### Simulated production systems and nutritional environments

The simulation of phenotypic trajectories also requires inputs for feed resource availability (quantity and quality). DM intake of cows can be restricted in simulations if the feed offer is limiting compared to cows' acquisition potential. Hence, DMI corresponds to the minimum value between total acquisition targeted by the cow (basal and lactation) and the feed offer. As a case study, we modelled the same production system as Puillet et al. (2021), i.e. a grass-based production system with seasonal calving typical of New Zealand context. The population of 20 000 cows was simulated from birth to death as a single cohort. The mating season started each year on the same day (October 10th) and lasted for 10 weeks. Gestation lasted 282d and cows were dried-off 90d before calving or at latest on May 15th. First mating of heifers

occurred at 424d of age. Females that were not pregnant at the end of the mating season were culled. In addition, females dropped out of the simulated herd when their body reserves were completely depleted due to insufficient energy acquisition or too high allocation to growth or lactation.

Different nutritional environments were simulated. Seasonal variation in feed quality was kept constant across environments and defined to be consistent with the variation in metabolisable energy content of grass (Roche et al., 2009b). Metabolisable energy content varied from 10.85 to 12.45 MJ/kg of DM with a yearly average of 11.70 MJ/kg of DM. Three nutritional scenarios were simulated by changing the DM offer with seasonal changes over a year corresponding to values found in the literature (Doole et al., 2013). In the baseline scenario, a high and non-limiting environment (HS) was defined mimicking *ad libitum* access to feed. A second moderate nutritional environment (MS) was calibrated so that DM offer could be limiting for high-acquisition cows. The yearly average DM offer was 12.2 kg DM/d per cow with values ranging from 10 to 16.8 kg DM/d depending on seasonality of grass production. Lastly, a low nutritional environment (LS) was simulated with a strong constraint on DM offer. The yearly average DM offer was 9.8 kg DM/d per cow with values ranging from 8 to 13.4 kg DM/d per cow. These nutritional environments mimicked plausible situations encountered in more unfavourable grazing conditions with moderate and low feed availability (Dairy NZ, 2022).

### Definition of phenotypes

In this study, we derived phenotypes from simulated trajectories for ten traits estimated during third lactation. These traits comprised: total energy corrected milk production (Milk, in kg), BW at calving (BW<sub>calv</sub>, in kg), DMI averaged over the whole lactation (in kg/d) and lactation efficiency (Lact\_Eff, in % points), expressed as the ratio of the total energy allocated to milk production over the total energy intake for the whole lactation, and the interval from first insemination to conception (IFC, in days). The timing of oestrus was simulated for all cows during the mating period. The reproduction success at each mating was stochastically

simulated using the conception probability that was estimated based on milk production, energy balance and BCS ([Annex 1 in Supplementary Material](#)). IFC spanned from 0d to 63d due to the 10-week mating period. To avoid data censoring for cows that failed to reproduce, a penalty value of 84d was set by default for cows that were not pregnant after the 4th oestrus as in [Puillet et al. \(2021\)](#). Five traits were derived from body reserve trajectories to evaluate the ability of cows to mobilise and reconstitute their body reserves during lactation. In this simulation study, body reserve traits were estimated as the ratio of labile mass over empty BW and expressed in percentage points. We considered the level of body reserves at calving (**BRcalv**) and at nadir (**BRmin**), as well as the time between calving and nadir (**TimeNadir**, in days). The change in body reserve levels was calculated during early lactation (**dBRearly**, in % points) as the difference between BRcalv and BRmin. The total change in body reserves over the whole lactation (**dBRTot**, in % points) was also estimated as the difference of body reserve level between the beginning and the end of lactation. Phenotypes were only considered for lactations longer than 220d. Finally, lifetime efficiency (**Life\_Eff**, in % points) was estimated for all simulated cows as the ratio of the total energy allocated to milk production over the total energy intake over their whole life from birth to culling. In the following, we will refer to Lact\_Eff as short-term lactation efficiency and Life\_Eff as lifetime efficiency.

#### Estimation of variance components

All traits were analysed using the following animal linear mixed model:

$$Y = Xb + Zu + e$$

With  $b$  the vector of fixed effects that comprised the week of calving (four levels) for all traits except AAP traits and Life\_Eff, and the number of days in milk as covariate for Milk, Lact\_Eff, and dBRTot traits to correct for shorter lactations;  $X$  was the incidence matrix relating performances to the fixed effects;  $u$  was the vector of additive genetic values following a normal distribution  $N(0, A\sigma_g^2)$  where  $A$  was the additive relationship matrix and  $\sigma_g^2$  the genetic variance of the trait;  $Z$  was the incidence matrix relating performances to animals, and  $e$  was the vector of residuals following a normal distribution  $N(0, I\sigma_e^2)$  where  $\sigma_e^2$  was the residual variance of the trait and  $I$  the identity matrix. Variance components were estimated for all four AAPs and for the above-mentioned traits. Initially, univariate analyses were carried out to estimate heritabilities. Then, bivariate analyses were carried out to estimate genetic and phenotypic covariances between traits within a given environment. Within each replicate, the same 200-daughter groups were simulated in each of the environments allowing us to estimate genetic correlations for the same trait between environments. All calculations were performed using the Average Information ReML algorithm implemented in the DMU software ([Madsen and Jensen, 2013](#)).

#### Comparison of simulated phenotypes and genetic parameters across scenarios

Each scenario was replicated 20 times to reduce deviations that may occur due to stochasticity in simulations, that arises from the sampling of reproduction success at each mating, and to refine estimates of genetic correlations between traits of low heritability. Performance, heritabilities, and genetic and phenotypic correlations were compared across environments. The normality of response variables was checked within each scenario using the Shapiro-Wilks test. Then, the homogeneity of variance across scenarios was evaluated using the Levene test. In most cases, variances were different across scenarios. Therefore, a one-way Welch's ANOVA was carried out followed by a Games-Howell post-

hoc test to test pairwise differences between nutritional environments. Those statistical analyses were undertaken with the rstatix package ([Kassambara, 2021](#)) in R ([R Core Team, 2021](#)). A compiled version of the simulation software and R programs to generate simulated datasets were made available as a data paper ([Bouquet et al., 2022a](#)).

## Results

### Description of simulated performance

The environment had a large impact on the mean production and reproduction performance of cows, all changes being significant between environments ([Table 1](#)). On average, DMI was reduced by 13 and 28% in the MS and LS environments compared to the HS environment. The inter-individual variance of DMI strongly decreased due to simulated reduction in the DM offer. In the LS environment, the CV of DMI was close to zero, meaning that all cows had the same intake, irrespective of their acquisition potential. The differences in mean performance for other simulated traits were moderate between the HS and MS environments ( $-646$  kg milk,  $-0.7\%$  of Lact\_Eff,  $+2.2$  d of IFC) and large between the MS and LS environments ( $-907$  kg milk,  $-1.2\%$  of Lact\_Eff,  $+4.9$  d of IFC). Life\_Eff was moderately lower in the MS environment compared to the HS environment ( $-2.5\%$  points) and very much lower in the LS environment compared to the MS environment ( $-5.7\%$  points). All changes in CV between environments were generally small yet significant, except for Lact\_Eff in the HS and MS environments. Finally, the numbers of cows starting and completing third lactation were also influenced by the nutritional environment ([Table 1](#)). They were slightly higher in the HS than in the MS environment. Nonetheless, the proportion of cows not completing third lactation was comparable in both environments ( $<1\%$ ). On the contrary, numbers of cows starting and completing third lactation were much lower in the LS than in other environments and the proportion of cows failing during third lactation was also much higher (16.7%).

Body reserve levels at calving and nadir significantly decreased whilst TimeNadir clearly increased along the gradient of nutritional constraint ([Table 2](#)). Similarly, dBRearly was significantly more negative in limiting environments. In the HS environment, dBRTot was close to zero meaning that, on average, cows were able to fully restore body reserves to the initial level at calving. Finally, cows were not able to fully restore body reserves during third lactation both in the MS ( $\text{dBRTot} = -3.23 \pm 4.10\%$  points) and LS environments ( $\text{dBRTot} = -9.04 \pm 4.40\%$  points).

### Phenotypic trajectories of cows with high lifetime efficiency

The average profile of body reserve levels over the lactation was plotted for the whole population and the 10% best cows on lifetime efficiency in each environment using the first replicate of simulations ([Fig. 2](#)). The average AAP traits for both groups of cows are presented in [Table S1 in supplementary material](#). The best cows for lifetime efficiency had higher body reserve levels at calving and mobilised more reserves in early lactation in the HS and MS environments. They were also able to restore body reserves at a faster pace during the second half of lactation. In the HS environment, the group of best cows for lifetime efficiency had slightly lower DMI over the whole lifetime, produced slightly more milk especially around the lactation peak, and were much lighter than average ([Fig. S1 in Supplementary Material](#)). In the MS environment, DMI was very similar for both groups of cows due to the restricted feed offer. On average, cows were lighter than in the HS environment due to energy restriction occurring in previous

**Table 1**  
Mean performance and CV averaged across replicates for production and reproduction traits of cows in all three nutritional environments.

Variable	Units	Statistics	Nutritional environment		
			High	Moderate	Low
Number of cows					
Starting third lactation		Mean	14 771 ± 20.0	13 486 ± 22.3	9 707 ± 33.9
Completing third lactation		Mean	14 653 ± 21.1	13 392 ± 25.5	8 085 ± 36.7
Traits					
Milk	Kg	Mean	5 072 ± 2.33 <sup>a</sup>	4 426 ± 1.33 <sup>b</sup>	3 519 ± 1.18 <sup>c</sup>
		CV	11.1 ± 0.02 <sup>a</sup>	8.5 ± 0.01 <sup>b</sup>	8.1 ± 0.01 <sup>c</sup>
Lact_Eff	% units	Mean	55.5 ± 0.01 <sup>a</sup>	54.8 ± 0.01 <sup>b</sup>	53.6 ± 0.02 <sup>c</sup>
		CV	7.5 ± 0.01 <sup>a</sup>	7.5 ± 0.01 <sup>a</sup>	7.0 ± 0.01 <sup>b</sup>
BWcalv	Kg	Mean	551.5 ± 0.33 <sup>a</sup>	527.2 ± 0.25 <sup>b</sup>	467.4 ± 0.21 <sup>c</sup>
		CV	11.3 ± 0.02 <sup>a</sup>	9.3 ± 0.02 <sup>b</sup>	7.6 ± 0.01 <sup>c</sup>
DMI	Kg/day	Mean	14.1 ± 0.01 <sup>a</sup>	12.5 ± 0.01 <sup>b</sup>	10.2 ± 0.01 <sup>c</sup>
		CV	7.1 ± 0.01 <sup>a</sup>	1.9 ± 0.01 <sup>b</sup>	0.5 ± 0.01 <sup>c</sup>
IFC	Days	Mean	42.0 ± 0.05 <sup>a</sup>	44.2 ± 0.06 <sup>b</sup>	49.1 ± 0.09 <sup>c</sup>
		CV	55.5 ± 0.03 <sup>a</sup>	55.0 ± 0.04 <sup>b</sup>	52.4 ± 0.08 <sup>c</sup>
Life_Eff	% units	Mean	37.5 ± 0.01 <sup>a</sup>	35.2 ± 0.02 <sup>b</sup>	29.5 ± 0.03 <sup>c</sup>
		CV	16.0 ± 0.02 <sup>a</sup>	15.9 ± 0.02 <sup>b</sup>	17.9 ± 0.02 <sup>c</sup>

Abbreviations: BWcalv = BW at calving; DMI = Daily DM intake on the whole lactation; Milk = Milk production; Lact\_Eff = Energy conversion ratio during third lactation; IFC = Interval between first insemination and conception; Life\_Eff = Lifetime energy conversion ratio.

<sup>a-c</sup> Mean values within a row with different superscripts differ significantly at  $P < 0.05$  based on 20 replicates.

**Table 2**  
Mean performance and mean SD across replicates for body reserve levels of cows and changes during lactation stages in all three nutritional environments.

Trait	Units	Statistics	Nutritional environment		
			High	Moderate	Low
BRcalv	Kg/kg, in % points	Mean	29.44 ± 0.04 <sup>a</sup>	27.38 ± 0.03 <sup>b</sup>	22.30 ± 0.03 <sup>c</sup>
		SD	8.08	7.40	6.05
BRmin	Kg/kg, in % points	Mean	24.91 ± 0.04 <sup>a</sup>	20.07 ± 0.04 <sup>b</sup>	11.64 ± 0.04 <sup>c</sup>
		SD	9.40	9.31	7.84
TimeNadir	Days	Mean	39.08 ± 0.07 <sup>a</sup>	78.02 ± 0.17 <sup>b</sup>	115.41 ± 0.26 <sup>c</sup>
		SD	17.20	43.69	64.63
dBRearly	Kg/kg, in % points	Mean	-4.53 ± 0.01 <sup>a</sup>	-7.31 ± 0.01 <sup>b</sup>	-10.66 ± 0.02 <sup>c</sup>
		SD	1.93	3.02	3.53
dBRtot	Kg/kg, in % points	Mean	0.60 ± 0.01 <sup>a</sup>	-3.23 ± 0.02 <sup>b</sup>	-9.04 ± 0.02 <sup>c</sup>
		SD	3.06	4.10	4.40

Abbreviations: BRcalv = Body reserves at calving; BRmin = Body reserves at nadir; TimeNadir = Lactation day when body reserves reach nadir; dBRearly = Change in body reserves between calving and nadir; dBRtot = Change in body reserves between calving and end of lactation.

<sup>a-c</sup> Values within a row with different superscripts differ significantly at  $P < 0.05$  based on 20 replicates.

lactations, but the difference in BW between the best cows on Life\_Eff and the average was conserved. The group of best cows mobilised more body reserves than average in early lactation but fully restored them by the end of lactation. On the contrary, the best cows for lifetime efficiency in the LS environment had similar body reserve levels at calving compared to average but experienced a smaller drop in body reserves in early lactation. After nadir, their body reserve levels remained higher throughout lactation (Fig. 2).

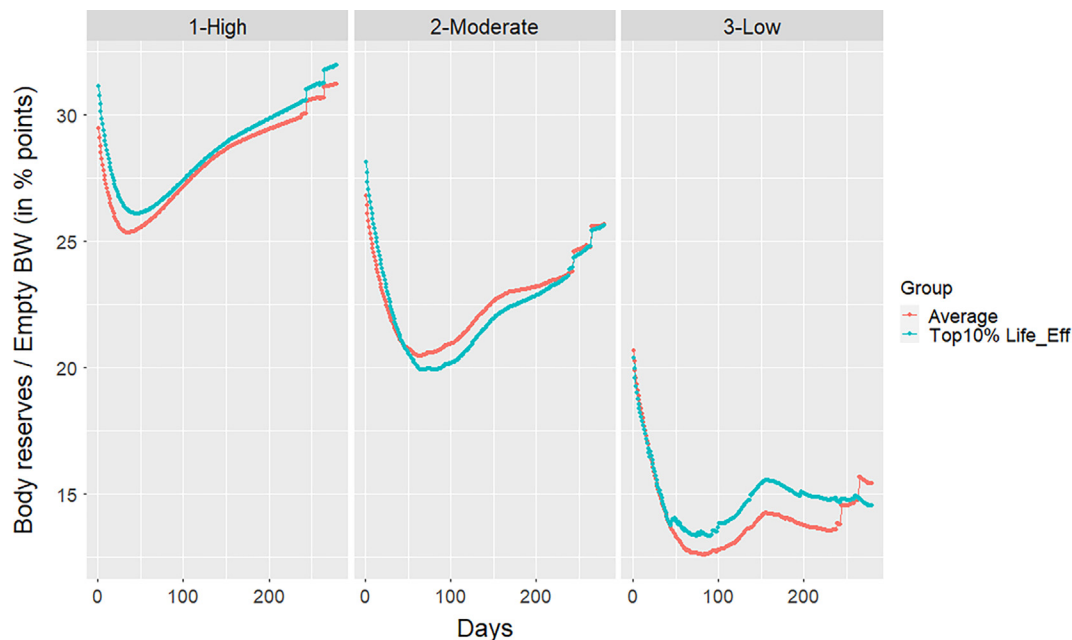
#### Heritabilities estimated for simulated traits

Heritabilities averaged over 20 replicates are presented in Table 3. The detailed variance components estimated for each trait and environment can be found in Table S2. On average, heritabilities estimated for the four AAP traits were equal to  $0.35 \pm 0.03$  as defined in the simulation (results not presented). Average heritabilities estimated for BWcalv ranged from 0.32 to  $0.34 \pm 0.04$  in all three environments. Heritability of DMI was moderate ( $0.35 \pm 0.04$ ) in the HS environment and decreased along the gradient of nutritional constraint to reach  $0.22 \pm 0.03$  in the LS environment. Heritability estimates of Milk and Lact\_Eff were moderate in the HS environment and decreased to slightly lower values in limiting environments. Heritabilities estimated for body reserve levels and

changes in body reserve levels were moderate in the HS and MS environments (from 0.24 to  $0.30 \pm 0.03$ ) and low to moderate in the LS environment (from  $0.14 \pm 0.02$  to  $0.25 \pm 0.03$ ). Heritabilities estimated for TimeNadir were also moderate in the HS environment but dropped to lower and not significantly different values in the MS and LS environments. Finally, heritabilities of lifetime efficiency were low in the HS environment ( $0.07 \pm 0.01$ ) and increased along the gradient of nutritional constraint to reach  $0.17 \pm 0.02$  in the LS environment.

#### Correlations between efficiency, and production and reproduction traits

Genetic and phenotypic correlations estimated between efficiency, production and reproduction traits are presented in Table 4 for all nutritional environments. In the HS environment, Lact\_Eff was highly genetically correlated with Milk, not correlated with DMI ( $0.04 \pm 0.08$ ), and negatively correlated with BWcalv ( $-0.45 \pm 0.04$ ). Positive and unfavorable correlations were estimated between Lact\_Eff and IFC at the genetic and phenotypic level. High genetic and phenotypic correlations were estimated between Lact\_Eff and Life\_Eff ( $\geq 0.81 \pm 0.04$ ). Life\_Eff was highly genetically correlated with Milk ( $0.67 \pm 0.06$ ), positively with DMI ( $0.25 \pm 0.09$ ) and negatively with BWcalv ( $-0.31 \pm 0.09$ ) and IFC ( $-0.25 \pm 0.13$ )



**Fig. 2.** Profile of the ratio of body reserves to empty BW for all cows in third lactation, and the top 10% best for lifetime efficiency (Life\_Eff), in the high, moderate and low nutritional environments.

**Table 3**

Averaged heritabilities (along with average SE) estimated based on twenty replicates for the different traits recorded for cows in the high (HS), moderate (MS) and low (LS) nutritional environments.

Trait	Nutritional environment					
	HS		MS		LS	
	Heritability	SE	Heritability	SE	Heritability	SE
Milk	0.33 <sup>a</sup>	0.04	0.29 <sup>b</sup>	0.03	0.27 <sup>c</sup>	0.03
Lact_Eff	0.32 <sup>a</sup>	0.04	0.30 <sup>a</sup>	0.03	0.27 <sup>b</sup>	0.03
BWcalv	0.34 <sup>a</sup>	0.04	0.33 <sup>a</sup>	0.04	0.32 <sup>a</sup>	0.04
DMI	0.35 <sup>a</sup>	0.04	0.26 <sup>b</sup>	0.03	0.22 <sup>c</sup>	0.03
IFC	0.01 <sup>a</sup>	0.01	0.01 <sup>a</sup>	0.01	0.01 <sup>a</sup>	0.01
BRcalv	0.28 <sup>a</sup>	0.03	0.25 <sup>b</sup>	0.03	0.16 <sup>c</sup>	0.03
BRmin	0.27 <sup>a</sup>	0.03	0.24 <sup>b</sup>	0.03	0.14 <sup>c</sup>	0.02
TimeNadir	0.26 <sup>a</sup>	0.03	0.15 <sup>b</sup>	0.03	0.14 <sup>b</sup>	0.02
dBRearly	0.26 <sup>a</sup>	0.03	0.25 <sup>a</sup>	0.03	0.21 <sup>b</sup>	0.03
dBRTot	0.30 <sup>a</sup>	0.03	0.29 <sup>a</sup>	0.03	0.25 <sup>b</sup>	0.03
Life_Eff	0.07 <sup>a</sup>	0.01	0.09 <sup>b</sup>	0.01	0.17 <sup>c</sup>	0.02

Abbreviations: Milk = Milk production; Lact\_Eff = Lactation efficiency in third lactation; BWcalv = BW at calving; DMI = Daily DM intake on the whole lactation; IFC = Interval between first insemination and conception; Life\_Eff = Lifetime energy conversion ratio; BRcalv = Body reserves at calving; BRmin = Body reserves at nadir; TimeNadir = Lactation day when body reserves reach nadir; dBRearly = Change in body reserves between calving and nadir; dBRTot = Change in body reserves between calving and end of lactation.

<sup>a,b,c</sup> Values within a row with different superscripts differ significantly at  $P < 0.05$  based on 20 replicates.

). Genetic and phenotypic correlations between Lact\_Eff and Life\_Eff remained at a high level in the MS and LS nutritional environments, yet slightly lower than in the HS nutritional environment. However, we observed some changes in the correlation pattern between efficiency measures and other traits. The genetic and phenotypic correlations between Lact\_Eff and Milk increased to higher values in both MS and LS environments. A progressive decrease in genetic correlations was observed between Lact\_Eff and BWcalv as the nutritional constraint increased. Although phenotypic correlation between Lact\_Eff and IFC remained at a moderate level in all three nutritional environments, genetic correlation dropped to a much lower value in the LS environment. Genetic and phenotypic correlations between Life\_Eff and Milk remained high in the three nutritional environments. The genetic correlations between

Life\_Eff and DMI progressively decreased to reach moderate and negative values in the LS environment. Finally, genetic correlations between Life\_Eff and BWcalv as well as IFC became highly negative in the MS and LS environments.

*Correlations between efficiency measures and body reserve traits*

Genetic and phenotypic correlations estimated between efficiency measures and body reserve traits are presented in Table 5 for all nutritional environments. Genetic and phenotypic correlations estimated between all groups of traits are presented in Table S3 of Supplementary Material for the HS environment. Moreover, genetic correlations between all traits estimated in the MS and LS environments and the significance of changes in genetic

**Table 4**

Average genetic<sup>1,2</sup> and phenotypic correlations (respectively  $r_g$  and  $r_p$ ) estimated between efficiency, production and reproduction traits of cows in the different nutritional environments.

Nutritional environment	Trait	Correlation	Milk	DMI	BWcalv	IFC	Life_Eff
High (HS)	Lact_Eff	$r_g$	0.72	0.04	-0.45	0.63	0.81
		$r_p$	0.73	0.04	-0.46	0.21	0.87
	Life_Eff	$r_g$	0.67	0.25	-0.31	-0.25	-
		$r_p$	0.77	0.19	-0.54	-0.60	-
Moderate (MS)	Lact_Eff	$r_g$	0.97	-0.03	-0.58	0.59	0.71
		$r_p$	0.97	0.00	-0.58	0.27	0.82
	Life_Eff	$r_g$	0.63	-0.17	-0.68	-0.51	-
		$r_p$	0.78	-0.19	-0.77	-0.61	-
Low (LS)	Lact_Eff	$r_g$	1.00	-0.12	-0.67	0.36	0.73
		$r_p$	0.99	-0.05	-0.67	0.24	0.77
	Life_Eff	$r_g$	0.71	-0.45	-0.83	-0.79	-
		$r_p$	0.76	-0.35	-0.84	-0.64	-

Traits: Milk = milk production; Lact\_Eff = energy conversion ratio in third lactation; Life\_Eff = Lifetime energy conversion ratio; BWcalv = BW at calving; DMI = daily DM intake on the whole lactation; IFC = interval between first insemination and conception.

<sup>1</sup> Average SE of genetic correlation estimates ranged from 0.04 to 0.10, except for genetic correlations between IFC and other traits where it ranged from 0.19 to 0.32.

<sup>2</sup> SEM of genetic correlation estimates ranged from 0.01 to 0.04, except for genetic correlations between IFC and other traits where it ranged from 0.03 to 0.08.

**Table 5**

Average genetic<sup>1,2</sup> and phenotypic correlations (respectively  $r_g$  and  $r_p$ ) estimated between efficiency and body reserve traits of cows in the high, moderate and low nutritional environments.

Nutritional environment	Trait	Correlation	BRcalv	BRmin	TimeNadir	dBRearly	dBRTot
High	Lact_Eff	$r_g$	-0.32	-0.46	0.86	-0.92	-0.74
		$r_p$	-0.38	-0.51	0.77	-0.86	-0.74
	Life_Eff	$r_g$	0.51	0.39	0.40	-0.37	-0.27
		$r_p$	-0.05	-0.20	0.59	-0.64	-0.60
Moderate	Lact_Eff	$r_g$	-0.26	-0.51	0.57	-0.88	-0.60
		$r_p$	-0.38	-0.58	0.42	-0.85	-0.63
	Life_Eff	$r_g$	0.67	0.54	0.00	-0.14	0.03
		$r_p$	0.12	-0.08	0.15	-0.48	-0.29
Low	Lact_Eff	$r_g$	0.03	-0.36	0.35	-0.78	-0.53
		$r_p$	-0.25	-0.51	0.29	-0.78	-0.60
	Life_Eff	$r_g$	0.87	0.82	-0.22	0.02	0.24
		$r_p$	0.43	0.22	-0.22	-0.32	-0.08

Abbreviations: Lact\_Eff = Energy conversion ratio in third lactation; Life\_Eff = Lifetime energy conversion ratio; BRcalv = Body reserves at calving; BRmin = Body reserves at nadir; TimeNadir = Lactation day when body reserves reach nadir; dBRearly = change in body reserves between calving and nadir; dBRTot = change in body reserves between calving and end of lactation

<sup>1</sup> Average SE of genetic correlation estimates ranged from 0.02 to 0.10.

<sup>2</sup> SEM of genetic correlation estimates ranged from 0.01 to 0.04.

correlation compared to the HS environment are presented in [Table S4 of Supplementary Material](#). High genetic correlations were estimated between BRcalv and BRmin but also between TimeNadir, dBRearly and dBRTot in all three nutritional environments ([Tables S3 and S4](#)). Lact\_Eff was moderately correlated with BRcalv and BRmin and highly correlated with TimeNadir, dBRearly and dBRTot in the HS environment ([Table 5](#)). Genetic correlations between Lact\_Eff and BRmin remained moderate in the MS and LS environments whereas they were close to zero between Lact\_Eff and BRcalv in the LS environment ( $0.03 \pm 0.03$ ). Genetic correlations between Lact\_Eff and dBRearly remained highly negative in the MS and LS environments ( $\leq -0.78 \pm 0.04$ ). Genetic correlations between Lact\_Eff and dBRTot were slightly reduced in the limiting environments compared to the HS environment. Genetic correlations between Lact\_Eff and TimeNadir progressively decreased from high to moderate values along the gradient of nutritional environments.

Genetic correlations between Life\_Eff and all body reserve traits were moderate in the HS environment; the highest genetic correlation was estimated with BRcalv ( $0.51 \pm 0.08$ ). Interestingly, the phenotypic correlations between Life\_Eff and BRcalv, as well as BRmin, were slightly negative. Finally, genetic correlations between Life\_Eff and BRcalv as well as BRmin increased to high and positive values in the limiting environments. Phenotypic

correlations between these traits also increased progressively to reach moderate and positive values in the LS environment. Genetic correlations between Life\_Eff and dBRearly, as well as dBRTot, increased from moderately negative values in the HS environment to slightly positive values in the LS environment. Phenotypic correlations between these traits followed the same trend although they remained negative in the LS environment.

#### Genotype-by-environment interactions

Genotype-by-environment interactions were assessed as the genetic correlation for a given trait measured in two different environments ([Table 6](#)). Genetic correlations estimated between the HS and MS environments were high yet significantly different from unity for all traits except Lact\_Eff. Milk production was the trait that was the most affected by GxE interactions with a genetic correlation of  $0.83 \pm 0.05$  between the HS and MS environments. Genetic correlations estimated between HS and LS environments remained high for most traits although at a slightly lower level than between the HS and MS environments. The trait that was the most affected by GxE interactions between the HS and LS scenarios was Life\_Eff ( $0.66 \pm 0.07$ ), followed by Milk ( $0.70 \pm 0.07$ ). Genetic correlations estimated between HS and LS environments were higher than 0.80 for all the other traits. Correlations could



**Table 6**

Average genetic correlations ( $r_g$ ) estimated for cow traits recorded in the high and moderate environments, and in the moderate and low nutritional environments.

Trait	High vs Moderate		High vs Low	
	$r_g$	SE	$r_g$	SE
Milk	0.83	0.05	0.70	0.07
BWcalv	0.98	0.01	0.94	0.01
Lact_Eff	0.99 <sup>1</sup>	–	0.99 <sup>1</sup>	–
BRcalv	0.97	0.01	0.90	0.02
BRmin	0.94	0.01	0.82	0.03
TimeNadir	0.93	0.01	0.87	0.02
dBRearly	0.91	0.01	0.87	0.02
dBrtot	0.86	0.02	0.86	0.02
IFC	NC <sup>2</sup>	–	NC <sup>2</sup>	–
Life_Eff	0.92	0.05	0.66	0.07

Abbreviations: Milk = Milk production; Lact\_Eff = Energy conversion ratio; BWcalv = BW at calving; IFC = Interval between first insemination and conception; BRcalv = Body reserves at calving; BRmin = Body reserves at nadir; TimeNadir = Lactation day when body reserves reach nadir; dBRearly = Change in body reserves between calving and nadir; dBrtot = Change in body reserves between calving and end of lactation; Life\_Eff = Lifetime energy conversion ratio.

<sup>1</sup> Genetic correlation fixed at the border of the parameter space.

<sup>2</sup> NC: No convergence of the Restricted Maximum Likelihood algorithm due to low heritability and dataset size.

not be estimated for IFC as the heritability and dataset size were too low to enable proper convergence of the REML algorithm in bivariate analyses.

#### Genetic drivers of lifetime efficiency and body reserve traits

The relative importance of energy acquisition and allocation traits to achieve high lifetime efficiency in contrasting nutritional environments was reflected by the genetic correlations estimated between efficiency and AAP input traits (Table S5). The pattern of genetic correlations between Life\_Eff and AAP input traits changed along the gradient of nutritional environments. In all three environments, estimated genetic correlations between AAP input traits were not significantly different from zero (i.e. the assumed values). In the HS environment, Life\_Eff was poorly genetically correlated with BasAcq, moderately correlated with LactAcq and LactAll, and highly correlated with  $f_{\text{prio}}G2S$ . In limiting environments, the genetic correlation between Life\_Eff and LactAcq dropped to values close to zero whereas the genetic correlation between Life\_Eff and BasAcq became moderately negative. The genetic correlation between Life\_Eff and LactAll clearly decreased along the gradient of nutritional constraint from a positive and moderate value in the HS environment to a slightly negative value in the LS environment. On the contrary, the genetic correlation between Life\_Eff and  $f_{\text{prio}}G2S$  increased to very high values. Similarly, the magnitude of genetic correlations between body reserve and AAP input traits changed along the gradient of nutritional constraint (Table S5). Genetic correlations between LactAcq and all body reserve traits decreased from moderate values in the HS environment to low values in the limiting environments. Genetic correlations sharply increased between TimeNadir and BasAcq whereas it decreased from high to moderate values between TimeNadir and LactAll along the gradient of nutritional constraint. Genetic correlations between BasAcq and dBRearly, as well as dBrtot, became also moderately to highly negative in the limiting nutritional environments.

## Discussion

This study is an extension of the work published by Puillet et al. (2021) with the objective of evaluating how lifetime efficiency and body reserves covary in dairy cows under contrasting nutritional

environments. Results of this study confirmed that the level of body reserves of cows, especially during early lactation, is a robust proxy of lifetime efficiency regardless of the nutritional environment. However, the best cows on lifetime efficiency exhibited different body reserve profiles in contrasting nutritional environments. In environments with little to moderate energy restriction, the mobilisation of body reserves in early lactation is a good indicator of lactation efficiency that can translate to lifetime efficiency if the cow is able to bounce back to the initial body reserve level to prepare for next calving. Thus, cows with high lifetime efficiency had both a large drop in body reserves in early lactation and a minimal change in body reserves over the whole lactation. However, when the ability to reconstitute reserves is compromised by insufficient energy intake, a stronger focus is put on the maintenance of body reserves to maximise reproduction success and extend productive life. In such nutritional environments, it is critical for cows to limit the mobilisation of body reserves in early and then over the entire lactation.

#### Relevance of body reserves as a proxy of lifetime efficiency

Body reserve traits are interesting life-history traits that inform about the magnitude of energetic trade-offs that occurred during the current lactation but also the preceding ones (Roche et al., 2009a). In this study, we focused on traits estimated in third lactation so that cows had already experienced trade-offs during the first two lactations. Results of this study confirmed that cows with high lifetime efficiency exhibited different body reserve profiles in contrasting nutritional environments. Interestingly, the best cows for lifetime efficiency in the HS and MS environments started from a higher level of body reserves at calving, mobilised more body reserves and over a longer period. Having higher BRcalv than average allowed them to maintain body reserves at a sufficient level during the mating period to limit the risk of reproduction failure. In the low nutritional environment, since energy offer was too limiting to enable cows restoring body reserves during lactation, cows with high lifetime efficiency had a lower energy allocation to lactation than average to limit the decrease in conception probability. Although the nutritional constraint increased linearly in the three environments (reduction of DMI by 13 and 28% in the MS and LS environments, respectively, compared to the HS environment), the change in IFC was more than twice larger between the MS and LS than between the HS and MS environments. This result highlighted a non-linear evolution of conception probability along the gradient of nutritional constraint due to a mismatch between the energy offer and cows' nutritional requirements.

Based on estimated genetic correlations, body reserve levels were confirmed as consistent indicators of fertility across the range of nutritional environments considered in this study. Similarly, changes in body reserves were good indicators of short-term lactation efficiency in all environments. However, the genetic correlation between short-term and lifetime efficiency tended to decrease and became even detrimental in environments with moderate to high energy shortage. Therefore, indicator traits describing body reserve mobilisation must be used in close connection with the target production environments, for instance by considering dBRearly or dBrtot as different traits in environments with different nutritional constraints.

#### Critical evaluation of model assumptions

The AQAL mechanistic model was designed to account for the main physiological processes impacting lactation efficiency on different timescales (lactation versus lifetime) and under-contrasted nutritional environments. Heritability estimates obtained for milk production, BW, DMI and efficiency measures simulated in the HS

environment were consistent with those found in the literature for grass-based production systems (Berry et al., 2003a). Moderate heritability values were estimated for body reserve levels, in agreement with literature values reported for body condition score (Berry et al., 2003a; Loker et al., 2011). Heritability estimated for changes in body reserves and TimeNadir were low to moderate in the HS and MS environments. They were higher than estimates reported by (Berry et al., 2002) for change in BCS during early lactation and over the whole lactation (0.07–0.10) in dairy cattle. The heritability estimated for IFC in the current study was very low in all environments (<0.02) and slightly lower than the literature estimates (Muuttoranta et al., 2019). This was expected as IFC was stochastically simulated based on conception probability at the time of insemination. This probability was derived deterministically and mainly captured the effects of energy balance and milk production on reproduction success, disregarding other genetic factors influencing fertility. Although heritability was slightly lower than usual, we believe that it would not change the trend in genetic correlations estimated between IFC, lifetime efficiency and other production traits across nutritional environments.

For all traits resulting from interactions between acquisition and allocation processes, the genetic correlations between environments were significantly different from unity due to the reduction in variance of DMI. Thus, the magnitude of G×E interactions remained low to moderate. Estimates were consistent with values found in the literature for milk production and BW at calving (Berry et al., 2003b; Nauta et al., 2006) but also for BCS around calving ( $\geq 0.70$ ) or at 180 d postcalving ( $\geq 0.84$ ) between extreme groups of herds defined based on a herd milk production average environmental gradient (Berry et al., 2003a).

Even though there is a good agreement between genetic parameters estimated in this study and those reported in the literature, the AQAL mechanistic model relies on a few simplifying assumptions that warrant further attention. First, cows were reared as a single cohort in a common herd because the version of simulation software used in this study could not assign cows to specific herds. As a result, all cows were offered the same amount of feed in the simulation. In the case of competition for feed, we may expect that cows with higher acquisition potential can acquire more energy than their counterparts. Thus, these cows may have been more constrained than what would be observed in practice. In practice, we would also expect differences in feed supply across herds within nutritional environments that should add some noise in the estimation of variance components. If fluctuations around the mean energy offer are small, we expect a negligible impact on (co-)variances estimated between traits. Considering a single herd may also lead to lower standard errors for estimated genetic parameters compared to models including contemporary groups of smaller size. Tests of significance carried out for estimated genetic parameters may therefore be slightly more permissive than observed with real data. However, we expect that this effect is limited in situations where progenies of sires are randomly distributed over contemporary groups of sufficient and balanced size.

Secondly, it was assumed that the four genetically driven acquisition and allocation traits were uncorrelated. It was shown that violation of this assumption can substantially modify the phenotypic response to an environmental challenge (Doeschl-Wilson et al., 2008; Descamps et al., 2016). Real datasets with longitudinal records on several successive lactations for milk production, energy intake, BW and BCS of hundreds of cows are needed to validate these assumptions. Finally, lactation acquisition that describes the innate increase in DMI triggered by lactation, was not associated with higher maintenance requirements. This can explain why lactation acquisition was positively correlated with lifetime efficiency in the non-limiting environment and had no adverse effect in the limiting environments. Hence, the model

needs to be further refined to account for the increased energy costs associated with higher lactation acquisition due to, for instance, increased foraging or digestion.

#### *Genetic drivers of lifetime efficiency under contrasting nutritional environments*

Performances of cows and potential energetic trade-offs were simulated explicitly as the result of interactions between the acquisition and allocation processes under given environmental conditions. Interestingly, high lifetime efficiency was obtained with different combinations of acquisition and allocation parameters under contrasting nutritional environments. When feed offer was not limiting, energy intake was determined by acquisition traits and was therefore only limited by the cow's ability to acquire feed. Hence, the variance of milk production, growth and body reserves depended on both the variance of acquisition and allocation input traits in agreement with van Noordwijk and de Jong (1986). In constrained environments, where the variance of energy intake was much reduced due to the simulated energy restriction, cows with high basal acquisition potential were less efficient over their lifetime. Indeed, these cows exhibited higher BW because they developed their structural mass faster due to higher energy intake during earlier periods without energy restriction. They had higher energy maintenance requirements and experienced more severe energy deficits in early lactation as well as extended periods of negative energy balance. In limiting environments where nutritional requirements could not be covered by energy acquisition, cows that reduced earlier their energy allocation to growing structural mass (higher  $f_{\text{prioG2S}}$ ) were favoured compared to other cows. This gave them the possibility to restore body reserves more quickly during lactation due to lower maintenance requirements. On the contrary, the relative importance of LactAll input trait to achieve high Life\_Eff decreased along the gradient of nutritional constraint. In the non-limiting environment, cows with higher LactAll were more efficient in their lifetime yet slightly less fertile due to higher milk production and body reserve mobilisation. In limiting environments, the same cows had a much higher risk of reproduction failure. Hence, the benefits of breeding cows with higher short-term efficiency were offset by their shorter productive life. In these simulations, fertility had a large impact on lifetime efficiency due to the simulated production system, with all cows not pregnant within the 10-week mating period being culled. In production systems without seasonal calving, we think that genetic and phenotypic correlations between lifetime efficiency and fertility will be of lower magnitude, but the change in genetic correlations observed across nutritional environments should remain valid.

#### *Implications and perspectives*

Until recently, breeding goals have mainly focused on improving lifetime milk production by simultaneously selecting both milk yield and functional traits. In non-limiting environments, such selection is expected to favour cows with higher acquisition potential (higher DMI), higher energy allocation to milk production and lower energy investment in growth. Results of this study suggest that selecting for higher milk production under non-limiting conditions may be suboptimal when cows are reared in harsher environments. Indeed, improved cows might fail in acquiring enough energy to cover their nutritional requirements, leading to longer periods of negative energy balance and higher rates of reproductive failure. Such a situation was observed in trials comparing the milk production, growth and puberty onset of different Holstein subpopulations under pasture conditions in New-Zealand (Roche et al., 2006; Macdonald et al., 2007). Consequently, specific breeding goals were developed to account for genetic parameters

that better reflected the magnitude of energetic trade-offs affecting the traits and give more emphasis to functional traits important to maintain cows' productive life (Roche et al., 2018). The magnitude of GxE interactions estimated for lifetime efficiency between HS and LS environments in this study would justify developing a dedicated breeding program, the correlation being lower than 0.80 (Mulder and Bijma, 2005). Genotype-by-environment interactions were more limited between the HS and MS environments for this simulated population of medium-sized cows with moderate milk production. There is a need to explore how cows of other breeds with different acquisition potential and energy allocation strategies would respond to the different levels of nutritional constraint and in other current or future production systems. Indeed, the advent of climate change is expected to impact nutritional environments and technical efficiency of dairy production systems (Quideville et al., 2022). Our approach of coupling mechanistic and genetic modelling enables investigating this issue in a cost-effective manner.

Estimating the gain in selection accuracy and genetic progress obtained by including new indicator traits in genomic evaluations of dairy cattle was out of the scope of this study. Using genetic parameters published in literature, (Bengtsson et al., 2022) showed that a typical dairy cattle breeding goal including BCS in early lactation as an indicator of resilience in the breeding goal generated more genetic gain on functional traits but had a substantial cost on genetic gain achieved on milk production. These genetic trends were expected in environments with little or moderate nutritional constraints. The benefits of increasing resilience of cows might be larger in harsher environments with severe nutritional constraints. Moreover, Bengtsson et al. (2022) could not predict the impact of breeding goals on lifetime efficiency due to the absence of genetic parameters. To predict long-term selection response for traits affected by trade-offs, mechanistic models can also be advantageously coupled with breeding scheme simulation (Cooper et al., 2021). Such an approach explicitly accounts for GxE interactions that can emerge due to changes in the energy balance induced by selection and environmental changes (Bouquet et al., 2022b). The simulation of phenotypic trajectories with the mechanistic models also enables evaluating lactation efficiency for different timescales. Considering the same dairy cattle breeding scheme as Bengtsson et al. (2022) and genetic parameters presented in this study, Zira et al. (2023) confirmed that including body reserve traits (BRmin, dBRTot) in the breeding goal reduced the selection response achieved on milk production and lifetime efficiency when cows were reared in a non-limiting nutritional environment. However, the same improved cows were better at coping with a severe feed shortage in third lactation than cows selected for the baseline breeding goal due to reduced energetic trade-offs. As a result, they were more efficient over their lifetime and emitted less methane per kg of produced protein.

In conclusion, the use of mechanistic models is a promising approach to derive and benchmark novel proxies of lactation efficiency in dairy cows in a cost-effective way, as well as their sensitivity to changes in nutritional environments. Those changes can originate from more diversified production systems but also climate change. Body reserve levels were confirmed as relevant indicators of lifetime efficiency because they were closely related to reproductive success irrespective of the environment. Changes in body reserves during lactation were highly correlated with lactation efficiency. However, the importance of increasing lactation efficiency decreased along the gradient of nutritional constraint. The use of changes in body reserves as indicators of lifetime efficiency must therefore be carried out in close connection with the target environment.

## Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.animal.2023.101035>.

## Ethics approval

Not applicable.

## Data and model availability statement

A compiled version of the simulation software and R programs to generate simulated datasets were made available as a data paper (Bouquet et al., 2022a) and can be retrieved from: <https://doi.org/10.1016/j.anopes.2022.100017>.

## Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence assisted technologies in the writing process.

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## Declaration of interest

None.

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