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## Research article

# Coupling genetic and mechanistic models to benchmark selection strategies for feed efficiency in dairy cows: sensitivity analysis validating this novel approach



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## ABSTRACT

Coupling genetic and mechanistic models is appealing to explore the impact of energy trade-offs on the expression of feed efficiency traits in dairy cattle and predict selection response. The objective of this study was to evaluate the sensitivity of genetic (co)variances among milk production and feed efficiency (FE) traits simulated with a mechanistic dairy cow model depending on the genetic variability assumed for input parameters. The cow model was calibrated for a grass-based production and included a genetic module. Four genetically driven input parameters described the energy acquisition and allocation to different biological functions of cows. In each simulation, a population of 20 000 cows from 200 unrelated sires was simulated. The nutritional environment was an input of the model and was tailored by modulating feed offer and quality. A non-limiting nutritional environment was simulated to mimic a situation of *ad libitum* feeding and was used as a reference. Two other scenarios were simulated by imposing a moderate and a high DM intake restriction on simulated cows. Five phenotypes related to milk production and FE were considered: milk production, BW at calving, DM intake, lactation efficiency and body reserves during early lactation. These traits were estimated both in first and third lactations. A baseline scenario was defined considering a heritability of 0.35 and a phenotypic CV of 10% for acquisition and allocation parameters (AAPs). Different scenarios were explored by reducing the heritability to 0.15 or increasing CV to 20 and 30% or both. Heritabilities and genetic correlations between simulated traits were estimated using animal linear mixed models. Each scenario was replicated 20 times. Simulated performance and genetic parameters for these traits were compared across scenarios using an ANOVA. The heritability of AAPs only influenced the heritability of simulated traits. The phenotypic CV of AAPs mainly influenced the variability of simulated traits. However, increasing the CV also affected the number of cows reaching first and third lactation, due to the early culling of females with extreme AAPs profiles. Compared to other input parameters, the nutritional environment had the largest effect on both performance and genetic correlations between traits. Using a heritability value of 0.35 and a CV of 10% for all four AAPs enabled the simulation of milk production and FE performance with a realistic mean, variance and genetic correlations among traits in the three considered environments.

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## Implications

Due to the scarcity of feed efficiency datasets in dairy cattle, using simulated datasets is an option to explore the relevance of breeding strategies under different environments. This study capi-

talises on a mechanistic model that simulates phenotypic trajectories of dairy cows over their lifetime. We identified genetic parameters to consider as inputs in the model to simulate traits with realistic means and genetic parameters. The nutritional environment was the input parameter with the highest influence on genetic correlations among simulated traits. This simulation tool is promising to benchmark selection strategies for feed efficiency in dairy cows under various nutritional environments.

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## Specification table

Subject	Breeding and Genetics
Type of data	Compiled Python code to simulate phenotypic data of milk production and feed efficiency traits in dairy cows, R code to manipulate datasets and carry out statistical analysis, shell script to chain all analyses.
How data were acquired	Datasets simulated with AQAL software (Puillet et al., 2016; 2021) compiled under Linux system with pyinstaller (Python 3.8 interpreter). Scripts launched with SLURM load manager. Genetic analysis was undertaken with DMU v5.2 ( <a href="https://dmu.ghpc.au.dk/dmu/DMU/Linux/Previous/">https://dmu.ghpc.au.dk/dmu/DMU/Linux/Previous/</a> ) and statistical analyses with R 4.0.3 programs. Codes were developed and run on the GHPC cluster at QGG centre (Aarhus University, Denmark)
Data format	Linux executable for the simulation software. Text files for analysis pipeline Output of the simulation software in SQLite database. All results after statistical analysis are in text files.
Parameters for data collection	Phenotypic trajectories of dairy cows were simulated for a grass-based production system with seasonal calving. Three nutritional environments simulated by changing the quantity of feed offered to cows.
Description of data collection	Simulated datasets
Data source location	Fill in the information available, and delete from this list as appropriate: Institution: QGG Centre, Aarhus University City/Town/Region: Tjele Country: Denmark
Data accessibility	Repository name: Mendeley Data Data identification number: <a href="https://doi.org/10.17632/txx9zkbd2g.2">https://doi.org/10.17632/txx9zkbd2g.2</a>
	URL: <a href="https://data.mendeley.com/datasets/txx9zkbd2g/2">https://data.mendeley.com/datasets/txx9zkbd2g/2</a>
Related research article	Puillet, L., Ducrocq, V., Friggens, N.C., Amer, P.R., 2021. Exploring underlying drivers of genotype by environment interactions in feed efficiency traits for dairy cattle with a mechanistic model involving energy acquisition and allocation. <i>Journal of Dairy Science</i> , 104, 5805–5816.

## Introduction

For decades, mechanistic models (MMs) have been used to assist decision-making in agriculture. In the livestock sector, such models were developed to help optimising the technical performance of herds and reducing both costs and the environmental footprint of production (Ellis et al., 2020). In animal nutrition, MMs has been a useful tool to predict animal responses to changes in environmental factors (e.g. feed composition, feed restriction, herd management, climate). So far, the use of MMs have been limited in animal breeding. However, there is increased interest in combining mechanistic and genetic modelling to investigate how energy trade-offs could hamper selection response achieved in breeding schemes, either by exacerbating genetic antagonisms between traits or by generating genotype-by-environment (G×E) interactions (Douhard et al., 2014). Such an approach could be beneficial for the genetic improvement of feed and lactation efficiency in dairy cattle. These complex traits are highly dynamic and are affected by trade-offs between different biological functions. Such trade-offs occur when energy intake is restricted and prevent the cows from expressing their full potential for the different biological functions, for example during lactation in low-input production systems. Increasing milk production and efficiency traits in dairy cows may thus impair fitness traits such as reproduction (Pryce et al., 1998) and health (Becker et al., 2021) and lead to a shorter productive life. The magnitude and nature of trade-offs between biological functions are expected to differ across production systems and change phenotypic and genetic covariances between traits, thus generating G×E interactions (Friggens et al., 2013). Moreover, the collection of feed intake data is costly and difficult, e.g. in outdoor production systems, leading to a scarcity of data needed for estimating reliable genetic parameters under a broad range of environments.

To broaden the scope of nutrition MMs to animal breeding issues, Puillet et al. (2021) developed a model based on the resource acquisition and allocation theory which includes a genetic module. Four genetically driven parameters describe the variability in the way cows acquire and allocate energy for different functions such as lactation, growth, and reproduction over their lifetime. This model was used to explore the relative contribution of energy acquisition and allocation parameters (AAPs) on lactation efficiency in dairy cows and to evaluate the magnitude of G×E interactions for these traits under various environments (Puillet et al., 2021). In this study, the genetic parameters of AAPs were defined empirically with typical values for production traits (Hill et al., 2007). Therefore, more insight is needed on the relative influence of genetic parameters assumed for AAPs and the effect of the nutritional environment on simulated traits before the model can be used in breeding applications. The objective of this study was to perform a sensitivity analysis to identify genetic parameters to be used as input for the simulation of dairy cow performance with realistic mean, variance and genetic correlation patterns among traits.

## Material and methods

The sensitivity analysis applied in this study made intensive use of stochastic simulations. The compiled executable of the simulation tool and scripts to reproduce simulations and analyses can be retrieved from: <https://data.mendeley.com/datasets/txx9zkbd2g/2>. This code needs to be run under Linux with the SLURM

**Table 1**  
Effect of the different scenarios on the average number of cows reaching first and third calving in the simulated dataset.

Scenario <sup>1</sup>	Heritability		CV		Number of cows starting first lactation			Number of cows starting third lactation		
	Acquisition <sup>2</sup>	Allocation <sup>3</sup>	Acquisition <sup>2</sup>	Allocation <sup>3</sup>	Mean	SEM	% of born heifers	Mean	SEM	% of primiparous cows
High nutritional environment (HS)										
HS_3535_1010	35	35	10	10	19 730	3.0	98.6%	14 771	20.0	74.9%
HS_3515_1010	35	15	10	10	19 730	2.9	98.7%	14 773	16.1	74.9%
HS_1515_1010	15	15	10	10	19 730	3.0	98.6%	14 774	17.0	74.9%
HS_3535_2020	35	35	10	30	19 039	9.0	95.2%	11 953	31.1	62.8%
HS_3535_1030	35	35	20	20	18 238	12.8	91.2%	10 768	37.9	59.0%
HS_3535_2030	35	35	20	30	17 885	14.3	89.4%	10 457	31.6	58.5%
Moderate nutritional environment (MS)										
MS_3535_1010	35	35	10	10	19 730	2.9	98.7%	13 486	22.3	68.4%
MS_1515_1010	15	15	10	10	19 730	3.0	98.6%	13 848	18.6	70.2%
MS_3535_2020	35	35	20	20	19 039	9.0	95.2%	10 973	30.5	57.6%
Low nutritional environment (LS)										
LS_3535_1010	35	35	10	10	19 730	2.9	98.7%	9 707	33.9	49.2%
LS_1515_1010	15	15	10	10	19 730	3.0	98.6%	9 686	25.6	49.1%
LS_3535_2020	35	35	20	20	19 030	9.0	95.1%	8 267	33.7	43.4%

<sup>1</sup> Abbreviations of scenarios were obtained by concatenating abbreviations of the nutritional environment, heritabilities of the two acquisition and allocation parameters and CV of the two acquisition and allocation parameters.

<sup>2</sup> Parameter value for both basal acquisition and lactation acquisition parameters.

<sup>3</sup> Parameter value for both allocation priority from growth to survival and lactation allocation parameters.

workload manager. In addition, it requires R statistical software (R Core Team, 2021) for data manipulations and statistical analyses as well as DMU version 5.2 (Madsen and Jensen, 2013) for the estimation of variance components. In this code, the seeds used for sampling random numbers were fixed at the beginning of each replicate to ensure the reproducibility of data.

Datasets were generated for 12 different scenarios, considering different combinations of input parameters based on three different nutritional environments, two levels of heritability and three levels of CV for AAPs (Table 1).

#### Dairy cow mechanistic model

The AQAL bioenergetic dairy cow model simulates phenotypic trajectories over a cow's lifetime for milk production, DM intake, body mass components including body reserves, as well as the timing of estruses and success of reproduction events (Puillet et al., 2016). The model can accommodate different nutritional environments by modulating the DM offer and metabolisable energy (ME) content of feed over time. The dynamics of energy acquisition and allocation for the main energy sinks (maintenance, lactation, gestation, body reserves) is described deterministically (Puillet et al., 2016). Four input parameters can be tuned to describe different dynamics of energy acquisition and allocation as observed for instance in different breeds. The first two acquisition parameters relate to the maximal potential DM intake of a non-lactating cow (basal acquisition abbreviated as **BasAcq**, in kg of DM/d) and the potential increase in DM intake during lactation (lactation acquisition or **LactAcq**, in kg of DM/d) in a non-limiting environment. The two other input parameters relate to the dynamics of energy allocation. The first one drives the dynamic of allocation to growth and corresponds to the rate of transfer between allocation to growth and allocation to survival ( $f_{\text{prioG2S}}$ , dimensionless). A high value implies a fast decrease in allocation to growth when the female ages. The second one drives the allocation to lactation and corresponds to the intensity of the charge of allocation to lactation at parturition (**LactAll**, dimensionless). The mean values of BasAcq, LactAcq,  $f_{\text{prioG2S}}$  and LactAll were determined to fit real data using a calibration procedure as described in Puillet et al. (2016). They were set to 7.00 kg/d, 10.25 kg/d,  $3.5 \cdot 10^{-3}$  and 0.56 as in Puillet et al. (2021). Based on the individual cow model, a genetic module was developed to simulate phenotypic and genetic variability

around the mean AAPs in a population of related cows. Thus, the variance observed around mean phenotypic trajectories at the population level was induced by assuming genetic and phenotypic variability for the AAPs. Only those four AAPs were assumed to be genetically driven as they were linked to the main energy acquisition processes and energy sinks. Further details concerning the model and its implementation can be found in Puillet et al. (2016 and 2021).

#### Simulated production systems

As a case study, a grass-based production system with seasonal calving was modelled following the same set-up as Puillet et al. (2021). The population was simulated as a single cohort of females from birth to death. It comprised 20 000 cows reared in the same environment. The mating season started on October 10th each year and lasted for 10 weeks. Gestation lasted 282 d, and cows were dried-off 90d before calving or at latest on May 15th. First mating of heifers occurred at 424 d of age. The probability of conception was derived based on deterministic equations accounting for milk production and energy balance (Puillet et al., 2016). Females that were not pregnant at the end of the mating season were culled. Moreover, females were culled when their body reserves were completely depleted due to insufficient energy acquisition or too high allocation to growth and lactation. Seasonality of feed resources in terms of quality and quantity was accounted for in the simulations. Variation in feed quality was defined to be consistent with ME content of grass in New Zealand (Roche et al., 2009). The ME content varied from 10.85 to 12.45 MJ/kg DM with a yearly average of 11.70 MJ/kg DM. Three nutritional environments were defined by changing the DM offer as simulated by Puillet et al. (2021). The high and non-limiting environment (**HS**) was defined to provide sufficient energy to cover the nutritional requirements of all cows during lactation and gestation. Secondly, a moderate scenario (**MS**) was defined so that DM offer could be limiting for high acquisition cows. The yearly average DM offer was 12.2 kg/d per cow with values ranging from 10 to 16.8 kg/d depending on the seasonality of grass production. Finally, a low nutritional environment (**LS**) was also simulated with a high constraint on DM offer. The yearly average DM offer was 9.8 kg/d per cow with values ranging from 8 to 13.4 kg/d per cow.

### Genetic determinism of acquisition-allocation parameters

In AQAL, the variance of simulated traits was induced by assuming phenotypic variance for AAP. These parameters were assumed to be genetically driven meaning that part of phenotypic variability was explained by additive genetic effects. A half-sib pedigree structure was simulated in this study. The true breeding values (TBVs) of AAPs were sampled for a set of 200 unrelated sires and 20 000 unrelated dams from a multivariate normal distribution with assumed genetic parameters. Sires were mated to dams to generate a single generation of 200 half-sib families comprising 100 daughters each. Procedures to sample TBV of cows and reconstruct acquisition and allocation phenotypes are described in Puillet et al. (2021).

First, the same genetic parameters for AAPs as in Puillet et al. (2021) were used, *i.e.* heritability of 0.35, a phenotypic CV of 10% and no genetic or phenotypic correlation between the input traits. These parameters were used to simulate milk production and FE data in all three nutritional environments and served as a baseline.

Then, different sets of genetic parameters were considered (Table 1) to evaluate how sensitive the genetic and phenotypic correlations between simulated traits were to changes in the genetic parameters of AAPs. In all three environments, the effect of heritability was evaluated by decreasing it to 0.15 for all four AAPs. Alternatively, the effect of CV was evaluated by increasing it to 20% for all four AAPs, whilst keeping heritability to 0.35. These lower heritabilities and higher CVs are typical of fitness traits (Hill et al., 2007). To have a better understanding on how the heritabilities (and CVs) of acquisition and allocation respectively influenced the (co)variances of simulated traits, we considered additional scenarios in the high nutritional environment only. First, we maintained heritabilities of acquisition to 0.35 and reduced heritabilities of allocation traits to 0.15, keeping CVs to 10% for all four parameters. Then, the CV of allocation parameters was increased to 30% whilst the CV of acquisition parameters kept to lower values (10 and 20%). Abbreviation of scenarios were built by concatenating the abbreviation of the nutritional environment, the heritability assumed for both acquisition and both allocation traits, and the CV assumed for both acquisition and both allocation traits (for instance HS\_3535\_2030).

### Definition of phenotypes

Phenotypic trajectories for milk production, feed efficiency and body reserves were generated using the mechanistic model described above and the sampled AAPs for each nutritional environment. Thus, no TBVs were sampled for milk production, feed efficiency and body reserve traits. Five simulated phenotypes were considered for further genetic analyses and were estimated for cows in first and third lactation (variable names were suffixed with L1 and L3). These traits comprised total lactation milk production (Milk), BW at calving (BWcalv), daily DM intake across lactation (DMI), lactation efficiency (Lact\_Eff), expressed as the ratio of energy invested in milk production over total energy intake during the lactation, and the minimum weight of body reserves during lactation (BRmin), expressed as the proportion of labile mass over empty BW. These traits were measured in first and third lactations. Records in both lactations were not analysed as repeated measurements but as two distinct traits.

### Estimation of variance components

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

$$Y = Xb + Zu + e$$

where  $X$  is the incidence matrix-relating performances to the fixed effects;  $b$  is the vector of fixed effects that comprised the calving group (four levels) that defined the nutritional environment at the time of parturition for all traits and the number of days in milk as a covariate for Milk and Lact\_Eff to correct for shorter lactations;  $Z$  is the incidence matrix-relating performances to animals;  $u$  is the vector of additive genetic values following a normal distribution  $N(0, A\sigma_g^2)$  where  $A$  is the additive relationship matrix and  $\sigma_g^2$  is the genetic variance of the trait; and  $e$  is the residual term following a normal distribution  $N(0, I\sigma_e^2)$  where  $\sigma_e^2$  is the residual variance of the trait and  $I$  the identity matrix.

Variance components were estimated using the Average Information Restricted Maximum Likelihood algorithm. At first, univariate analyses were carried out to estimate heritabilities, followed by bivariate analyses to estimate genetic and phenotypic covariances between traits. All calculations were carried out using the DMU software (Madsen and Jensen, 2013) that can be retrieved from <https://dmu.ghcp.au.dk/dmu/DMU/Linux/Previous/>.

### Comparison across scenarios

Each scenario was replicated 20 times to reduce the uncertainty around genetic correlation estimates that could be large for low heritability trait. Performances, heritabilities, and genetic and phenotypic correlations were compared across scenarios using a 1-way ANOVA to evaluate the impact of each scenario, *i.e.* each combination of genetic parameters assumed for AAPs and environment. The normality of the response variable was checked at first within each scenario using the Shapiro-Wilks test. Then, the homogeneity of variances across scenarios was evaluated using the Levene test. In most cases, variances were different across scenarios. Therefore, a Welsh 1-way ANOVA was carried out followed by Games-Howell posthoc tests to determine the significance of contrasts between all pairs of scenarios. Statistical analyses were performed with the rstatix package (Kassambara, 2021), and matrices were represented with the corplot package (Wei and Simko, 2021) in R (R Core Team, 2021).

## Results

### Comparison of performance mean and variability

The number of cows starting their first and third lactation is presented in Table 1 for all scenarios. The number of heifers starting first lactation was not affected by the environment or heritability of AAPs. However, it was highly affected by the CV of AAPs. When CV of AAPs was increased to 20%, the number of heifers failing due to acute energy imbalance (*i.e.* too few body reserves) before starting first lactation increased from 1.4 to 4.8%. In the most extreme scenario regarding CV (HS\_3535\_2030), the proportion of heifers failing prematurely increased to 10.6%. These animals with a combination of too high allocation to growth and low basal acquisition failed to acquire and maintain sufficient body reserves to allow them to transition to viable lactation. The number of cows reaching third lactation depended on the nutritional environment and the CV assumed for AAPs but not on their heritability. In scenarios with a heritability of 0.35 and a CV of 0.10 for all AAPs, the proportion of primiparous cows reaching third calving was 74.5, 68.4 and 49.2% in the high, moderate and low nutritional environments. When CV of AAPs was increased to 20%, the proportion of primiparous cows reaching third lactation decreased to 62.8, 57.6 and 43.3% in the high, moderate and low nutritional environments.

The high nutritional environment mimicked a situation of *ad libitum* feeding. In the moderate nutritional environment, realised

DMI was reduced by 2.0% compared to target intake during the first lactation meaning that DM offer was only slightly limiting compared to cow potential intake. This constraint was more important for third lactation cows which had higher nutritional requirements for maintenance and production (-12.9%). The LS environment was rather extreme with a DM offer that was much lower than potential intake both in first lactation (-12.5%) and third lactation (-27.8%).

Mean performances of cows were affected by the environment as well as the CV of AAPs but not their heritability. This was observed for first-parity cows (Table 2) as well as third-parity cows (Supplementary Table S1). However, for a given set of AAPs genetic parameters, average milk production, BW at calving and lactation efficiency measured in first lactation were significantly reduced in the MS and LS environments compared to the HS environments.

When CV of AAPs was increased from 10 to 20%, no significant difference was observed in milk production in first lactation in the high nutritional environment although BW at calving slightly increased, and lactation efficiency slightly decreased (Table 2). In the MS and LS environments, mean performance significantly differed for all traits when CV was increased from 10 to 20%. For third lactation cows, increasing CV of AAPs also induced small yet significant changes in all traits (Supplementary Table S1).

The environment also had a significant effect through restrictions exerted on DM intake in the suboptimal environments. Consequently, the CV of Milk was reduced in the MS and LS environments whereas CV of Lact\_Eff and BRmin was increased, regardless of cow parity. In scenarios where different values were allocated to AAPs, the CVs of DMI and BWcalv were generally close to the CV of acquisition parameters in the non-constraining nutritional environment, whereas the CV of Milk and Lact\_Eff was comprised between values set for CV of AAPs.

Comparison of heritabilities estimated across scenarios

Heritabilities estimated for the different traits and scenarios are presented in Table 3 for first-parity cows and in Supplementary Table S2 for third-parity cows. Heritability values estimated for the simulated traits depended simultaneously on the heritability and CV assumed for AAPs and on the environment.

In the high nutritional environment, the heritability of BWcalv was close to the one assumed for acquisition parameters. The her-

itability estimates for Milk and BRmin were close to the average of assumed heritabilities for acquisition and allocation parameters. Indeed, these estimates were close to 0.35 and 0.15 when the heritability of all four AAPs was set to either 0.35 or 0.15, and they took intermediate values when the heritability of acquisition parameters was set to 0.35 and the heritability of allocation parameters was set to 0.15. Heritabilities estimated for Milk and BRmin were slightly reduced when considering the MS and LS environments. Unlike milk production, heritability estimated for BRmin was sensitive to the CV of AAPs, with lower estimates when CV increased.

As expected, the heritability of DMI was highly dependent on both assumed heritability for acquisition traits and the environment. In the high and non-constraining nutritional environment, the estimated heritability was close to heritabilities assumed for acquisition parameters. Estimated heritabilities were markedly reduced in the limiting nutritional environments, especially in the LS environment.

Heritability of lactation efficiency was lower than the heritability values assumed for AAPs. Furthermore, heritability estimates were slightly increased when the CV of allocation parameters was increased. Heritabilities estimated in the HS and MS nutritional environments were not significantly different whereas these estimates were slightly lower in the LS environment with an increased CV.

Change in genetic correlation patterns among traits across scenarios

The average of genetic and phenotypic correlations estimated in the baseline scenario are presented in Fig. 1 for the high nutritional environment. High genetic correlations were estimated between Milk and Lact\_Eff as well as Milk and DMI regardless of cow parity. The genetic correlation between Milk and BWcalv was moderate to high in first lactation and much lower, but still positive, in third lactation. The genetic correlation between lactation efficiency and DMI was close to zero for both lactations. Genetic correlations between Lact\_Eff and BWcalv, as well as BRmin, were negative and low in first lactation although phenotypic correlations were of higher magnitude. Genetic correlations between these traits were higher in third than in first lactation. The genetic correlation between DMI and BWcalv was high in first and third lactation. The genetic correlations between BRmin and DMI as well as

Table 2 Mean and CV across replicates of simulated performances of cows in first lactation for the simulated traits and the different scenarios.

Scenario <sup>1</sup>	DMI_L1			BWcalv_L1			Milk_L1			Lac_Eff_L1			BRmin_L1		
	Mean	SEM	CV <sup>2</sup>	Mean	SEM	CV <sup>2</sup>	Mean	SEM	CV <sup>2</sup>	Mean	SEM	CV <sup>2</sup>	Mean	SEM	CV <sup>2</sup>
High nutritional environment (HS)															
HS_3535_1010	14.1 <sup>a</sup>	0.01	9.37 <sup>d</sup>	501.7 <sup>a</sup>	0.34	10.91 <sup>e</sup>	4 001.9 <sup>a</sup>	2.03	11.64 <sup>f</sup>	41.9 <sup>a</sup>	0.01	10.86 <sup>g</sup>	24.4 <sup>b</sup>	0.04	30.91 <sup>h</sup>
HS_3515_1010	14.1 <sup>a</sup>	0.01	9.37 <sup>d</sup>	501.7 <sup>a</sup>	0.34	10.91 <sup>e</sup>	4 002.6 <sup>a</sup>	1.69	11.65 <sup>f</sup>	41.8 <sup>a</sup>	0.01	10.86 <sup>g</sup>	24.4 <sup>b</sup>	0.03	30.93 <sup>h</sup>
HS_1515_1010	14.1 <sup>a</sup>	0.00	9.36 <sup>d</sup>	501.6 <sup>a</sup>	0.24	10.91 <sup>e</sup>	4 003.7 <sup>a</sup>	1.34	11.65 <sup>f</sup>	41.9 <sup>a</sup>	0.01	10.85 <sup>g</sup>	24.4 <sup>b</sup>	0.03	30.91 <sup>h</sup>
HS_3535_1030	14.1 <sup>a</sup>	0.01	9.52 <sup>c</sup>	501.5 <sup>a</sup>	0.37	11.00 <sup>e</sup>	3 856.0 <sup>d</sup>	3.42	25.16 <sup>b</sup>	40.3 <sup>f</sup>	0.04	25.11 <sup>a</sup>	26.1 <sup>a</sup>	0.06	53.13 <sup>c</sup>
HS_3535_2020	14.3 <sup>b</sup>	0.01	15.20 <sup>a</sup>	511.8 <sup>b</sup>	0.68	20.20 <sup>b</sup>	4 001.2 <sup>a</sup>	3.73	21.92 <sup>c</sup>	41.4 <sup>c</sup>	0.03	18.38 <sup>d</sup>	24.0 <sup>c</sup>	0.05	51.19 <sup>e</sup>
HS_3535_2030	14.3 <sup>b</sup>	0.01	15.15 <sup>a</sup>	512.0 <sup>b</sup>	0.69	20.38 <sup>a</sup>	3 907.0 <sup>b</sup>	4.22	28.17 <sup>a</sup>	40.3 <sup>f</sup>	0.04	25.26 <sup>a</sup>	26.0 <sup>a</sup>	0.06	55.12 <sup>b</sup>
Moderate nutritional environment (MS)															
MS_3535_1010	13.8 <sup>c</sup>	0.01	8.57 <sup>e</sup>	501.8 <sup>a</sup>	0.35	10.91 <sup>e</sup>	3 884.2 <sup>c</sup>	1.68	10.39 <sup>g</sup>	41.5 <sup>b</sup>	0.01	11.17 <sup>f</sup>	23.1 <sup>d</sup>	0.04	32.00 <sup>g</sup>
MS_1515_1010	13.8 <sup>c</sup>	0.00	8.57 <sup>e</sup>	501.9 <sup>a</sup>	0.24	10.91 <sup>e</sup>	3 885.7 <sup>c</sup>	1.09	10.40 <sup>g</sup>	41.5 <sup>b</sup>	0.01	11.17 <sup>f</sup>	23.1 <sup>d</sup>	0.03	32.01 <sup>g</sup>
MS_3535_2020	13.7 <sup>d</sup>	0.01	12.45 <sup>b</sup>	511.0 <sup>b</sup>	0.66	20.08 <sup>c</sup>	3 799.7 <sup>e</sup>	2.89	19.32 <sup>d</sup>	40.9 <sup>d</sup>	0.03	18.66 <sup>c</sup>	22.7 <sup>e</sup>	0.05	52.46 <sup>d</sup>
Low nutritional environment (LS)															
LS_3535_1010	12.3 <sup>e</sup>	0.00	8.03 <sup>f</sup>	501.0 <sup>a</sup>	0.33	10.61 <sup>f</sup>	3 398.7 <sup>f</sup>	1.10	9.30 <sup>h</sup>	40.7 <sup>e</sup>	0.01	12.83 <sup>e</sup>	17.5 <sup>g</sup>	0.04	42.67 <sup>f</sup>
LS_1515_1010	12.3 <sup>e</sup>	0.00	8.02 <sup>f</sup>	501.0 <sup>a</sup>	0.23	10.61 <sup>f</sup>	3 399.5 <sup>f</sup>	0.73	9.29 <sup>h</sup>	40.7 <sup>e</sup>	0.01	12.84 <sup>e</sup>	17.5 <sup>g</sup>	0.03	42.72 <sup>f</sup>
LS_3535_2020	12.2 <sup>f</sup>	0.00	9.54 <sup>c</sup>	501.7 <sup>a</sup>	0.56	18.26 <sup>d</sup>	3 286.7 <sup>g</sup>	1.96	17.10 <sup>e</sup>	40.0 <sup>g</sup>	0.03	19.41 <sup>b</sup>	18.7 <sup>f</sup>	0.05	60.38 <sup>a</sup>

Milk\_L1 = milk production in first lactation; Lac\_Eff\_L1 = lactation efficiency in first lactation; DMI\_L1 = DM intake in first lactation; BWcalv\_L1 = BW at first calving; BRmin\_L1 = minimal body reserves during first lactation.

<sup>a-h</sup> Values within a column with different superscripts differ significantly at P < 0.05.

<sup>1</sup> See Table 1 for scenario abbreviations.

<sup>2</sup> SEM of CV ranged from 0.01 to 0.13% for the five analysed traits.

**Table 3**  
Heritabilities estimated for simulated traits measured on dairy cows in first lactation across scenarios.

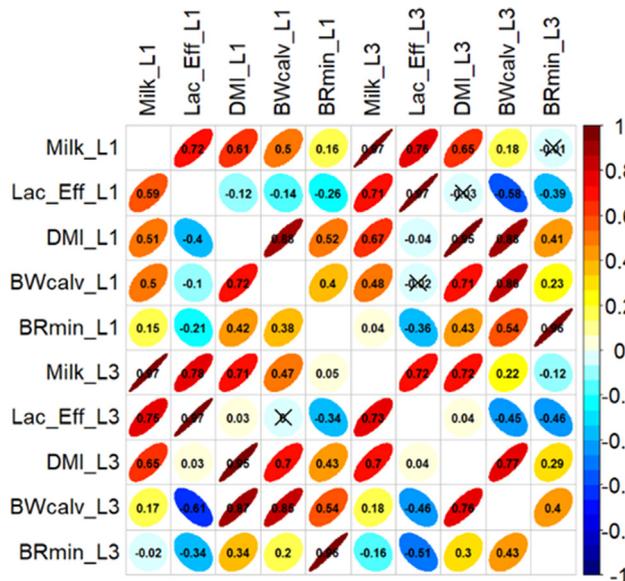
Scenario <sup>1</sup>	Milk_L1 <sup>2</sup>	BWcalv_L1 <sup>2</sup>	Lac_Eff_L1 <sup>2</sup>	DMI_L1 <sup>2</sup>	BRmin_L1 <sup>2</sup>
HS_3535_1010	0.34 <sup>a</sup>	0.35 <sup>a</sup>	0.22 <sup>b</sup>	0.24 <sup>b</sup>	0.34 <sup>a</sup>
HS_3515_1010	0.23 <sup>d</sup>	0.35 <sup>a</sup>	0.10 <sup>d</sup>	0.24 <sup>b</sup>	0.19 <sup>c</sup>
HS_1515_1010	0.15 <sup>e</sup>	0.15 <sup>c</sup>	0.10 <sup>d</sup>	0.15 <sup>d</sup>	0.14 <sup>d</sup>
HS_3535_1030	0.29 <sup>bc</sup>	0.35 <sup>a</sup>	0.26 <sup>a</sup>	0.21 <sup>b</sup>	0.19 <sup>c</sup>
HS_3535_2020	0.32 <sup>ab</sup>	0.32 <sup>ab</sup>	0.27 <sup>a</sup>	0.27 <sup>a</sup>	0.23 <sup>b</sup>
HS_3535_2030	0.29 <sup>bc</sup>	0.33 <sup>ab</sup>	0.26 <sup>a</sup>	0.28 <sup>a</sup>	0.18 <sup>c</sup>
MS_3535_1010	0.34 <sup>a</sup>	0.35 <sup>a</sup>	0.22 <sup>b</sup>	0.19 <sup>c</sup>	0.33 <sup>a</sup>
MS_1515_1010	0.14 <sup>e</sup>	0.15 <sup>c</sup>	0.10 <sup>d</sup>	0.08 <sup>ef</sup>	0.14 <sup>d</sup>
MS_3535_2020	0.31 <sup>ab</sup>	0.32 <sup>ab</sup>	0.26 <sup>a</sup>	0.22 <sup>b</sup>	0.23 <sup>b</sup>
LS_3535_1010	0.34 <sup>a</sup>	0.35 <sup>a</sup>	0.18 <sup>c</sup>	0.05 <sup>f</sup>	0.30 <sup>a</sup>
LS_1515_1010	0.15 <sup>e</sup>	0.15 <sup>c</sup>	0.07 <sup>e</sup>	0.02 <sup>g</sup>	0.13 <sup>d</sup>
LS_3535_2020	0.30 <sup>bc</sup>	0.31 <sup>b</sup>	0.23 <sup>b</sup>	0.09 <sup>e</sup>	0.19 <sup>c</sup>

Milk\_L1 = milk production in first lactation; Lac\_Eff\_L1 = lactation efficiency in first lactation; DMI\_L1 = DM intake in first lactation; BWcalv\_L1 = BW at first calving; BRmin\_L1 = minimal body reserves during first lactation.

<sup>a-g</sup> Values within a row with different superscripts differ significantly at  $P < 0.05$ .

<sup>1</sup> See Table 1 for scenario abbreviations; HS = high nutritional environment; MS = moderate nutritional environment; LS = low nutritional environment.

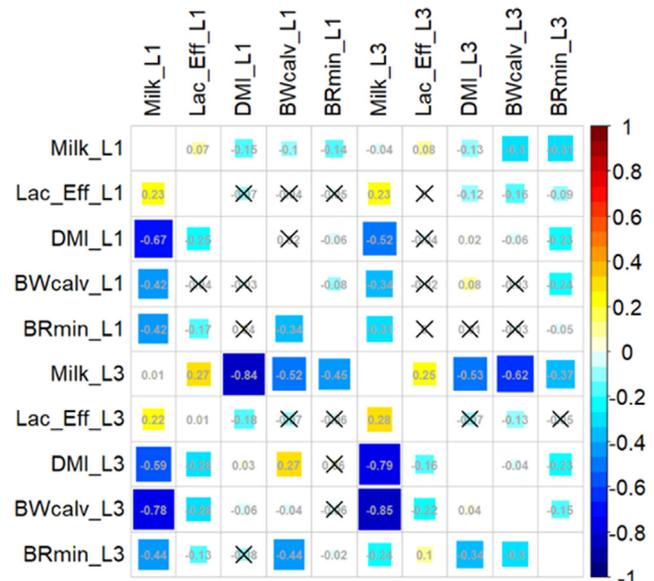
<sup>2</sup> SEs of the mean ranged from 0.004 to 0.01 for all traits and scenarios.



**Fig. 1.** Mean genetic and phenotypic correlations (upper and lower triangular matrices, respectively) estimated between simulated traits of dairy cows in the high nutritional environment. Traits: Milk\_L1 = milk production in first lactation; Lac\_Eff\_L1 = lactation efficiency in first lactation; DMI\_L1 = dry matter intake in first lactation; BWcalv\_L1 = BW at first calving; BRmin\_L1 = minimal body reserves during first lactation; Milk\_L3 = milk production in third lactation; Lac\_Eff\_L3 = lactation efficiency in third lactation; DMI\_L3 = DM intake in third lactation; BWcalv\_L3 = BW at third calving; BRmin\_L3 = minimal body reserves during third lactation. Correlations that were not significantly different from 0 at a 5% threshold based on the 20 replicates were crossed. SEs of mean genetic correlations ranged from 0.01 to 0.10 where SEs of genetic correlation estimates ranged from 0.05 to 0.58 for individual estimates within replicates.

BWcalv were moderate in first and third lactation. All genetic correlations estimated between the same trait measured in first and third lactation were very high (>0.86).

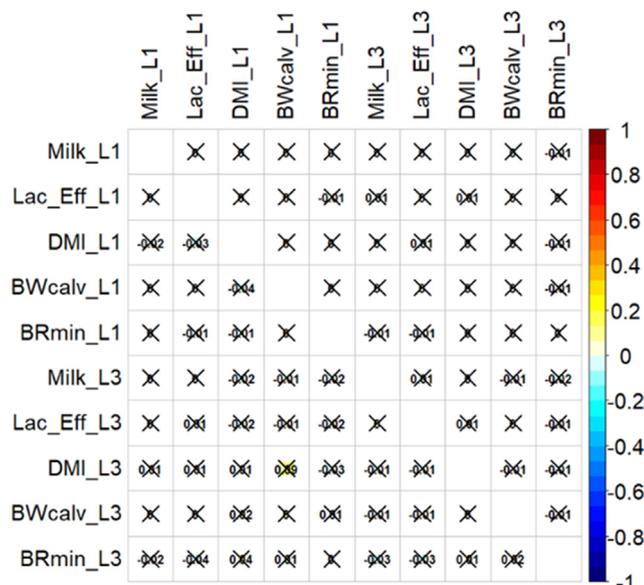
The nutritional environment had a large impact on the shaping of genetic correlations among simulated traits, as already shown by Puillet et al. (2021). When comparing the high and moderate nutritional environments, most changes in genetic correlations between traits measured in first lactation were limited (Fig. 2). The contrasts were larger for third lactation traits because third-parity cows experienced higher feed restriction and hence stronger trade-offs than first-parity cows in the MS environment. The genetic correlations most impacted by the change in nutritional



**Fig. 2.** Contrasts between genetic correlations estimated for each trait measured on dairy cows in the moderate vs high nutritional environment (upper triangular) and in the low vs high nutritional environment (lower triangular), considering heritability of 0.35 and coefficient of variation of 10% for acquisition and allocation parameters. Traits: Milk\_L1 = milk production in first lactation; Lac\_Eff\_L1 = lactation efficiency in first lactation; DMI\_L1 = DM intake in first lactation; BWcalv\_L1 = BW at first calving; BRmin\_L1 = minimal body reserves during first lactation; Milk\_L3 = milk production in third lactation; Lac\_Eff\_L3 = lactation efficiency in third lactation; DMI\_L3 = DM intake in third lactation; BWcalv\_L3 = BW at third calving; BRmin\_L3 = minimal body reserves during third lactation. Contrasts that were not significantly different from 0 at a 5% threshold based on the 20 replicates were crossed.

environment were those estimated between milk production and other traits, especially DMI, BWcalv and BRmin. These traits were generally more unfavourably correlated in more constraining environments due to increased trade-offs. In third lactation, the drop in genetic correlation between DMI and BRmin was also notable.

When comparing HS and LS environments, large changes in genetic correlations were observed whatever the cow parity. The genetic correlation between Milk and Lact\_Eff increased and the genetic correlations between Milk and DMI, as well as BWcalv, strongly decreased and became negative indicative of a trade-off between milk production and BW. The genetic correlation between BRmin and BWcalv in third lactation was also substantially reduced.

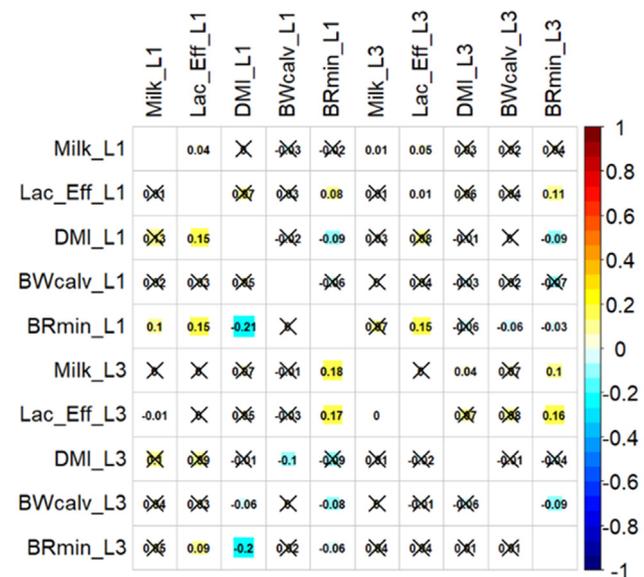


**Fig. 3.** Contrasts between genetic correlations estimated for each trait measured on dairy cows in scenarios with heritability of acquisition and allocation parameters set to 0.35 vs 0.15 in the high nutritional environment (upper triangular) and in the low nutritional environment (lower triangular), considering a CV of 10% for acquisition and allocation parameters. Traits: Milk\_L1 = milk production in first lactation; Lac\_Eff\_L1 = lactation efficiency in first lactation; DMI\_L1 = DM intake in first lactation; BWcalv\_L1 = BW at first calving; BRmin\_L1 = minimal body reserves during first lactation; Milk\_L3 = milk production in third lactation; Lac\_Eff\_L3 = lactation efficiency in third lactation; DMI\_L3 = DM intake in third lactation; BWcalv\_L3 = BW at third calving; BRmin\_L3 = minimal body reserves during third lactation. Contrasts that were not significantly different from 0 at a 5% threshold based on the 20 replicates were crossed.

Independently from the environment, the heritability defined for AAPs did not impact genetic correlations among simulated traits neither in first nor in third lactation (Fig. 3). Finally, changes in genetic correlations among simulated traits were limited when increasing the CV from 10 to 20% in the HS environment (Fig. 4). The largest change was observed between BRmin and lactation efficiency in third lactation. In the LS environment, increasing the CV of AAPs from 10 to 20% had a larger effect on estimated genetic correlations. However, those changes remained limited and much smaller than the changes induced by the change in environment.

**Author’s point of views**

- The main outcome of this study is a suite of scripts and a compiled version of the AQAL software to (1) simulate phenotypic trajectories of milk production and feed efficiency traits in a population of related cows and (2) estimate genetic parameters for traits derived from simulations.
- The sensitivity analysis performed in this study gives insight into the tuning of genetic parameters of AQAL input traits to simulate datasets of phenotypes with realistic means and genetic parameters. It confirmed that a heritability of 0.35 for all four AAPs and a phenotypic CV of 10% permitted to simulate datasets of phenotypes with realistic variance and covariance components, as suggested empirically by Puillet et al. (2021). Such genetic parameters are typical for production traits in domesticated species in farm or natural conditions (Hill et al., 2007).
- As expected, the heritability of AAPs did not influence the mean or variability of simulated performances but only the heritability of simulated underlying traits. The heritability of basal acquisition was the main driver of the heritability of BW at first calving. It had to be set to 0.35 to match heritability of BW at first calving reported in the literature (Liinamo et al., 2012). The heritability of other traits depended jointly on the heritability of acquisition and allocation parameters. Defining a heritability of 0.35 for allocation parameters ensured reaching heritability in the range of 0.30–0.40 for milk production and 0.25–0.35 for body reserves as usually reported in the literature based on real data (Vallimont et al., 2010; Liinamo et al., 2012; Manzanilla-Pech et al., 2014; Manzanilla-Pech et al., 2016; Manafiazar et al., 2016; Li et al., 2016). Based on this parameterisation, the heritability obtained for lactation efficiency was equal to 0.22 in the high nutritional environment which is consistent with values reported in the literature for other measures of lactation and feed efficiency, such as feed conversion ratio or residual feed intake (Manzanilla-Pech et al., 2016; Manafiazar et al., 2016).
- As expected, the CV of AAPs mainly influenced the variability of simulated traits. However, it had also an impact on the phenotypic mean and genetic parameters of simulated traits due to increased loss or early culling of females presenting extreme acquisition and allocation values. Even in the high non-limiting nutritional environment, the proportion of females lost before first lactation was very high when CV of acquisition or allocation was set to 20% or higher. Those high culling rates are not realistic for heifers which suggested that, to be realistic, CV of acquisition and allocation input traits should be kept to values lower than 20%.
- This study confirmed that the nutritional environment has a much larger influence in the shaping of genetic and phenotypic covariances between traits than heritability and phenotypic CV of acquisition and allocation input parameters. Such information is critical for using the mechanistic AQAL software for breeding applications in the context of G×E interactions.



**Fig. 4.** Contrasts between genetic correlations estimated for each trait measured on dairy cows in scenarios with CV for acquisition and allocation parameters set to 20 vs 10% in the high nutritional environment (upper triangular) and in the low nutritional environment (lower triangular), considering heritability of 0.35 for all acquisition and allocation parameters considering a CV of 10% for acquisition and allocation parameters. Traits: Milk\_L1 = milk production in first lactation; Lac\_Eff\_L1 = lactation efficiency in first lactation; DMI\_L1 = DM intake in first lactation; BWcalv\_L1 = BW at first calving; BRmin\_L1 = minimal body reserves during first lactation; Milk\_L3 = milk production in third lactation; Lac\_Eff\_L3 = lactation efficiency in third lactation; DMI\_L3 = DM intake in third lactation; BWcalv\_L3 = BW at third calving; BRmin\_L3 = minimal body reserves during third lactation. Contrasts that were not significantly different from 0 at a 5% threshold based on the 20 replicates were crossed.

Indeed, the simulation of milk and feed efficiency performances should be relatively robust to deviations from true values of heritability and CV of AAP. The  $G \times E$  interactions emerging from the simulations are then mostly dependent on the nutritional environment specifications and resulting trade-offs in case of energy restriction.

- The significant changes in correlation among traits across environments suggest that the model adequately captures effects arising from  $G \times E$  interactions that are consistent with expectations, *i.e.* more unfavourable genetic correlations between traits conflicting for access to energy (for example Milk and BW) and a higher emphasis on allocation to fitness-related traits than milk production to achieve higher lifetime lactation efficiency in more unfavourable environments.
- The set of parameters used for the four AAPs enabled the simulation of cows with moderate BW and milk production in a typical grass-based production system. Hence, trade-offs for access to energy between production and reproduction traits were low in the non-limiting nutritional environment. This was consistent with the literature on trade-offs in ecology as does the increasing trade-offs in poorer environments leading to more unfavourable genetic correlations between traits conflicting for energy access.
- We expect that the script and software attached to this study will help breeders (1) explore the interest in novel phenotypes derived from phenotypic trajectories and (2) define new breeding strategies for feed efficiency in dairy cows, with a focus on the influence of  $G \times E$  interactions on the trait expression.

In conclusion, the code associated to this article enables the simulation of datasets of cow phenotypic trajectories for milk production and feed efficiency traits in different nutritional environments. The present sensitivity analysis confirmed the relevance of defining a heritability value of 0.35 and a CV of 10% for acquisition and allocation input parameters in the AQAL simulation tool to simulate traits with realistic heritability and genetic correlation structure. Furthermore, the heritability and CV of AAPs had a more limited impact than the nutritional environment on genetic correlations among simulated traits. Hence, the release of such a mechanistic simulation tool, coupled with genetic simulation, is an opportunity to explore the interest in new traits for genetic improvement and to define new breeding strategies under various environmental scenarios.

### Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.anopes.2022.100017>.

### Ethics approval

This study did not require ethics approval because it relied on simulated data.

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### Declaration of interest

None.

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### Reader comments

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