

Mechanistic-based prediction of selection response on resilience and feed efficiency traits in dairy cattle

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Abstract

The objective of this study was to present a new methodology to predict selection response on resilience and feed efficiency (FE) in dairy cattle. This approach combines genetic and mechanistic modelling to describe the biological mechanisms underlying these traits. A dairy cattle breeding scheme was simulated considering a non-limiting nutritional environment and two different breeding goals focusing either on milk production or FE. Selection response was predicted within the non-limiting environment but also for a prospective low-input system (LS). Predictions obtained with conventional and mechanistic-based methods were consistent for milk production, body weight and FE within the non-limiting environment. However, genetic trends predicted for fertility were different. Selection response achieved on milk production was much smaller in the LS than in the breeding nucleus due to the increased nutritional constraint. The breeding goal with emphasis on FE enabled a better transfer of genetic gain to the LS environment.

Introduction

Breeding for resilience and feed efficiency (FE) in dairy cattle is difficult because these traits result from a subtle balance between biological functions aiming at maintaining a cow's ability to produce and reproduce. This balance is also highly dependent on the nutritional environment: trade-offs between production and fitness traits are exacerbated when energy intake is limiting (Puillet et al., 2021). With climate change and societal demands for expanding grass-based production systems, nutritional environments might be more uncertain and diverse in the future. When defining novel breeding strategies on resilience and FE, it is critical to anticipate these changes and select cows that can cope with various production systems. This paper describes a new mechanistic-based method (MM) combining genetic and mechanistic modelling to predict selection response on cow milk production and FE traits. This approach can be used within a given breeding environment but also facilitates predicting selection response that would be expected in more challenging environmental scenarios.

Material & Methods

General approach to predict selection response. In this study, we capitalize on the AQAL bioenergetic model to simulate phenotypic trajectories of milk production and FE traits over the lifetime of dairy cows depending on energy available in the environment (Puillet et al., 2016; 2021). This dynamic mechanistic model of a single cow is grounded on the resource acquisition and allocation (AA) theory to describe cows' responses to nutritional challenges. Variability in the response observed at the population level is induced by assuming genetic and phenotypic variance for a set of four input parameters describing energy AA strategies of cows. Acquisition parameters correspond to the maximal intake of a non-reproducing cow (basal acquisition: BasAcq) and the increase of intake during lactation (lactation acquisition: LactAcq) expected in a non-limiting environment. Allocation parameters correspond to the

rate of transfer of energy from growth to survival (RTGS) defining the trade-off between structural mass and body reserves and the allocation to lactation (LactAll) defining the energy investment in milk production. Mean values of these four parameters were determined by a calibration procedure using real data as described by Puillet et al. (2021). The effect of the nutritional environment - an input of the model - on the variability of traits was modelled through stochastic simulations. To predict genetic gain, it was assumed that selection on usual production and functional traits changes the mean genetic level of energy acquisition and allocation variables. Thus, updating AA parameters considering this correlated response is a way to simulate new performance datasets mimicking the effects of selection with AQAL. The method comprises three steps. First, datasets with a pedigree structure were simulated with AQAL considering the same AA parameters as Puillet et al. (2021) and a non-limiting nutritional environment typical of breeding herds. This environment corresponded to the “high & stable” (HS) scenario in Puillet et al. (2021). Simulated data were used to estimate genetic parameters between simulated traits and AA input traits. Second, the ADAM breeding scheme simulation tool (Pedersen et al., 2009) was used to estimate the correlated selection response expected on AA traits for a given breeding goal and a typical dairy cattle breeding scheme structure. Finally, new levels of milk production and FE traits were simulated by updating the AQAL AA input parameters with the correlated selection response to estimate the change in performance due to selection.

Considered traits and genetic parameters. Four traits were analyzed in this study and were estimated for primiparous cows: milk production (MP), body weight at calving (BW), energy conversion efficiency (ECE) and the interval between first mating and conception (IFC). The four AA input traits were assumed to have a heritability of 0.35, a phenotypic coefficient of variation of 10% and to be genetically uncorrelated as assumed by Puillet et al. (2021). Genetic parameters were estimated between AA traits and simulated traits using restricted maximum likelihood applied to bivariate linear animal mixed models (Table 1). Genetic correlations were close to 1 between BasAcq and BW, as well as LactAll and ECE. Hence, we considered these pairs of traits as single traits.

Table 1. Genetic parameters for acquisition, allocation and simulated traits (heritability on the diagonal, genetic and phenotypic correlations above and below the diagonal).

	BasAcq / BW	LactAcq	RTGS	LactAll / ECE	MP	IFC
BasAcq / BW	0.35	0.00	0.00	0.00	0.50	-0.23
LactAcq	0.00	0.35	0.00	0.00	0.38	-0.12
RTGS	0.00	0.00	0.35	0.00	0.24	-0.64
LactAll / ECE	0.00	0.00	0.00	0.35	0.72	0.56
MP	0.52	0.39	0.23	0.73	0.34	0.12
IFC	-0.05	-0.02	-0.13	0.11	0.06	0.01

Simulation of dairy cattle breeding scheme. A large-scale breeding nucleus was simulated over a 30-year period with ADAM (Pedersen et al., 2009). It comprised 20,000 females equally distributed in 200 herds and mated with 100 sires each year. True breeding values (TBV) and phenotypes were sampled based on genetic parameters in Table 1. Milk production, BW and IFC were recorded on all cows. Genomic selection was simulated using the pseudo-genomic selection approach (Buch et al., 2012). The accuracy of genomic breeding values (GEBV) was estimated using selection index theory to combine information from bull and cow reference populations (Buch et al., 2012). We assumed a reference population of 10,000 bulls with 100 daughters each, 50,000 cows with performance for MP, BW, IFC, and

5000 cows with ECE phenotypes. The GEBV accuracy of candidates without performance was 0.68 for MP and BW, 0.60 for ECE and 0.58 for IFC. Using simulated phenotypes, pseudo-genomic phenotypes and pedigree, GEBV were predicted using DMU software (Madsen and Jensen, 2013).

Each year, the best 4000 male and 4000 female calves were assumed to be genotyped based on parental breeding values. After genotyping, the best 100 1-year old males were selected to be used as sires for one year. Within each herd, the best 100 females aged from 1 to 5 years were selected using estimated breeding values. Selection decisions were based on a total merit index. Two simple breeding goals were defined to reflect a balance between different production and functional traits. In the first breeding goal, called M-FER, equal weight was given to MP and IFC. In the second breeding goal, called EFF-FER, equal weight was given to ECE and IFC. Annual genetic gain was predicted for each trait by regressing mean TBV of selection candidates on their birth year over the last ten years of simulation. The first 20 years were considered as burn-in period and were discarded. All presented results were averaged based on 30 replicates.

Genetic gain predictions based on the mechanistic model. Mean values of the four AA parameters were updated considering the correlated selection response expected over a 20-year period. Changes in heritability and phenotypic variance of AA traits due to selection were also estimated as observed in ADAM stochastic simulations. Changes in genetic covariance between AA traits were small (≤ 0.04 in absolute value) and were ignored. Selection response was estimated for each trait on an annual basis as the change in performance simulated with the initial and updated sets of AA parameters within the non-limiting HS environment.

Selection response that would be expressed in a low nutritional environment following selection in the HS environment was estimated in the same way but simulating datasets with AQAL considering the “low & stable” (LS) environment in PUILLET et al. (2021). In this environment, the nutritional constraint was substantial: dry matter intake was on average 14.7% lower than total potential acquisition.

Results and discussion

Correlated selection responses on AA traits predicted for the two breeding goals are presented in Table 2. With the M-FER breeding goal, high genetic gain was achieved on basal acquisition because this trait was positively correlated to MP and IFC. Indeed, when access to feed is non-limiting, increasing feed intake by selection is an option to improve both MP and IFC. Therefore, although a high weight was given to MP, genetic gain on lactation allocation was only limited. Selecting on the EFF-FER breeding goal led to a more balanced genetic gain on the four AA traits, with a shift in genetic gain from basal acquisition to lactation allocation. In both scenarios, similar positive genetic gain was achieved on RGTS meaning that selection favors cows allocating more energy for body reserves accretion than growing structural mass. Selection responses predicted for simulated traits with the conventional and mechanistic-based methods are presented in Table 3. With the conventional method, high genetic gain was estimated on MP, BW and IFC for the M-FER breeding goal in the HS environment. Genetic gain on ECE was much more limited.

Table 2. Mean annual genetic gain¹ (in genetic standard deviation units) estimated for acquisition and allocation traits in the breeding environment for the two breeding goals.

Breeding goal	BasAcq	LactAcq	RTGS	LactAll
M-FER	0.34	0.13	0.20	0.09
EFF-FER	0.22	0.14	0.21	0.23

¹Standard error of the mean ranged from 0.002 to 0.003 for all predictions

Table 3. Annual genetic gain (expressed in genetic standard deviation units) predicted for simulated traits with the conventional (CONV) and mechanistic-based (MM) methods in the breeding environment (HS) and the low nutritional scenario (LS).

Trait	CONV prediction – HS		MM prediction – HS		MM prediction – LS	
	Breeding goal		Breeding goal		Breeding goal	
	M-FER	EFF-FER	M-FER	EFF-FER	M-FER	EFF-FER
MP	0.33	0.38	0.34	0.41	0.15	0.28
BW	0.34	0.22	0.30	0.19	0.23	0.16
ECE	0.09	0.23	0.08	0.22	0.09	0.23
IFC	-0.21	-0.11	-0.01	0.06	0.00	0.06

With the EFF-FER breeding goal, genetic gain was much higher on ECE and more limited on BW and IFC. This was consistent with genetic correlations estimated between AA input traits and simulated traits. Selection response predictions were consistent across methods and breeding goals within the HS environment for MP, BW and ECE, with annual genetic gain differences lower than 0.04 genetic standard deviation units (σ_g). Differences were larger on IFC. Indeed, annual genetic gain was reduced from -0.21 to -0.01 σ_g in the M-FER scenario and from -0.11 to 0.06 σ_g in the EFF-FER scenario, *i.e.* a zero or even unfavorable trend was predicted on fertility in the M-FER and EFF-FER scenarios with the MM approach.

Genetic gain that would be expressed in the LS environment given selection in the HS environment was estimated with the MM approach (Table 3). In the LS environment, selection response predicted on MP and BW with the M-FER breeding goal was reduced by 56% and 23% relative to the HS environment. The reduction in genetic gain was more limited in the EFF-FER scenario (-32% and -16% for MP and BW). Indeed, increasing basal acquisition by selection in the HS environment led to further increase the nutritional constraint in the LS scenario due to increased maintenance requirements. This also explains the larger reduction in selection response on BW and MP with the M-FER breeding goal due to faster genetic progress on basal acquisition. Hence, a larger proportion of genetic gain was transferred from the high to the low nutritional environment with the EFF-FER breeding goal.

In conclusion, this study showed the feasibility of combining mechanistic and genetic modelling to predict selection response on milk and FE traits in dairy cattle. The mechanistic-based method gave consistent predictions of selection response for milk production and FE traits within the breeding environment. Compared to the standard approach, it also cast light on the AA strategies used to achieve genetic gain. Furthermore, it enabled the estimation of genetic gain that could be transferred from the breeding environment to a prospective environment accounting for both genetic trends and the magnitude of physiological trade-offs on production and reproduction traits.

References

- Buch L.H., Kargo M., Berg P., Lassen J., and Sørensen, A. C. (2012) *Animal* 6(06):880-886. <https://doi.org/10.1017/S1751731111002205>
- Madsen P., and Jensen J. (2013) DMU: A package for analyzing multivariate mixed models. User's guide - Version 6, release 5.2. QGG Center, Aarhus University, Tjele, Denmark.
- Pedersen L.D., Sørensen A.C., Henryon M., Ansari-Mahyari S., and Berg P. (2009) *Livest. Sci.* 121(2-3):343-344. <https://doi.org/10.1016/j.livsci.2008.06.028>
- Puillet L., Réale D., and Friggens N.C. (2016) *Genet. Sel. Evol.* 48:72. [10.1186/s12711-016-0251-8](https://doi.org/10.1186/s12711-016-0251-8)
- Puillet L., Ducrocq V., Friggens N.C., and Amer P.R. (2021) *J. Dairy Sci.* 104(5):5805–5816. <https://doi.org/10.3168/jds.2020-19610>