Selection for low or high feed intake cows: genotype by environment interaction for milk yield, live weight and dry matter intake in dairy cows

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Summary

Selection for feed efficiency is of increasing interest for cattle breeders, and countries are combining data to develop genomic breeding values to be used across feeding systems. Also a classical question is if we should breed cows with a higher feed intake (capacity) so they can convert more roughage into milk, or should we breed cows that are efficient and have a lower feed intake for a given yield, i.e. that are more profitable (milk yield - feed intake). To answer this question genotype by environment (GxE) was investigated. Experiments with a total of 1,602 cows recorded for dry matter intake (DMI), fat-protein corrected milk (FPCM) and liveweight) (LW) were grouped into a high, medium and low nutritional environment to estimate genetic parameters. Heritability for DMI and LW were constant across the environments, for milk yield there was a decrease in h^2 from high to low environment. Genetic correlations between the environments ranged between 0.68 to 0.90 for DMI, and were slightly lower for FPCM, and higher for LW. Selection index calculations demonstrated that selection for higher intake gave heavier cows, and when selecting for a higher intake relatively to milk yield on a higher density diet there was no benefit in terms of profit on lower density diets. Therefore, the breeding goals should always be for profit (FPCM – DMI) independent of the nutritional environment.

Keywords: R.F. Veerkamp, feed intake, genotype by environment interaction, breeding goal, dairy cattle

Introduction

Genomic prediction enables selection for scarcely recorded traits, since training of the prediction equations can happen in research populations. Feed efficiency is one of these traits for which recently genomically predicted breeding values were introduced. In the Netherlands we introduced the breeding value for DMI, which combines daughter information with genomic prediction for DMI with the information coming from other predictor traits (LW and milk production).

The first reason why GxE is of interest, is the question if breeding values for DMI are representative across all feeding systems. DMI records in the training population are collected across many different experiments in the Netherlands, but also more and more data will be combined across countries (Berry *et al.* 2013, De Haas *et al.* 2015). Hence, the question is if all data can be treated as one trait, or if multi-trait models should be used across countries, as suggested by de Haas *et al.* (2012). Also, farmers apply very different feeding systems. Therefore, it is also important to investigate the scale of the breeding values and the ranking of animals across different systems. Especially when breeding values for DMI are combined with breeding values for milk yield in a measure of feed efficiency or profit.

The second reason why GxE could be relevant, is the question if we should select cows that can eat and produce more, or if we should select cows that eat less for the same amount of milk yield (profit). Based on nutritional models, it could be argued that cows that eat more roughage per kg milk can be fed less concentrates, and can also convert more grass into milk (Groen & Korver, 1989, Harrison *et al.* 1990, Veerkamp, R.F., 1998). This hypothesis is also partly used to support the argument of type breeders that big and heavy cows are more favourable than smaller cows, as they can eat more roughage. The answer to the question if we should breed for higher or lower feed intake is partly economic and depends on the cost price of roughage versus concentrates (Koenen at al. 2000). However, the cost of a kg roughage or concentrate is not very different for most farmers in the Netherlands. The other part of the answer to the question if we should select for a higher intake (capacity) or a lower feed intake requires knowledge on GxE for DMI and milk yield. To justify selecting for cows that can eat relatively more on a high concentrate system (at the same yield), these cows should benefit from the higher intake capacity on a roughage-based diet, and a re-ranking should be observed. If no re-ranking is observed we should simply select for the most profitable cows across environments. Therefore the objective of this paper was to estimate the extent of GxE for milk yield, DMI and LW across a range of feeding experiments, grouped in low, medium and high energy density diets.

Material and methods

A unique large dataset was available on 1,602 cows with daily records on DMI, FPCM and LW recorded in 2,652 lactations and 281 experiments between 1990 and 2015. This is a subset of all records available, as initially only experiments with an explicit recording of a separate concentrate gift were used. Recording frequencies of DMI varied by experiment: it was recorded either one, two, three or five times per week. An overview of the experiments, treatments and diets is given in Manzanilla-Pech et al. (2014).

Environments were defined by classifying each experiment as high, medium or low energy density diet. As the diet composition or energy content was not for all experiments readily available, the energy content was estimated based on the within experiment response of FPCM on DMI. The regression of FPCM on DMI was estimated for each experimental treatment by fitting an interaction in a model that adjusted across the whole dataset for lactation stage, breed, parity and age at calving. The pedigree file contained 7,642 animals; 131 sires had progeny with data, and 413 dams had own data and daughters with data recorded.

A nine traits model (FPCM, DMI and LW in three environments) was fitted in ASREML (Gilmour *et al.* 2015) to estimate variance components. The model included fixed effect adjustments within each trait for breed (up to 0.25 none HF was allowed), days in milk (5^{th} order polynomial), experimental treatment, herd by month of calving, herd by year of calving, and an age at calving effect within parity. Next to the additive genetic effect including the pedigree relationship matrix, a permanent environmental effect was fitted for each animal. The permanent environmental effect was correlated between the traits within each environment, but not across environments.

Estimates of the variance components were used to judge the extent of GxE. Selection index calculations were used to compare the response in the high and low environment from selection on FPCM, profit (assuming a milk price of €0.34 and the cost of a kg DMI of €0.20), feed intake (capacity) (DMI) and different weights for feed costs (€0.20 to -€0.20) relative to FPCM. The latter scenarios should answer the question if selection for high feed intake capacity should give more profit when allowing the energy density of the diet to decrease.

Results and discussion

Classification of the experiments in the three environments based on response in FPCM per kg DMI, resulted in a high environment with nearly 10 kg per day higher FPCM than the low environment, and a 2.3 kg higher DMI (Table 1). This is a large contrast in environment compared to practical farms. The medium group had a lower FPCM, but similar intake as the high group, and a 20 kg higher LW than the other two groups. These trends can also be seen when the means for each experiment were plotted (Figure 1). Concentrate fed outside the total mixed ratio (TMR) appeared to be different and not very suitable criteria to classify the experiments.

Heritability for DMI and LW were constant across the environments, for milk yield there was a decrease in h^2 from high to low environment (Table 2). The lower number of records (weekly versus daily) for FPCM is reflected in the higher SE. Despite the larger differences in mean FPCM between the environments, the phenotypic variance was relatively constant. For DMI the standard deviation dropped from 3.5 to 2.8 from high to low energy density diets.

Genetic correlations (Table 3) between the environments ranged between 0.68 to 0.90 for DMI, were lower for FPCM (0.56 to 0.82) and much higher for LW (0.90 to 0.97). These genetic correlations for FPCM were somewhat lower than expected. Genetic correlations between FPCM and DMI were between 0.61 and 0.72 when measured in the same environment, when measured in the most contrasting environment these correlations dropped to 0.26 and 0.35, respectively. Correlations between DMI and LW were less sensitive to the environment where the traits were measured.

Selection for FPCM gave the highest response in the same environment (Table 4), and halved when selection was in the contrasting environment. With selection for FPCM, the marginal feed cost increased by €0.07 per kg milk, but with selection for profit with €0.04 per kg milk in an environment with high energy density diets. The maximal response for FPCM and profit was larger in high than in low energy density diets. Interestingly, the response in profit increased with 5-6% compared to selection for FPCM, when selection was for profit in the same environment. However, 11% extra response (compared to selection for FPCM) was observed in profit on low energy density diets with selection on profit on high energy density diets, and 19% extra response in profit on high energy density diets when selection was on profit on low energy density diets.

Selection for a high intake (capacity), or a high milk yield combined with a high feed intake (“milk from roughage”), always gave a higher response for LW than selection for FPCM or profit. Obviously the response in profit was lower for the high intake (capacity) and “milk from roughage” scenarios. The hypothesis was (based on preferred cow type and nutritional models) that this extra weight and intake capacity would be advantageous on a lower concentrated diet with more roughage. However, also when selection was in the high environment and response was measured in the low environment, response was highest from selection for profit in the high environment. This holds for the full range of weights for DMI (Figure 2). Therefore, there is no extra benefit of selecting for a higher intake (capacity) on a concentrated diet, to anticipate on a lower density diet in the future.

Conclusion

From the genetic parameters estimated in this study, it can be concluded that the extent of GxE for DMI is expected to be similar as found for FPCM. Data can be combined across environments as one trait, but in extreme nutritional environments a multi-trait model should be considered. The breeding goals should always be for profit (FPCM – DMI) independent of the environment for which is selected and there is no benefit on lower density diets of selecting for a higher intake (capacity) relatively to milk yield.

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Table 1. Number of records, mean and standard deviation across the three groups of experiments: high, medium and low response for milk yield to extra DMI.

	High environment			Medium environment			Low environment		
	#	Mean	Std	#	Mean	Std	#	Mean	Std
DMI (kg?)	83,366	21.8	4.9	98,081	21.7	4.4	66,281	19.5	3.8
FPCM ??	8,180	38.8	8.5	9,681	32.9	8.7	54,99	27.9	8.3
LW (kg)	81,848	635	77	64,988	653	80	31,861	633	89

Table 2. Phenotypic standard deviation (σ_p), heritability (h^{2}[1]) and permanent environmental effect (c^2) across the three groups of experiments: high, medium and low response for milk yield to extra DMI.

	High environment			Medium environment			Low environment		
	σ_p	h^2	c^2	σ_p	h^2	c^2	σ_p	h^2	c^2
DMI	3.51	0.14	0.17	3.37	0.12	0.21	2.81	0.15	0.21
FPCM	5.67	0.19	0.35	5.99	0.13	0.47	5.66	0.09	0.32
LW	63.5	0.64	0.17	59.6	0.62	0.16	58.1	0.60	0.13

[1] Standard errors for h^2 and c^2 0.02 for DMI and LW and 0.04 for FPCM.

Table 3. Phenotypic and genetic(below diagonal) correlations for DMI, FPCM and LW across the three groups of experiments: high, medium and low response for milk yield to extra DMI (± standard error)

		DMI			FPCM			LW		
		High	Med	Low	High	Med	Low	High	Med	Low
DMI	High	-	0.12 ±0.02	0.10 ±0.03	0.34 ±0.02	0.08 ±0.03	0.04 ±0.04	0.21 ±0.02	0.14 ±0.02	0.14 ±0.03
	Med	0.90 ±0.11	-	0.11 ±0.02	0.08 ±0.03	0.36 ±0.02	0.06 ±0.03	0.13 ±0.03	0.16 ±0.02	0.14 ±0.03
	Low	0.68 ±0.14	0.82 ±0.13	-	0.04 ±0.04	0.06 ±0.03	0.37 ±0.02	0.17 ±0.03	0.19 ±0.03	0.24 ±0.02
FPCM	High	0.62 ±0.09	0.56 ±0.15	0.26 ±0.20	-	0.13 ±0.04	0.08 ±0.06	0.16 ±0.03	0.08 ±0.04	0.07 ±0.05
	Med	0.60 ±0.16	0.72 ±0.10	0.43 ±0.20	0.82 ±0.18	-	0.08 ±0.05	0.03 ±0.04	0.02 ±0.03	0.05 ±0.05
	Low	0.35 ±0.24	0.55 ±0.23	0.61 ±0.12	0.56 ±0.30	0.76 ±0.31	-	0.04 ±0.04	0.07 ±0.04	0.08 ±0.03
LW	High	0.44 ±0.07	0.48 ±0.09	0.56 ±0.10	0.14 ±0.09	0.09 ±0.13	0.15 ±0.17	-	0.58 ±0.02	0.55 ±0.03
	Med	0.47 ±0.08	0.56 ±0.08	0.62 ±0.09	0.22 ±0.10	0.21 ±0.12	0.29 ±0.16	0.93 ±0.03	-	0.59 ±0.03
	Low	0.47 ±0.10	0.53 ±0.10	0.56 ±0.07	0.21 ±0.12	0.19 ±0.14	0.21 ±0.14	0.90 ±0.04	0.97 ±0.03	-

Table 4. Selection response in the high and low response environment, from selection for FPCM, profit (=0.34 FPCM - 0.20 DMI), intake capacity (DMI), and "milk from roughage" (=0.34 + 0.20 DMI).

	Response in High environment				Response in Low environment			
	Milk (€)	Feed (€)	Profit (€)	LW (kg)	Milk (€)	Feed (€)	Profit (€)	LW (kg)
Selection in High environment on:								
FPCM	0.84	-0.16	0.68	7.1	0.29	-0.05	0.23	10.0
Profit	0.80	-0.10	0.71	0.1	0.27	-0.01	0.26	3.8
Intake capacity	0.52	-0.26	0.25	22.3	0.19	-0.14	0.05	21.7
Milk from roughage	0.82	-0.20	0.62	11.6	0.28	-0.08	0.20	13.8
Selection in Low environment on:								
FPCM	0.41	-0.08	0.32	10.0	0.59	-0.14	0.44	11.3
Profit	0.41	-0.03	0.39	-0.2	0.55	-0.08	0.47	2.6
Intake capacity	0.21	-0.17	0.04	27.8	0.39	-0.22	0.17	25.3
Milk from roughage	0.39	-0.11	0.28	14.3	0.58	-0.17	0.41	14.9

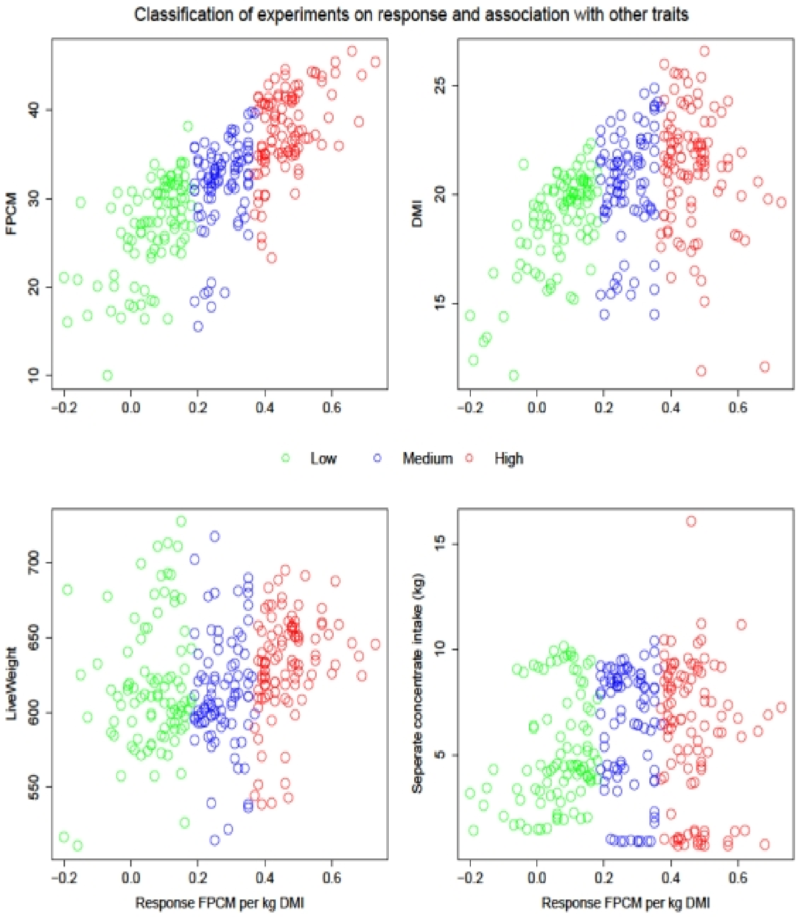

Figure 1. Experiments classified in high, medium and low environment based on the response for FPCM per kg DMI, and the association of the response per experiment with average FPCM, DMI, LW and the amount of concentrate fed separate from the mixed ration.

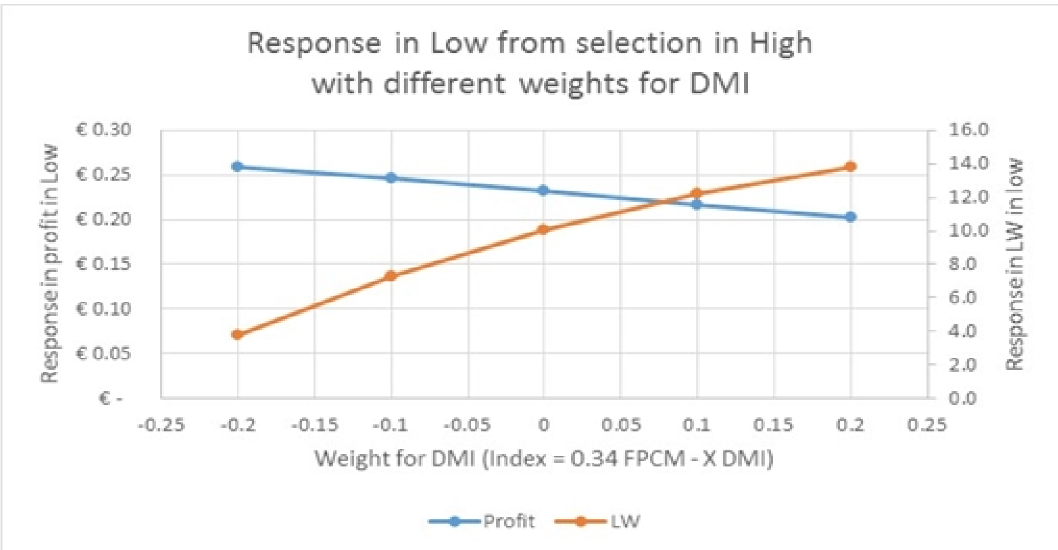

Figure 2. Selection response in profit and LW in the Low environment, from selection in the High environment using different weights for DMI (X ranges from -0.2 to 0.2 in 0.34 FPCM

+ X DMI).