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Latent phenotype potential: Modelling response to selection for dairy cattle productivity traits considering genetic correlations

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Abstract. The aim of the study was to analyse the dynamics of changes in economically important traits of dairy cattle: milk fat and protein content, daughter pregnancy rate, productive longevity, residual feed intake, live weight, somatic cell score, when modelling selection for dairy productivity traits such as milk yield, milk fat and protein content. The research material consisted of data from a reference herd of Holstein cows at the “Terezyne” dairy farm (Kyiv region, Ukraine). The total number of cows observed was 14,712 across seven lactations. MRS software was used for modelling. When selecting for milk yield at selection differentials of 100 kg, 300 kg and 500 kg, the genetic response of the next generation for milk yield was 31.59 kg, 94.77 kg and 157.97 kg, respectively. At the same time, there was an increase in such traits as productive longevity, from 0.59 months to 2.94 months, live weight – from 0.36 to 1.79 kg, and the score for somatic cell content in milk – from 0.03 to 0.13. Genetic changes in milk fat and protein content, signs of daughter fertility and residual feed intake had reverse values. Significant phenotypic correlations were obtained between the milk yield of first-calf heifers and milk fat content (-0.2985), milk fat content (+0.9631), milk protein content (-0.2642), milk protein (+0.9924), open days period (+0.0989), productive longevity (+0.0989) and live weight (+0.2199). There were mixed levels of correlation in the daughters of sires between milk yield and milk protein content from -0.1229 to +0.1708, and between milk yield and open days from -0.0726 to +0.1836. Modelling of possible changes in genetic correlations in the range from -0.10 to -0.95 between milk yield and daughter pregnancy rate (DPR) was performed. The rates of correlated response when selecting for milk yield, depending on the values of genetic correlation between these traits, affected the reduction in the level of pregnancy in cows from -0.51 to almost -5.0 points. The impact on the strength and direction of the established relationships can contribute to the stabilisation or deterioration of reproductive traits when selecting for milk yield. The proposed modelling method makes it possible to predict changes in the main traits used for selection, depending on the genetic correlations between them

Keywords: genetic parameters; phenotypic correlations; dairy productivity; reproduction

Introduction

An important aspect of breeding work in dairy cattle farming is modelling the response to the selection of a set of economically important traits, taking into account the genetic links (correlations) between them. P. VanRaden (2020) pointed out that the global trend in dairy cattle selection programmes is to increase the number of control traits, due to their impact on production profitability. For a comprehensive assessment, indices are used to determine the selection rank of individual animals within a breed. According to official data from the United States Department of Agriculture (USDA), several methods are used to evaluate dairy cattle, the main one being NM\$ – Lifetime Net Merit (VanRaden *et al.*, 2021). This is

the official evaluation for Holstein animals, and the NM\$ value is considered a measure of the expected additional net profit in US dollars that the sire's daughters can earn during their lifetime. P. VanRaden *et al.* (2021) note that the total NM\$ value is based on the Predicted Transmitting Ability (PTA), which is equal to half of the breeding value for 17 traits with the corresponding economic weight of each. Most traits are negatively correlated, but at the same time, predicted PTA values remain one of the main tools for genetic evaluation. PTA allows comparing sires for a specific trait that can be observed in 50% of offspring. The remaining 50% of “success” will depend on the successful selection of pairs, sires and brood stock, according

to the ranks of such evaluation, which also affects the level of genetic correlations between traits in the next generation.

The Holstein Association USA uses its own productivity index, TPI (Type-Production Index), whose formula has a slightly different weighting of traits compared to the PTA index, and the overall performance is aimed at obtaining a profitable cattle herd. It should be noted that similar or even identical results of a comprehensive assessment can be obtained with different values for individual traits included in the index, which are characterised by different directions of genetic relationships between these traits. However, changes in some traits in the index do not always lead to positive changes in others, which requires constant verification of this effect over several generations based on phenotypic or genetic correlations. According to A. Caballero (2020) and S. Xu (2022), the genetic correlation between two quantitative traits is defined as the relationship between the breeding values of animals for these traits, and their significance lies in the ability to predict genetic changes when selecting for one of them.

M. Satoh (2024) used three methods for predicting response to truncated selection based on BLUP (Best Linear Unbiased Prediction), where only a certain percentage of fit individuals are selected from the population for reproduction and the rest are culled: (1) based on the mean value of the estimated breeding values (EBV) in the candidate population for selection (Δg_1); (2) based on the variance of EBV in the candidate population for selection (Δg_2); (3) based on the diagonal elements of the inverse matrix on the left side of the mixed model equation (Δg_3). The author concluded that it is desirable to use Δg_1 or Δg_2 to predict the response to truncated selection based on BLUP BV. However, in populations where selection is ongoing, the accuracy of predicting the selection response is likely to depend on distribution bias and the Balmer effect for Δg_2 , when generalised descriptions of a specific situation are

applicable to many others. L. Brito *et al.* (2021) noted that for the development of milk production, it is necessary to improve current breeding indices and breeding goals, paying more attention to traits related to animal welfare, health, longevity, environmental performance (e.g., methane emissions and feed efficiency) and overall resilience. This should be done by identifying selection criteria (traits) that accurately reflect the biological mechanisms underlying the relevant phenotypes, are heritable, and can be measured quickly and cost-effectively in large numbers of animals.

N. Lopez-Villalobos *et al.* (2024) assessed the value of continuous genetic improvement using a model covering all dairy producers in an industry where dairy prices were determined by supply and demand curves for a specific product. Over 10 years of genetic improvement, the present value of the benefits was estimated at USD 123,000 per farm. The corresponding benefit, when assuming that markets had fixed commodity prices, was USD 183,000 per farm. The model showed that systematic genetic gains have a limited duration, during which additional benefits gradually decline and eventually disappear. T. Niehoff *et al.* (2024) proposed a new selection criterion that describes the genetic level of selected grandprogenitors produced by the offspring of a given cross. The authors compared this criterion with other published criteria in a stochastic simulation of the current breeding programme over 21 generations to validate the concept. The proposed result showed better results than all other tested criteria. Thus, the new selection option offers a tool for accelerating genetic progress for modern genomic breeding programmes. It preserves more genetic variation than previously published criteria. Taking into account future gametic Mendelian sampling variations in the selection process also appears promising for maintaining greater genetic variation.

The aim of this study was to establish the nature of correlated genetic changes in a complex

of economically valuable traits in Holstein cattle under conditions of targeted selection for increased milk productivity of the herd.

Literature Review

B. Cuyabano *et al.* (2024) suggested considering genetic correlations not only as one of the genetic parameters used in assessing the breeding value of animals based on a set of traits, but also as a certain “latent phenotype”, based on the fact that the values of genetic correlations may vary in the offspring of different sires. If genetic correlations are specific values inherent in each individual, then they can be considered as a phenotype of a hidden regulatory trait that controls the relationship between selection traits. For such antagonistic traits in dairy cattle as productivity – fertility, somatic cell count, live weight – residual feed intake, it can be assumed that animals at the extreme ends of the rank distribution are likely to represent different breeding values for a particular hidden regulatory trait and, especially, when generations change. B. Olasege *et al.* (2024), using the “correlation scanning” method, identified regions of the Australian Holstein cattle genome that determine antagonistic genetic correlations between traits. Several such regions were identified, most of which were related to muscle development, body weight, and milk quality traits. Future studies may identify such “antagonistic regions” as potential genomic areas to alter unfavourable correlations and improve milk quality, milk production, fertility traits, and milk urea levels.

Between 1930 and 2015, dairy cattle selection criteria focused on increasing milk production, which led to a decline in health and fertility and triggered metabolic diseases (Egger-Danner *et al.*, 2015). As noted by O. Fedota *et al.* (2020), growing concern for animal welfare, consumer demands for food quality and product composition, and reduced exposure to veterinary drugs have prompted changes in breeding strategies. The health and production

efficiency of different breeds and species of animals are becoming increasingly important due to growing competition for high-quality plant sources of energy and protein. Agro-economic and climatic characteristics of milk production and genetic heterogeneity of breeds influence the target function of the selection index, which will be constantly aimed at total profit and minimisation of losses. Thus, according to V. Danshin *et al.* (2017), these estimates make it possible to determine the approximate expected effect of breeding stock. At the same time, it is important to take into account the productive and adaptive qualities of animals in different natural and climatic zones, especially when using interbreeding (Nogoev *et al.*, 2025). The assessment of genetic correlations requires the use of highly accurate methods, such as REML (Residual Maximum Likelihood) – a method of limited maximum likelihood. The method involves the use of model fitting techniques in which all observations are expressed additively through fixed and random effects (Misztal *et al.*, 2024).

A negative effect of genomic selection may be unfavourable genetic correlations between the performance traits for which selection is carried out and the so-called secondary traits, which include adaptation traits. This phenomenon was noted by I. Misztal & D. Lourenco (2024), who pointed out that such adaptation traits in dairy cattle include heat stress resistance, which should also be included in selection indices. An important advantage of genomic selection is the possibility of genetic improvement of traits that are difficult or costly to measure. Such traits can be measured in small numbers of animals in reference populations designated specifically for this purpose. One such trait is feed efficiency, i.e. the ability of cows to produce the same amount of milk with less feed (Brito *et al.*, 2020). Recently, this trait has received a lot of attention, which, according to M. Madilindi *et al.* (2022), is due to its economic and environmental significance.

As a modern mainstream, it is worth noting software solutions based on artificial intelligence (AI) that are used in dairy farming for various purposes (De Vries *et al.*, 2023; Neethirajan, 2023). H. Monteiro *et al.* (2024) proved that the composition of the rumen microbiome describes a significant part of the variability in residual feed intake by dairy cows. According to the scientists' conclusion, the application of AI and the development of sensor technologies have radically changed traditional sectors of the economy, including dairy farming (Akash *et al.*, 2022). Precision livestock farming using AI and sensor technologies offers innovative solutions in the field of milk production. According to G. Koutouzidou *et al.* (2022), such approaches have enabled real-time monitoring and management decisions to improve animal welfare and increase their productivity. Measuring individual animal characteristics, which, according to B. Martins *et al.* (2020), is important for assessing their health and productivity, remains a challenging task that takes time when using conventional routine methods. That is why artificial intelligence and sensor technologies automate individual accounting based on cow behaviour during feeding, including time spent at the feeder, feeding frequency and amount of feed consumed (Lee & Seo, 2021). According to A. De Vries *et al.* (2023), the main areas of application for artificial intelligence technologies in dairy farming are: (1) building expert systems to improve feeding, culling, mastitis control, and individual selection of breeding bulls; (2) literature reviews on management areas; (3) disease diagnosis; (4) detection of cows in oestrus and prediction of the probability of successful insemination; (5) prediction of future milk productivity of cows;

(6) assessment of individual feed consumption by cows based on data on productivity, behaviour and metabolic characteristics; (7) voluntary milking systems or milking robots. Thus, modelling and predicting probable changes in dairy cattle populations can be based on genetic correlations between traits.

Materials and Methods

The research was based on individual records of a reference herd of Holstein cows at the "Terezyne" dairy farm in the Kyiv region for the period from January 2020 to May 2025. The study did not involve any experimental interventions in animals; all data were obtained from the farm's routine accounting system and collected in accordance with ICAR (2014) requirements. The herd consists of 1,350 cows descended from sires of the Chief 1427381.62, Elevation 1491007.65, Starbuck 352790.79, Bell 1667366.74, Montfretch 91779b72, Hanover Red 1629391.72, Marshall 2290977.95, and J. Besne 5694028588.94 lines. The average annual productivity of cows is within 10,000 kg. The dry matter ration for the dairy cows consists of 9.55 kg of maize silage, 1.97 kg of lucerne haylage, 3.08 kg of soya bean meal, 3.05 kg of maize grain, 1.87 kg of sunflower meal, and 1.8 kg of wheat and barley grain, as well as mineral and vitamin supplements. The total weight of the ration was 45.8 kg at 23 kg of dry matter, with a protein content of 18%, a Neutral Detergent Fibre (NDF) level of 28%, and an Acid Detergent Fibre (ADF) level of 16.2%. Milking of cows ($n = 500$) was carried out on VMS DeLaval robotic milking systems, and the second part ($n = 850$) – in a 2×16 Parallel milking parlour. Table 1 shows descriptive statistics of the studied traits of cows.

Table 1. Descriptive statistics of the studied traits of cows for standard lactation, 305 days

Trait	N	M $\pm$ m	σ^2	σ	Cv, %
First lactation (5,105 head)					
Milk yield, kg	5,105	7,133.43 $\pm$ 24.63	3,097,643.56	1,760.01	24.7
Milk fat content, %	5,105	4.01 $\pm$ 0.01	0.10	0.31	7.8

Table 1. Continued

Trait	N	M ± m	σ^2	σ	Cv, %
First lactation (5,105 head)					
Milk fat amount, kg	5,105	287.90±1.14	6,621.95	81.38	28.3
Milk protein content, %	5,026	3.33±0.02	0.01	0.12	3.6
Milk protein amount, kg	5,026	239.71±0.87	3,767.58	61.38	25.6
Second lactation (4,032 head)					
Milk yield, kg	4,032	7,818.71±33.64	4,561,996.43	2,135.88	27.3
Milk fat content, %	4,032	4.07±0.01	0.10	0.31	7.6
Milk fat amount, kg	4,032	320.29±1.56	9,792.74	98.96	30.9
Milk protein content, %	3,991	3.35±0.01	0.02	0.14	4.1
Milk protein amount, kg	3,991	263.90±1.19	5,643.08	75.12	28.5
Third lactation (2,628 head)					
Milk yield, kg	2,628	7,461.29±47.33	5,886,521.69	2,426.22	32.5
Milk fat content, %	2,628	4.05±0.01	0.10	0.31	7.8
Milk fat amount, kg	2,628	304.86±2.15	12,188.14	110.40	36.2
Milk protein content, %	2,612	3.35±0.01	0.02	0.14	4.2
Milk protein amount, kg	2,612	251.09±1.66	7,178.99	84.73	33.7
Fourth lactation (1,542 head)					
Milk yield, kg	1,542	7,180.17±63.97	6,310,879.79	2,512.15	35.0
Milk fat content, %	1,542	4.05±0.01	0.10	0.32	8.0
Milk fat amount, kg	1,542	293.29±2.89	12,882.52	113.50	38.7
Milk protein content, %	1,531	3.35±0.01	0.02	0.14	4.3
Milk protein amount, kg	1,531	241.72±2.24	7,689.99	87.69	36.3
Fifth lactation (805 head)					
Milk yield, kg	805	6,775.39 ± 90.14	6,541,314.99	2,557.60	37.7
Milk fat content, %	805	4.04 ± 0.01	0.10	0.32	7.9
Milk fat amount, kg	805	276.48 ± 4.05	13,223.79	114.99	41.6
Milk protein content, %	799	3.34 ± 0.01	0.02	0.16	4.7
Milk protein amount, kg	799	227.38 ± 3.15	7,930.42	89.05	39.2
Sixth lactation (408 head)					
Milk yield, kg	408	6,478.12 ± 123.83	6,256,262.35	2,501.25	38.6
Milk fat content, %	408	4.01 ± 0.02	0.10	0.32	7.9
Milk fat amount, kg	408	262.76 ± 5.53	12,482.83	111.73	42.5
Milk protein content, %	404	3.33 ± 0.01	0.03	0.17	5.1
Milk protein amount, kg	404	216.99 ± 4.32	7,555.89	86.92	40.1
Seventh lactation (192 head)					
Milk yield, kg	192	6,137.05 ± 175.72	5,928,770.24	2,434.91	39.7
Milk fat content, %	192	3.97 ± 0.02	0.10	0.32	8.1
Milk fat amount, kg	192	245.96 ± 7.74	11,495.00	107.21	43.6
Milk protein content, %	191	3.30 ± 0.01	0.03	0.16	4.9
Milk protein amount, kg	191	203.74 ± 6.08	7,071.25	84.09	41.3
Open days period	2,201	233.22 ± 4.04	35,905.42	189.49	81.2
Live weight at first calving, kg	3,692	578.33 ± 0.74	1,998.61	44.71	7.7
Productive longevity, months	5,604	83.20 ± 4.21	99,165.23	314.91	3.8

Note: N – number of observations; M ± m – mean value of the trait and its standard error; σ^2 – variance of the trait; σ – standard deviation of the trait; Cv – coefficient of variation of the trait

Source: developed by the authors

The general algorithm for calculating the traits included in the test set is presented below. Daughter Pregnancy Rate (DPR) was calculated in points using formula (1):

$$DPR = \frac{21}{(SP - RWP) + 11} \times 100, \quad (1)$$

where 21 – the length of the cows' sexual cycle; SP – the service period; RWP – the required waiting period (at least 60 days); 11 – the correction factor.

The Somatic Cell Score (SCS) in milk was calculated in scores using formula (2):

$$SCS = \log_2 (NSC/100,000) + 3, \quad (2)$$

where NSC – the number of somatic cells per 1 ml of milk.

The somatic cell count indicators were assessed in scores: 100,000 cells/ml – 3 points; 400,000 cells/ml – 5 points; 200,000 cells/ml – 4 points; 500,000 cells/ml – 5.3 points; 300,000 cells/ml – 4.6 points. Residual Feed Intake (RFI) was defined as the difference

between actual and expected feed intake in terms of dry matter – Dry Matter Intake (DMI). The expected daily dry matter intake of a dairy cow was calculated based on its live body weight using a linear regression equation: $DMIE = -38.09 + 0.106 \times (\text{live weight})$. Residual feed intake was equal to: $RFI = DMIa - DMIE$, where $DMIa$ is the actual dry matter intake.

Animals with lower and, especially, negative residual feed intake are considered more economically efficient. According to I. Berro *et al.* (2019), the effectiveness of breeding programmes, including genomic ones, depends on the quality of recording and the volume of phenotypic data, the number and type of markers, and the size and composition of the Training Population (TR), in which a sufficient amount of such data has been accumulated. In addition, the structure and diversity of the population play a key role in compiling optimal sets for specific testing populations (TE). Phenotypic and genetic correlations between the traits studied that are characteristic of the Holstein breed were considered as TR (Tables 2, 3).

Table 2. Phenotypic correlations between investigated traits in the Holstein breed

Trait	1	2	3	4	5	6	7	8
1. Milk yield	1.0							
2. Milk fat	+0.619	1.0						
3. Milk protein	+0.901	+0.723	1.0					
4. Fertility rate	-0.342	-0.245	-0.307	1.0				
5. Productive longevity	+0.175	+0.144	+0.179	+0.544	1.0			
6. Residual feed intake	+0.040	+0.030	+0.030	+0.010	0.0	1.0		
7. Live weight	-0.066	-0.045	-0.055	-0.009	-0.041	0.0	1.0	
8. Somatic Cell Score	-0.159	-0.167	-0.148	-0.019	-0.163	0.0	+0.005	1.0

Source: P. VanRaden *et al.* (2021)

Table 3. Genetic correlations between the traits studied in the Holstein breed

Trait	1	2	3	4	5	6	7	8
1. Milk yield	1.0							
2. Milk fat	+0.399	1.0						

Table 3. Continued

Trait	1	2	3	4	5	6	7	8
3. Milk protein	+0.835	+0.591	1.0					
4. Fertility rate	-0.094	-0.075	-0.078	1.0				
5. Productive longevity	+0.113	+0.090	+0.128	+0.102	1.0			
6. Residual feed intake	+0.010	-0.070	+0.080	+0.020	-0.010	1.0		
7. Live weight	-0.131	-0.115	-0.100	-0.024	-0.221	+0.143	1.0	
8. Somatic Cell Score	+0.179	+0.080	+0.168	-0.313	-0.456	-0.124	-0.192	1.0

Source: P. VanRaden *et al.* (2021)

Multivariate Response to Selection (R) was calculated using the formula by B. Walsh & M. Lynch (2018) (3):

$$R = GP^{-1}s, \quad (3)$$

where G – the matrix of additive genetic variances and covariances between traits; P – the

matrix of phenotypic variances and covariances between traits; s – the vector of selection differentials.

The calculations were performed using proprietary software – MRS (Multivariate Response to Selection), where, when modelling selection based on two traits, the system of equations has the form (4):

$$MRS = \begin{bmatrix} R_1 \\ R_2 \end{bmatrix} = GP^{-1}s = \begin{bmatrix} G_{11} & G_{12} \\ G_{12} & G_{22} \end{bmatrix} \begin{bmatrix} P_{11} & P_{12} \\ P_{12} & P_{22} \end{bmatrix}^{-1} \begin{bmatrix} S_1 \\ S_2 \end{bmatrix}, \quad (4)$$

where R_1 and R_2 – responses to the selection of the first and second traits; G_{11} and G_{12} – genetic variances of the first and second traits; G_{12} – genetic covariance between traits; P_{11} and P_{12} – phenotypic variances of the first and

second traits; P_{12} – the phenotypic covariance between traits; S_1 and S_2 – the selection differentials of the first and second traits. Covariance $P_{12} = \rho_z(P_{11}P_{22})^{1/2}$, where ρ_z – the phenotypic correlation between two traits. Then:

$$\begin{aligned} P^{-1}s &= \frac{1}{P_{11}P_{22} - P_{12}^2} \begin{bmatrix} P_{22} & -P_{12} \\ -P_{12} & P_{11} \end{bmatrix} \begin{bmatrix} S_1 \\ S_2 \end{bmatrix} \\ &= \frac{1}{P_{11}P_{22}(1 - \rho_z^2)} \begin{bmatrix} S_1P_{22} - S_2P_{12} \\ -S_1P_{12} + S_2P_{11} \end{bmatrix}. \end{aligned} \quad (5)$$

Thus, the response to selection of the first trait is obtained from the above derivation.

The final form of this response is given in equation (6):

$$R_1 = \frac{h^2_1}{(1 - \rho_z^2)} \left[S_1 - S_2 \frac{P_{12}}{P_{22}} \right] + \frac{G_{12}(-S_1P_{12} + S_2P_{11})}{P_{11}P_{22}(1 - \rho_z^2)}, \quad (6)$$

where h_1^2 – the heritability coefficient of the first trait.

The correlated response of trait Y to selection for trait X was calculated using the formula by A. Caballero (2020) (7):

$$R_{YX} = i_X \cdot r_{Gxy} \cdot h_Y \cdot h_X \cdot \sigma_X, \quad (7)$$

where i_X – the intensity of selection for trait X; r_{Gxy} – the genetic correlation between traits X and Y; h_Y – the heritability coefficient of trait Y; h_{DPR} – the heritability coefficient of trait X; σ_X – the standard phenotypic deviation of trait X.

Results and Discussion

Tables 4-6 show the results of modelling genetic changes in the studied traits when selecting for milk productivity indicators such as milk yield, milk fat and protein content,

depending on the values of the corresponding selection differentials. When selecting for milk yield with corresponding selection differential values of 100 kg, 300 kg and 500 kg, the genetic response of the next generation for milk yield will be 31.59 kg, 94.77 kg and 157.97 kg, respectively. At the same time, the amount of milk fat will increase by 0.98 kg, 2.94 kg and 4.91 kg, and the amount of milk protein – by 0.29 kg, 0.88 kg and 1.46 kg. At the same time, there is an increase in indicators such as productive longevity – from 0.59 months to 2.94 months, live weight – from 0.36 to 1.79 kg, and the somatic cell score content in milk – from 0.03 to 0.13. At the same time, genetically determined changes in the fat and protein content of milk, signs of the fertility level of daughters and residual feed consumption had negative values (Table 4).

Table 4. Genetic changes in investigated traits under selection for milk yield

Traits	Selection differential for milk yield, kg		
	100	300	500
Milk yield, kg	31.59	94.77	157.95
Milk fat amount, kg	0.98	2.94	4.91
Milk protein amount, kg	0.29	0.88	1.46
Milk fat content, %	-0.005	-0.007	-0.009
Milk protein content, %	-0.003	-0.004	-0.006
Daughter pregnancy rate, scores	-0.19	-0.58	-0.97
Productive longevity, months	0.59	1.76	2.94
Residual feed intake, kg	-0.03	-0.08	-0.14
Live weight, kg	0.36	1.08	1.79
Somatic cell score content in milk	0.03	0.09	0.13

Source: developed by the authors

Similar patterns were observed when selecting by milk fat amount (Table 5), where milk fat amount at selection differentials of 10 kg, 30 kg and 50 kg was +2.46 kg, +7.37 kg and +12.29 kg, respectively. Genetic changes in all traits show a positive trend towards an increase with a decrease in the level of daughter

fertility (-0.02 – -0.11) and residual feed intake (-0.01 kg – -0.07 kg).

The level of milk protein has become one of the main indicators in determining the price of milk in many countries around the world, which prompts to model the consequences of selection based on this trait (Table 6).

Table 5. Genetically determined changes in the studied traits when selecting by milk fat amount

Traits	Selection differential for milk fat amount, kg		
	10	30	50
Milk yield, kg	3.24	9.71	16.18
Milk fat amount, kg	2.46	7.37	12.29
Milk protein amount, kg	0.32	0.97	1.62
Milk fat content, %	0.004	0.005	0.007
Milk protein content, %	0.002	0.003	0.005
Daughter pregnancy rate, scores	-0.02	-0.06	-0.11
Productive longevity, months	0.13	0.40	0.67
Residual feed intake, kg	-0.01	-0.04	-0.07
Live weight, kg	0.21	0.64	1.06
Somatic cell score content in milk	0.003	0.009	0.015

Source: developed by the authors

Table 6. Genetically determined changes in the studied traits when selecting for milk protein amount

Traits	Selection differential for milk fat amount, kg		
	10	30	50
Milk yield, kg	1.46	4.38	7.29
Milk fat amount, kg	0.49	1.46	2.44
Milk protein amount, kg	3.12	9.35	15.58
Milk fat content, %	0.002	0.003	0.004
Milk protein content, %	0.003	0.005	0.008
Daughter pregnancy rate, scores	-0.14	-0.41	-0.68
Productive longevity, months	0.21	0.61	1.02
Residual feed intake, kg	-0.04	-0.11	-0.19
Live weight, kg	0.47	1.40	2.33
Somatic cell score content in milk	0.003	0.009	0.015

Source: developed by the authors

When selecting for milk protein amount with selection differentials of 10 kg, 30 kg and 50 kg, genetic changes in milk protein amount were +3.12 kg, +9.35 kg and +15.58 kg, respectively. The level of fertility of daughters decreased by 0.14, 0.41 and 0.68 points. Residual feed consumption decreased by 0.04 kg, 0.11 kg and 0.19 kg. An increase in the absolute values of fat and protein content in milk was noted. Productive longevity increased by 0.21 months, 0.61 months and 1.02 months, and live weight increased by 0.47 kg, 1.40 kg and 2.33 kg. At the same time, the somatic cell concentration score increased by 0.003, 0.009 and 0.015 points. Thus, selection based on milk productivity traits contributes to an increase in productive longevity and live weight of cows while

reducing residual feed intake. At the same time, there is a deterioration in indicators such as the level of pregnancy in daughters and the concentration of somatic cells in milk.

The results obtained regarding the rate of genetic change are consistent with current trends in dairy cattle breeding. According to P. VanRaden (2020), genomic selection has been used in dairy cattle breeding since 2009, which has led to a significant reduction in generation intervals. Across four genetic improvement pathways, the average generation interval has decreased from 6-6.5 years to 2.5-3 years, i.e. by a factor of 2. According to G. Wiggins & J. Carrillo (2022), the largest reduction in the generation interval occurred in the category of bull sires – from 8 to 2-3 years, which led to

accelerated genetic progress in the main selection pathways. Genetic progress in milk fat content in Holstein bulls in the United States increased sixfold between 2009 and 2023, and the overall level of genetic progress nearly doubled. This explains the need for constant monitoring of correlated changes in fitness traits during intensive selection for productivity.

Assuming the existence of the “latent phenotype” phenomenon, modelling of possible

changes in genetic correlations during selection for milk yield and correlated response for DPR was performed. Changes in the values of genetic correlation between these traits in the range from -0.10 to -0.95 (Fig. 1) cause a decrease in the correlated response of the fertility level of cows from -0.51 to almost -5.0 points. Thus, the strength and direction of these relationships can influence the improvement or deterioration of reproductive traits when selecting for milk yield.

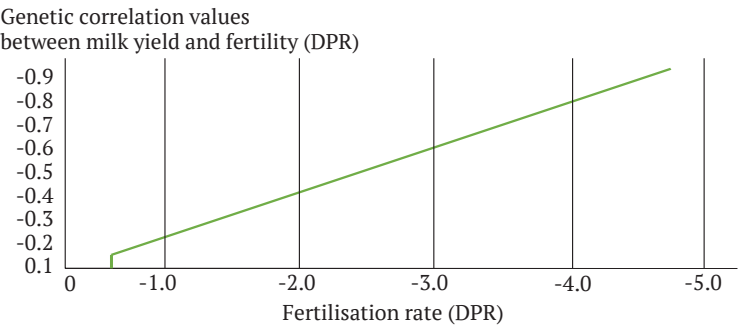


Figure 1. Correlated response of DPR change to selection for milk yield when genetic correlation values change

Source: developed by the authors

Table 7 shows phenotypic correlations between milk productivity traits, service period, productive longevity and live weight at first calving at the “Terezyne” farm.

Table 7. Phenotypic correlations between milk productivity traits, service period, productive longevity and live weight at first calving at the “Terezyne” farm (7,128 heads)								
Traits	1	2	3	4	5	6	7	8
1. Milk yield	1.00							
2. Milk fat content	-0.2985 ***							
3. Milk fat amount	+0.9631 ***	+0.5363 ***						
4. Milk protein content	-0.2642 ***	+0.6039 ***	+0.3860 ***					
5. Milk protein amount	+0.9924 ***	+0.3557 ***	+0.9740 ***	+0.3749 ***				
6. Service period	+0.0166 *	+0.2953 ***	-0.0714 ***	-0.1918 ***	-0.0050			
7. Productive longevity	+0.0989 ***	-0.1230 ***	+0.0559 ***	-0.0546 ***	+0.0901 ***	+0.8466 ***		
8. Live weight	+0.2199 ***	+0.1447 ***	+0.2233 ***	+0.2019 ***	+0.2095 ***	+0.0485 ***	+0.0875 ***	

Note: * – $p < 0.05$; ** – $p < 0.01$; *** – $p < 0.001$

Source: developed by the authors

At the “Terezyne” farm, reliability correlates positively with the amount of milk fat and protein, the length of the service period, productive longevity and live weight, and negatively with the fat and protein content of milk. The fat content in milk is positively correlated with all traits except productive longevity. The protein content in milk is negatively correlated with the service period and productive longevity. The amount of milk fat is positively correlated with the service period and live weight and

negatively correlated with productive longevity, while the amount of milk protein is negatively correlated with the service period and positively correlated with productive longevity and live weight. The service period is characterised by a high positive correlation with productive longevity. Within the framework of the assumption of “latent phenotype” possibilities, an assessment of phenotypic correlations between the studied traits in cows depending on their paternal origin was carried out (Table 8).

Table 8. Phenotypic correlations between milk productivity traits, open days period, productive longevity and live weight at first calving of different sires

Traits	Sires				
	CA 106627797 D. Kickball Et	CA 7746123 S. Stady Et	CA 9969495 V. Sophomore Et	NL 493726366 O. Gigant	NL 520913639 N. Saltie
Number of animals	69	105	34	22	29
Milk fat content	-0.0258	+0.0238	+0.0279	+0.2603***	+0.0730***
Milk fat amount	+0.9993***	+0.9948***	+0.9981***	+0.9533***	+0.9625***
Milk protein content	-0.0973**	+0.0345	+0.1708***	+0.0872***	-0.1229***
Milk protein amount	+0.9986***	+0.9971***	+0.9992***	+0.9962***	+0.9948***
Open days period	-0.0726	+0.1836***	+0.0512	+0.0529	+0.1332***
Productive longevity	+0.2441***	+0.1974***	+0.2014***	+0.0339	+0.0709***
Live weight	-0.1850*	-0.0014	-0.3563***	+0.2389***	+0.2378***

Note: * – $p < 0.05$; ** – $p < 0.01$; *** – $p < 0.001$

Source: developed by the authors

There are significant differences between the daughters of bulls of different origins in terms of phenotypic correlations between the above traits. In the offspring of the breeding bull CA 106627797 D. Kickball Et, the correlation between milk yield and milk protein content was -0.0973**, and in the offspring of the bull CA 9969495 V. Sophomore Et, it was +0.1708***, and in the offspring of the bull NL 520913639 N. Saltie, it was -0.1229***. Similar results were obtained for other traits. In the offspring of the breeding bull CA 9969495 V. Sophomore Et, the correlation between milk yield and live weight of cows was -0.3563***, and in the offspring of the breeding bull NL 520913639 N. Saltie, it was

+0.2378***. The results obtained indicate the possibility of a “latent phenotyp”, i.e. cows of different origins are characterised not only by different values of selection traits, but also by the values and direction of the relationships between them.

The reduction in residual feed intake obtained when selecting for productivity is of great practical importance. Iranian scientists S. Nadri *et al.* (2023) concluded that including feed efficiency in the breeding goals for dairy cattle is desirable in terms of increasing sustainability and profitability. A study of selection indices that include feed efficiency showed that this allows for the greatest economic effect.

At the same time, it is possible to use indicators such as certain characteristics of the cows' body structure, namely fatness, milk type, etc. A number of studies have shown that feed efficiency in dairy cows is related to their behaviour and the response of certain genotypes to environmental conditions (Fedota *et al.*, 2022). In a study by B. Nascimento *et al.* (2024), behavioural indicators such as chewing duration, lying duration and motor activity of cows were studied. Heritability was 0.19 for chewing and activity and 0.37 for lying duration. According to the authors, cows that spend more time lying down and are less active in movement are characterised by higher feed efficiency. This confirms the advisability of including feed efficiency indicators in breeding programmes.

It should be noted that modelling the response to selection is quite often used in modern breeding studies. J. Weller *et al.* (2022) used modelling to assess the effects of selecting Israeli dairy cattle based on reproduction and milk production indicators. In another study, J. Weller *et al.* (2023) used modelling to study the possibility of selecting cows based on viability, which was defined as the inverse of the probability of death. The viability of 523,954 cows was established for the period from 2000 to 2026, which was 89.6%, and according to this model, pregnancy reduced viability by 15%. The viability index increased with each calving, but was associated with an increase in the duration of lactation. The heritability coefficient of viability was 0.0082, and the phenotypic and genetic trends in viability over 14 years were -0.042% and -0.22% per year, respectively. A. Bouquet *et al.* (2022) presented a new methodology for predicting the response of selection for feed efficiency in dairy cattle. This approach combines genetic and mechanistic modelling to describe the biological mechanisms underlying these traits. A dairy cattle breeding scheme was modelled, taking into account an unrestricted feeding environment and two different selection goals, focused either on milk production

or feed efficiency. The selection response was predicted in an unrestricted environment as well as for a promising low-cost system. The predictions obtained using traditional and mechanistic methods were consistent for milk production, body weight and feed efficiency in an unrestricted environment.

The current study revealed a decrease in reproduction rate, or daughter pregnancy rate, when selecting for milk productivity traits, indicating genetic antagonism between these traits. The genetic basis of antagonism is evidenced by the results of studies by L. Ma *et al.* (2019). The authors conducted a genomic comparison of two lines of Holstein cows, where one line was selected for milk productivity for 40 years since 1964, and the other line was a control line without selection. The results showed that selection for milk productivity resulted in a deterioration in reproduction and fertility rates. Thanks to this work, 198 genes associated with milk productivity and reproduction rates in cows were identified.

Thus, the analysis of predictive traits that may differ within certain genetic groups and the improvement of tools for their assessment are promising. Existing contradictions in the objectives and selection criteria between traits call into question the relatively rapid improvement in those traits that are related to health, reproduction, feed efficiency, or that reduce methanogenesis in ruminants. Modelling processes based on mathematical patterns that describe the relationships between such traits and the use of accurate and predictive data makes it possible to optimise selection and breeding programmes by identifying economically important traits for each group of animals.

Conclusions

The proposed algorithm for modelling the correlated response to selection makes it possible to predict the dynamics of genetic changes for a complex of traits when selecting for individual traits. When selecting for milk yield with

corresponding selection differentials of 100 kg, 300 kg and 500 kg, the genetic response of the next generation for milk yield will be 31.59 kg, 94.77 kg and 157.97 kg, respectively. At the same time, the amount of milk fat will increase by 0.98 kg, 2.94 kg and 4.91 kg, and the amount of milk protein by 0.29 kg, 0.88 kg and 1.46 kg. At the same time, there is an increase in such characteristics as productive longevity – from 0.59 months to 2.94 months, live weight – from 0.36 to 1.79 kg, and the score for somatic cell content in milk – from 0.03 to 0.13. A decrease in the reproduction rate, or the level of pregnancy in daughters, was established when selecting for milk productivity traits, which indicates the presence of genetic antagonism between these indicators. When selecting for milk fat amount with selection differentials of 10 kg, 30 kg and 50 kg, the additional milk fat yield was +2.46 kg, +7.37 kg and +12.29 kg, respectively. Genetic changes in all traits have a positive dynamic of increase with a decrease in the level of daughter fertility (-0.02 – -0.11) and residual feed intake (-0.01 kg – -0.07 kg). When selecting for milk protein amount with selection differentials of 10 kg, 30 kg and 50 kg, genetic changes in milk protein amount were +3.12 kg, +9.35 kg and +15.58 kg, respectively. The daughter pregnancy rate decreased by 0.14, 0.41 and 0.68 points. Residual feed intake decreased by 0.04 kg, 0.11 kg and 0.19 kg. At the same time, an increase in the absolute values of fat and protein content in milk was observed. In the offspring of bulls of different origins, there are significant differences in phenotypic correlations between selection traits. In the daughters of the breeding bull CA 106627797 D. Kickball Et, the correlation between milk yield and milk protein content was -0.0973**,

and in the offspring of the bull CA 9969495 V. Sophomore Et, it was +0.1708***, and in the offspring of the bull NL 520913639 N. Saltie, it was -0.1229***. Similar results were obtained for other traits. In the offspring of the breeding bull CA 9969495 V. Sophomore Et, the correlation between milk yield and live weight of cows was -0.3563***, and in the offspring of the breeding bull NL 520913639 N. Saltie, it was +0.2378***.

Selection for milk productivity traits contributes to an increase in productive longevity and live weight of cows while reducing residual feed intake. The values of phenotypic correlations between the studied traits in cows descended from different breeding bulls show significant differences. Further research should be directed towards identifying genomic regions that determine antagonistic genetic correlations between productivity and reproduction traits, as well as on the development of selection indices that take into account the individual variability of genetic correlations in the offspring of different sires to optimise genetic progress for a complex of economically valuable traits in dairy cattle.

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Conflict of Interest

The authors declare no conflict of interest.

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Можливості латентного фенотипу: моделювання відповіді на відбір за ознаками продуктивності молочної худоби з урахуванням генетичних кореляцій

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Анотація. Метою досліджень був аналіз динаміки змін економічно важливих ознак молочної худоби: вмісту жиру та білка в молоці, рівня тільності дочок, продуктивного довголіття, залишкового споживання корму, живої маси, балу за вмістом соматичних клітин, при моделюванні відбору за такими ознаками молочної продуктивності, як надій, кількість молочного жиру та білка. Матеріалом для досліджень були дані референтного стада голштинських корів молочної ферми «Терезине» (Київська область, Україна). Загальна кількість спостережень корів склала 14 712 в розрізі семи лактацій. Для моделювання використане програмне забезпечення «MRS». При відборі за надоєм на рівні селекційних диференціалів 100 кг, 300 кг та 500 кг генетична відповідь наступного покоління по надою склала 31,59 кг, 94,77 кг та 157,97 кг відповідно. Одночасно спостерігалось збільшення таких ознак, як продуктивне довголіття, з 0,59 міс. до 2,94 міс., жива маса – з 0,36 до 1,79 кг, та бал за вміст соматичних клітин в молоці – з 0,03 до 0,13. Генетичні зміни вмісту жиру та білка в молоці, ознаки рівня тільності дочок та залишкового споживання корму мали зворотні значення. Отримано значущі показники фенотипових кореляцій між надоєм первісток

та вмістом жиру в молоці (-0,2985), кількістю молочного жиру (+0,9631), білка в молоці (-0,2642), молочного білка (+0,9924), періоду відкритих днів (+0,0989), продуктивним довголіттям (+0,0989) та живою масою (+0,2199). Відмічено різноспрямований рівень зв'язків у дочок плідників між надосем та вмістом білка в молоці від -0,1229 до +0,1708, надосем та періодом відкритих днів – від -0,0726 до +0,1836. Проведено моделювання можливих змін генетичних кореляцій в діапазоні від -0,10 до -0,95 між надосем та рівнем тільності (DPR). Темпи корельованої відповіді при відборі за надосем залежно від значень генетичної кореляції між цими ознаками вплинули на зменшення рівня тільності корів з -0,51 до майже -5,0 балів. Вплив на силу та спрямованість встановлених зв'язків може сприяти стабілізації або погіршенню ознак відтворення при відборі за надосем. Запропонований метод моделювання дає змогу прогнозувати зміни основних ознак, за якими проводиться відбір, в залежності від генетичних кореляцій між ними

Ключові слова: генетичні параметри; фенотипічні кореляції; молочна продуктивність; розмноження