



Genetic relationships between milk production, meat production, and cow size traits in Nordic Red dairy cattle

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ABSTRACT

The beef-on-dairy approach, which uses surplus dairy calves for meat production, is considered environmentally sustainable and an efficient use of dairy resources. Inseminating dairy cows with beef semen improves the meat traits of dairy-origin beef; however, the focus on crossbreeding with beef sires often overlooks the role of the cow's genetics on meat traits and does not directly target genetic improvement of the cow. This issue is further compounded in the Nordic countries, where a Saved Feed index is included in the Nordic Total Merit index. This index lowers maintenance energy requirement by applying a negative index weight on metabolic body weight. Although this improves feed efficiency, its influence on other economically important traits has not been addressed so far. In this study, we estimated genetic parameters for cow carcass traits (carcass weight, carcass conformation, carcass fatness), 305-d milk production traits (milk yield, protein yield, fat yield), cow size traits (stature, metabolic body weight), and bull calf growth traits (daily carcass gain, carcass conformation, carcass fatness) in Nordic Red dairy cattle using data from 18,757 cows and 41,838 bull calves. Variance components were estimated by fitting a multivariate animal model and applying a Monte Carlo expectation maximization restricted maximum likelihood algorithm implemented in MiX99 software. Heritability estimates for cow carcass traits ranged from 0.37 (carcass conformation) to 0.68 (carcass weight); for milk production traits from 0.31 (fat yield) to 0.38 (milk yield); and for cow size traits from 0.64 (stature) to 0.66 (metabolic body weight). Bull calf growth traits showed heritability estimates ranging from 0.19 (bull carcass conformation) to 0.34 (daily carcass

gain). Unfavorable genetic correlations were observed between cow carcass and 305-d milk production traits, ranging from -0.27 (carcass weight and protein yield) to -0.67 (carcass fatness and fat yield). In contrast, positive genetic correlations were noted between cow carcass and progeny growth traits, ranging from 0.20 (bull carcass conformation and cow carcass weight) to 0.67 (cow carcass weight and daily carcass gain), except for bull carcass fatness, which was positively correlated only with cow carcass fatness. Cow carcass traits were also positively correlated with metabolic body weight, ranging from 0.39 (cow carcass fatness) to 0.90 (cow carcass weight). These results provide insight into the genetic relationship among traits relevant for milk and dairy-beef production and may support the optimization of total merit index selection for balanced improvement of milk and meat traits.

Key words: beef-on-dairy, cow carcass, genetic correlation

INTRODUCTION

Improving the productivity of dairy cows has long been a central breeding goal and remains an ongoing process. In recent years, the focus has shifted toward sustainability, particularly through improving feed efficiency and reducing environmental impact. Several studies have examined the relationships between milk production and other important traits such as reproductive performance (Berry et al., 2014), feed efficiency (Lidauer et al., 2023), and health (Schmidtman et al., 2023). Despite the focus on sustainability in breeding programs, little attention has been paid to the effects of continuous selection for milk production traits on beef production traits. This is a relevant concern, given that dairy-beef systems offer a sustainable approach for beef production, with a substantially lower environmental footprint compared with conventional suckler herd systems (Nguyen et al.,

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The list of standard abbreviations for JDS is available at adsa.org/jds-abbreviations-26. Nonstandard abbreviations are available in the Notes.

2010). Accounting for beef traits in dairy cattle breeding programs could therefore reduce reliance on resource-intensive beef production and help address criticism of the livestock sector for its contribution to climate change. Surplus dairy calves and culled cows account for a large share of beef production in the Nordic countries (Åby et al., 2014). Therefore, neglecting carcass traits in total merit selection may represent a missed opportunity both economically and environmentally.

In the Nordic countries, the Nordic Total Merit (NTM) index is the primary breeding tool for balancing production, functionality, and sustainability in dairy cattle. The introduction of the Saved Feed index into the NTM index in 2020 (Lidauer et al., 2019; Stephansen et al., 2025) reflects an emphasis on improving feed efficiency by selecting cows that require less energy for maintenance—that is, cows with lower metabolic body weight (MBW) and cows that use feed more efficiently (Mehtiö et al., 2021). Though economically and environmentally beneficial, the Saved Feed index may also influence other traits not directly included in the breeding objective. For example, Mehtiö et al. (2021) reported a positive genetic correlation between MBW and cow carcass weight. Growth traits have also been linked to feed intake (Schenkel et al., 2004), another component of the Saved Feed index. Consequently, continued selection for improved efficiency achieved partly by favoring smaller cows could intensify potential antagonistic relationships with cow carcass traits and growth traits, especially if these traits are not included in the breeding goal. These relationships raise concerns that selection for higher production and efficiency could unintentionally reduce growth rate and carcass quality.

Although the Saved Feed index provides clear economic and environmental benefits, it is important to evaluate its broader consequences. Understanding the relationships between important traits under selection and cow carcass traits is essential for balancing progress in efficiency and milk production while maintaining cow carcass value. Therefore, this study aims to estimate the genetic correlations between cow carcass traits (carcass weight, carcass conformation, and carcass fatness), 305-d milk production traits (milk yield, protein yield, and fat yield), cow size traits (stature and MBW), and growth traits (bull calf daily carcass gain, bull calf carcass conformation, and bull calf carcass fatness) in Nordic Red dairy cattle.

MATERIALS AND METHODS

Data

Data on Nordic Red dairy cattle were provided by the Nordic Cattle Genetic Evaluation (NAV), the responsible

organization for dairy and beef cattle genetic evaluation in Nordic countries (Denmark, Finland, and Sweden). We considered 4 groups of traits: (1) cow carcass traits, comprising carcass weight, carcass conformation, and carcass fatness; (2) milk production traits measured over 305-d lactation period, including milk yield, protein yield, and fat yield; (3) cow size traits, stature, and MBW, calculated as the body weight raised to the power of 0.75; and (4) growth traits, namely daily carcass gain of bulls, bull carcass conformation, and bull carcass fatness.

The 11 traits considered in this study included 7 continuous traits and 4 ordinal categorical traits. The ordinal categorical traits were carcass conformation and carcass fatness for both dairy cows and dairy bull calves, and the remaining were continuous traits. Carcass conformation was scored on a 15-level European beef carcass conformation and fat class (E, U, R, O, P; **EUROP**) scale, with 1 representing poor conformation and 15 indicating high muscularity, and carcass fatness was scored on a 5-level EUROP scale, where 1 represented low fat and 5 indicated high fat level; moderate fat levels are generally considered economically optimal. These scores were visually assessed by trained personnel at registered slaughterhouses. Carcass weight was defined as cold carcass weight ($0.98 \times$ hot carcass weight) measured after removal of head, blood, hide, and internal organs. Milk yield, protein yield, fat yield, and daily carcass gain were all measured in kilograms. Metabolic body weight, also measured in kilograms, was derived from body weight measurements recorded using tapes during regular herd visits. When a cow had multiple measurements within 1 lactation, the last measurement was retained. Stature, measured in centimeters from the top of the spine to the ground by trained specialists after first parity, describes the cow's height at first lactation.

We applied a 2-step approach in the data sampling. First, we sampled cow datasets for carcass, 305-d milk production, and size traits from an initial 355,868 records. To ensure typical culling ages, records were retained only if age at slaughter was between 25 and 100 mo of age, and slaughter occurred less than 365 d after their last calving, retaining 268,024 records. To ensure high-quality data that were both reliable and representative of the average farm size, herds were required to have between 3 and 20 cow carcass records per year, at least 8 years of first-parity records, with a minimum average of 3 records per year, and at least an average of 4 size trait measurements per year, retaining 40,433 records. Herds whose records contained fewer than 45 unique sires were excluded, retaining 36,970 records. This criterion was set to ensure adequate genetic linkage across herds by restricting the analysis to herds primarily relying on artificial insemination rather than own sires. Because the size traits had the fewest records, only herds with MBW

Table 1. Descriptive statistics showing the number of records, mean, SD, and minimum (Min) and maximum (Max) values for each trait

Trait	No. of records	Mean	SD	Min	Max
Cow carcass traits (cows)					
Carcass weight (kg)	17,731	280.7	46.40	138.0	422.0
Carcass conformation	17,565	3.15	1.03	1.0	7.0
Carcass fatness	17,723	2.64	1.02	1.0	5.0
305-d milk traits (cows)					
Milk yield (kg)	41,795	8,885	1,686	3,699	14,111
Protein yield (kg)	38,595	321.5	58.2	145.1	498.2
Fat yield (kg)	38,595	395.0	74.5	167.5	623.9
Size traits (cows)					
Stature (cm)	10,299	140.6	3.7	129.6	151.8
Metabolic body weight (kg)	8,861	121.1	11.1	87.4	161.6
Growth traits (bull calves)					
Daily carcass gain (kg)	37,026	0.54	0.07	0.32	0.80
Carcass conformation	41,794	5.00	0.83	1.0	11.0
Carcass fatness	41,838	2.43	0.64	1.0	5.0

observation were retained, leaving 19,514 cows with observations. Finally, only data from 2010 to 2024 were included in the study, resulting in a cow dataset of 18,757 cows with observations.

In the second step, we examined the NAV growth data that was collected on bulls to assess growth performance in fattening herds. Bull calves whose dams were included in the cow dataset were identified to ensure genetic connectivity between the cow and bull calf datasets. These bull calves, together with their herd mates, were then selected for preprocessing. The bull calf data were trimmed by excluding animals born before 2007, as this was the earliest calving year in the cow dataset. In Finland, bull calves are typically slaughtered at an older age than in Sweden and Denmark. Therefore, the measurements used in this study reflected the growth of bull calves that underwent a long, extensive fattening period (>550 d). Consistent with the cow data, herds were required to have at least 8 yr of recorded data. To maintain genetic connectivity while avoiding excessively large and weakly connected datasets, herds were ranked by the percentage of bulls whose dams were present in the cow dataset. By prioritizing herds with the strongest connections, we included only herds with a minimum of 5 and maximum of 100 growth records from bull calves whose dams were present in the cow dataset. All sires of bull calves were also confirmed to be Nordic Red. To be included in the final data, the slaughter age was required to be between 200 to 900 d, and average daily carcass gain had to be less than 1 kg.

Both datasets were then merged, and observations of continuous traits that deviated more than 3 SD from the mean were considered outliers and discarded. The final dataset (Table 1) comprised a total of 64,271 animals: 18,757 cows and 45,514 bull calves. Observations for cows originated from 186 herds, and those for bull calves from 102 herds. Of the cow data, at least 3,175 cows had

both carcass and size records, 8,497 cows had both milk and size records, and 16,011 cows had both carcass and milk records. Pedigree information obtained from the NAV was pruned to 3 generations using RelaX2 software (v1.99; Strandén and Vuori, 2006). The resulting pedigree consisted of 172,480 animals.

Statistical Models

All 11 traits were analyzed in a single analysis by applying a multitrait linear mixed model with trait-specific models as follows.

Carcass traits:

$$y_{t,ihjvzd} = l_{t,i}\phi(d) + H5Y_{t,h} + SYM_{t,j} + hy_{t,v} + a_{t,z} + e_{t,ihjvz},$$

where $y_{t,ihjvzd}$ is an observation for trait t (carcass weight, carcass conformation, or carcass fatness score); $l_{t,i}\phi(d)$ is the fixed regression on days from calving to slaughter (d), nested within parity i (1 to 5), where $\phi(d)$ vector contains the covariates of a second-order Legendre polynomial for d ; $H5Y_{t,h}$ is the fixed effect of herd $\times$ 5-yr period (e.g., 2010–2014) h ; $SYM_{t,j}$ is the fixed effect of the slaughter year $\times$ month j ; $hy_{t,v}$ is a random effect of the herd $\times$ year v ; $a_{t,z}$ is the random additive genetic effect of animal z ; and $e_{t,ihjvz}$ is the random residual effect.

305-d milk yield traits:

$$y_{t,klhvz} = CYS_{t,k} + CAP_{t,l} + H5Y_{t,h} + hy_{t,v} + pe_{t,z} + a_{t,z} + e_{t,klhvz},$$

where $y_{t,klhvz}$ represents an observation for trait t (milk, protein, or fat yield in kg); $CYS_{t,k}$ is the fixed effect of calving year $\times$ season k ; $CAP_{t,l}$ is the interaction between calving age $\times$ parity l (1–3); $H5Y_{t,h}$ is the fixed effect of herd $\times$ 5-yr period h ; $hy_{t,v}$ is a random effect of the herd $\times$

year v ; $pe_{t,z}$ is the random permanent environment effect of animal z ; $a_{t,z}$ is the random additive genetic effect of animal z ; and $e_{t,klhvz}$ is the random residual effect.

Size traits stature and MBW, respectively:

$$\text{Stature}_{mnhopvz} = \beta_1 \times \text{cage}_m + \beta_2 + w_n + H5Y_h \\ + CLCY_o + CYM_p + hy_v + a_z + e_{mnhopvz}$$

and

$$\text{MBW}_{qrhuvzs} = l_q\phi(s) + \beta_3 \times AP_r + H5Y_h \\ + YM_u + hy_v + pe_z + a_z + e_{qrhuvz},$$

where $\beta_1 \times \text{cage}_m$ is a linear regression on calving age m ; $\beta_2 + w_n$ is a linear regression on lactation week n ; $l_q\phi(s)$ is a fixed regression function on days in milk s nested within parity (1–3) q , where $\phi(s)$ is the vector containing the covariates of a second-order Legendre polynomial for days in milk s ; $\beta_3 \times AP_r$ is a linear regression on calving age nested within parity (1–3) r ; $H5Y_h$, $CLCY_o$, CYM_p , and YM_u are fixed effects of herd $\times$ 5-yr period h , classifier $\times$ year of classification o , calving year $\times$ month p , and year $\times$ month of measurement u , respectively; hy_v , pe_z , a_z , $e_{mnhopvz}$, and e_{qrhuvz} are random effects of the herd-year v , permanent environment and additive genetic effect of animal z , residual (stature), and residual (MBW), respectively.

Growth traits:

$$y_{t,fugwz} = \beta_{t,z}h + AD_{t,f} + YM_{t,u} \\ + GH5Y_{t,g} + ghy_{t,w} + a_{t,z} + e_{t,fugwz},$$

where $y_{t,fugwz}$ is an observation for trait t (daily carcass gain, bull carcass conformation, or bull carcass fatness); $\beta_{t,z}h$ are fixed regressions on 8 founder breed shares plus 1 fixed regression on total heterozygosity of animal x . Total heterozygosity was calculated based on parents' breed compositions, considering 8 founder populations for the Nordic Red dairy cattle, and following Dickerson (1973); $AD_{t,f}$ is the fixed effect of age of dam f ; $YM_{t,u}$ is the fixed effect of year $\times$ month of measurement u , $GH5Y_{t,g}$ is the fixed effect of the growing herd $\times$ 5-yr period g ; $ghy_{t,w}$, $a_{t,z}$, and $e_{t,fugwz}$ are random effects of growing herd-year w , animal z , and residual respectively.

All random effects in the models were assumed to follow multivariate normal distributions (MVN) with a mean of zero. Their distributions of the respective random effects were defined as follows, with $\otimes$ denoting the Kronecker product:

$$\text{var}(hy) \sim MVN(0, \mathbf{I} \otimes \mathbf{M}),$$

where $\mathbf{I}$ is an identity matrix and $\mathbf{M}$ is an 8×8 matrix of herd-year variances [$\text{var}(hy)$] with diagonal block structure due to different recording time of cow carcass, 305-d milk production, and size traits;

$$\text{var}(ghy) \sim MVN(0, \mathbf{I} \otimes \mathbf{N}),$$

where $\mathbf{I}$ is an identity matrix and $\mathbf{N}$ is a 3×3 matrix for growth traits [$\text{var}(ghy)$];

$$\text{var}(pe) \sim MVN(0, \mathbf{I} \otimes \mathbf{P}),$$

where $\mathbf{I}$ is an identity matrix and $\mathbf{P}$ is a 4×4 matrix of permanent environmental effects [$\text{var}(pe)$] for milk yield, protein yield, fat yield, and MBW;

$$\text{var}(a) \sim MVN(0, \mathbf{A} \otimes \mathbf{G}),$$

where $\mathbf{A}$ is the numerator relationship matrix and $\mathbf{G}$ is an 11×11 matrix of additive genetic variances and covariances [$\text{var}(a)$]; and

$$\text{var}(e) \sim MVN(0, \mathbf{I} \otimes \mathbf{R}),$$

where $\mathbf{I}$ is an identity matrix and $\mathbf{R}$ is an 11×11 matrix of residual variances and covariances [$\text{var}(e)$].

Variance and co-variance components for all traits were estimated by applying the Monte Carlo expectation maximization restricted maximum likelihood (**MC-EM REML**) algorithm implemented in the MiX99 software suite (Matilainen et al., 2012). For each REML round, we generated 2 data samples, and convergence of estimated variance components was detected by the convergence criterion outlined in Matilainen et al. (2012). Variance components were considered converged once the criterion reached a value of 1.0×10^{-11} , which required 6,423 MC-EM REML rounds. Heritability was calculated as the ratio of additive genetic variance to total phenotypic variance.

RESULTS

In this study, the average carcass weight of cows was 280.7 kg, ranging from 138.0 to 422.0 kg, and the average slaughter age was 1,415 d (47 mo; Table 1). Bull calves had a higher average carcass weight of 343.5 kg and were slaughtered at a younger average age of 584 d. In addition, bull calves achieved higher average scores for both carcass conformation and carcass fatness (Table 1). The highest conformation score observed among bull calves in our data was 11, which corresponds to a carcass with very good muscle development, a convex body profile, and a rounded shape (Ruokavirasto, 2025). In

comparison, the highest conformation score recorded for cows was 7, representing a carcass with a straight profile and good muscle development (Ruokavirasto, 2025). Despite differences in conformation, both bull calves and cows had fat scores ranging from 1 to 5 (Table 1), where a score of 1 indicates little to no fat cover and a score of 5 indicates a carcass entirely fat-covered (Ruokavirasto, 2025). Overall, bull calves produced heavier, more muscular, and better-conformed carcasses compared with cows, with only minor difference in average fat levels (Table 1). The 305-d milk yield in this dataset ranged from 3,699 to 14,111 kg. Protein yield varied between 145 and 498 kg, and fat yield ranged from 168 to 624 kg. The average stature of cows was 140.6 cm, and the average MBW was 121.1 kg. The average daily carcass gain of bull calves was 0.54 kg, with a minimum of 0.32 kg and maximum of 0.80 kg.

Heritability

Among the 11 traits analyzed, the highest heritability estimates were observed for cow carcass weight (0.68), MBW (0.66), and stature (0.64), indicating strong genetic influence on these traits. Standard errors for heritability estimates generally ranged from 0.02 to 0.04 (Table 2). Carcass conformation and carcass fatness showed lower heritability estimates than the size traits, ranging from 0.19 to 0.43 across cows and bulls. Specifically, heritabilities for bull carcass conformation and fat were 0.19 and 0.20, respectively, whereas the corresponding estimates for cows were higher, 0.37 and 0.43. Among these carcass quality traits, carcass fatness exhibited higher heritability than conformation in both sexes. For the 305-d milk traits, moderate heritability estimates were obtained, ranging from 0.31 (fat yield) to 0.38 (milk yield), suggesting a reasonable genetic contribution to variation in milk production traits. Among

the growth traits, daily carcass gain exhibited the highest heritability (0.34).

Correlations

Genetic and phenotypic correlations are presented in Table 3. Genetic correlations ranged from -0.67 (cow carcass fatness and fat yield) to 0.90 (cow carcass weight and MBW), indicating diverse genetic relationships among traits. Phenotypic correlations similarly ranged from -0.27 (cow carcass fatness and milk yield) to 0.93 (milk yield and protein yield). Standard errors for genetic correlations ranged from 0.02 to 0.10 , with higher values mainly observed for correlations involving growth traits. The strongest within-trait group genetic correlations were observed among the 305-d milk production traits, which showed high favorable genetic correlations with each other, ranging from 0.75 (milk yield and fat yield) to 0.88 (milk yield and protein yield). The corresponding phenotypic correlations were similarly high (0.78 – 0.93), with the same trait pairs showing the lowest and highest correlations as observed genetically. This can be expected because protein yield and fat yield were formed by multiplying the milk samples' protein and fat contents by milk yield. Cow carcass traits, namely weight, conformation, and fatness, were also strongly correlated with one another, with a high positive genetic correlation of 0.76 between weight and conformation. The 2 cow size traits MBW and stature also exhibited a strong genetic correlation of 0.75 with one another. Conversely, growth traits showed weaker within-trait group genetic correlations, ranging from 0.02 (daily carcass gain and bull carcass fatness) to 0.42 (daily carcass gain and bull carcass conformation), suggesting weaker genetic ties. However, growth traits showed notably stronger within-trait group phenotypic correlations compared with the genetic correlations.

Table 2. Estimates of standard deviations, heritabilities, and standard errors for cow carcass traits, 305-d milk production traits, cow size traits, and bull calf growth traits in Nordic Red dairy cattle¹

Trait	Unit	σ_a ($\pm$ SE)	σ_{hy} ($\pm$ SE)	σ_{pe} ($\pm$ SE)	σ_e ($\pm$ SE)	h^2 ($\pm$ SE)
CarW	kg	35.34 ± 0.92	5.65 ± 0.91	—	23.67 ± 0.82	$0.68 (0.02)$
CarConf(C)	EUROP scale (1–15)	0.58 ± 0.03	0.18 ± 0.02	—	0.73 ± 0.02	$0.37 (0.03)$
CarFat(C)	EUROP scale (1–5)	0.63 ± 0.03	0.18 ± 0.03	—	0.69 ± 0.02	$0.43 (0.03)$
Milk yield	kg	865.7 ± 32.5	284.5 ± 14.9	465.74 ± 40.1	948.6 ± 9.8	$0.38 (0.02)$
Protein yield	kg	26.88 ± 1.22	10.89 ± 0.50	18.42 ± 1.23	31.68 ± 0.31	$0.33 (0.03)$
Fat yield	kg	34.89 ± 1.67	15.29 ± 0.79	21.14 ± 1.98	45.52 ± 0.43	$0.31 (0.03)$
Stature	cm	2.64 ± 0.10	0.47 ± 0.04	—	1.95 ± 0.10	$0.64 (0.04)$
MBW	kg	7.73 ± 0.23	2.07 ± 0.25	0.91 ± 1.32	5.12 ± 0.12	$0.66 (0.03)$
Daily carcass gain	kg/d	0.034 ± 0.002	0.016 ± 0.001	—	0.045 ± 0.001	$0.34 (0.03)$
CarConf(B)	EUROP scale (1–15)	0.341 ± 0.021	0.188 ± 0.013	—	0.674 ± 0.009	$0.19 (0.02)$
CarFat(B)	EUROP scale (1–5)	0.25 ± 0.02	0.16 ± 0.01	—	0.48 ± 0.01	$0.20 (0.03)$

¹CarW = cow carcass weight; CarConf(C) = cow carcass conformation; CarFat(C) = cow carcass fatness; MBW = metabolic body weight; CarConf(B) = bull carcass conformation; CarFat(B) = bull carcass fatness; σ_a = additive genetic SD; σ_{hy} = herd-year SD; σ_{pe} = permanent environmental SD; σ_e = residual SD, h^2 = heritability estimate.

Table 3. Estimates of genetic correlations (in upper triangle), and phenotypic correlations (in lower triangle) for cow carcass traits, 305-d milk production traits, size traits, and growth traits in Nordic Red dairy cattle¹

Trait	CarW	CarConf(C)	CarFat(C)	Milk	Protein	Fat	Stature	MBW	DCG	CarConf(B)	CarFat(B)
CarW											
CarConf(C)	0.65	0.76(0.03)	0.63 (0.03)	-0.34 (0.03)	-0.27 (0.02)	-0.34 (0.03)	0.62 (0.04)	0.90 (0.02)	0.67 (0.05)	0.20 (0.07)	-0.11 (0.08)
CarFat(C)	0.60	0.53	0.71 (0.04)	-0.57 (0.04)	-0.52 (0.04)	-0.58 (0.04)	0.09 (0.07)	0.51 (0.05)	0.37 (0.07)	0.53 (0.07)	-0.01 (0.10)
Milk	-0.13	-0.21		-0.66 (0.03)	-0.61 (0.03)	-0.67 (0.04)	0.03 (0.06)	0.39 (0.05)	0.16 (0.08)	0.14 (0.09)	0.35 (0.08)
Protein	-0.08	-0.17	-0.27		0.88 (0.01)	0.75 (0.02)	0.16 (0.04)	-0.06 (0.06)	0.15 (0.05)	-0.06 (0.09)	-0.10 (0.07)
Fat	-0.12	-0.19	-0.23	0.93		0.83 (0.02)	0.18 (0.05)	-0.01 (0.07)	0.18 (0.06)	-0.06 (0.10)	-0.08 (0.08)
Stature	0.45	0.05	-0.25	0.78	0.80		0.14 (0.04)	-0.06 (0.06)	0.12 (0.07)	-0.07 (0.09)	-0.01 (0.09)
MBW	0.58	0.24	0.01	0.14	0.15	0.12		0.75 (0.03)	0.54 (0.06)	-0.24 (0.09)	-0.29 (0.09)
DCG	0.32	0.13	0.21	0.00	0.03	0.01	0.49		0.71 (0.06)	0.10 (0.08)	-0.14 (0.10)
CarConf(B)	0.07	0.14	0.06	0.05	0.06	0.04	0.25	0.33		0.42 (0.06)	0.02 (0.08)
CarFat(B)	-0.04	-0.002	0.04	-0.02	-0.02	-0.02	-0.08	0.03	0.43		0.13 (0.10)
			0.10	-0.03	-0.02	-0.00	-0.10	-0.05	0.22	0.18	

¹Standard errors of phenotypic correlations were between 0.002 and 0.04. CarW = cow carcass weight; CarConf(C) = cow carcass conformation; CarFat(C) = cow carcass fatness; MBW = metabolic body weight; DCG = daily carcass gain; CarConf(B) = bull carcass conformation; CarFat(B) = bull carcass fatness.

Cow carcass traits showed negative, unfavorable genetic correlations with 305-d milk traits. The genetic correlations between cow carcass traits and MBW were positive and significant for all 3 carcass traits, whereas, among the genetic correlations with stature, only the estimate for carcass weight was significant (Table 3). Within growth traits, daily carcass gain and bull carcass conformation were positively genetically correlated with cow carcass traits. Correlations for daily carcass gain ranged from 0.16 (cow carcass fatness) to 0.67 (cow carcass weight), and correlations for bull carcass conformation ranged from 0.14 (cow carcass fatness) to 0.53 (cow carcass conformation). Among the cow carcass traits, only cow carcass fatness was significantly correlated with bull carcass fatness.

Although 305-d milk traits were negatively genetically correlated with carcass traits, their correlations with other trait groups varied. The milk traits showed a slight positive correlation with stature but no significant correlation with MBW. Within the growth traits category, 305-d milk traits were slightly positively correlated with daily carcass gain but uncorrelated with bull carcass conformation and fat (Table 3).

Growth traits also displayed varying relationships with size traits, ranging from strong positive to moderate negative and, in some cases, nonsignificant correlations (Table 3). Daily carcass gain was positively correlated with both stature and MBW, whereas bull carcass conformation and fat showed negative correlations with stature but were uncorrelated with MBW. Daily carcass gain also showed moderate favorable genetic correlations with carcass conformation in both cows (0.37) and their bull progeny (0.42), but a low genetic correlation with carcass fatness in cows (0.16). With bulls, the phenotypic correlation between daily carcass gain and carcass fatness was 0.22, whereas the genetic correlation was near zero and nonsignificant, suggesting that the association between daily carcass gain and fatness in bulls is largely driven by management factors rather than being under genetic control. Interestingly, both genetic and phenotypic correlations between carcass conformation and fat were stronger in cows than in bulls (Table 3).

DISCUSSION

Antagonistic relationships among economically important traits highlight the need to understand their genetic relationships. This knowledge is essential for guiding breeding decisions that promote balanced genetic improvement and prevent unfavorable responses in correlated traits. In this study, we estimated multivariate variance components for 11 important production traits in dairy cattle. Moderate to high heritabilities were estimated for all traits, consistent with earlier studies (Parkkonen et al., 2000; Lidauer et al., 2003, 2019; Hoque

et al., 2006; Johansson et al., 2009; Kause et al., 2015; Mehtiö et al., 2021; NAV, 2024).

Our results revealed negative genetic correlations between 305-d milk traits and all 3 cow carcass traits, ranging from -0.27 (protein yield and carcass weight) to -0.67 (fat yield and carcass fatness; Table 3). These correlations were substantially stronger than those reported by Liinamo et al. (1999), who found correlations between -0.01 and -0.38 in Finnish Ayrshire cattle. The estimated negative genetic correlations are reflected in our NAV data trends, where protein yield and fat yield increased at annual rates of 2.43 kg (genetic SD = 26.88) and 3.26 kg (genetic SD = 34.89), respectively, but carcass conformation and fatness declined at annual rates of 0.01 and 0.04 scale points, respectively. This suggests that intensification of dairy production has strengthened these genetic trade-offs, likely through energy partitioning, where high-producing cows direct more nutrients toward milk production at the expense of muscle and fat deposition. The moderate to high heritability estimates for carcass traits (Table 2) are consistent with previous findings (Eriksson, 2003; Hoque et al., 2006; Kause et al., 2015; Kelly et al., 2019; Mehtiö et al., 2021), indicating that a sufficient proportion of the phenotypic variation is attributable to genetic factors, suggesting potential for genetic improvement through selection. Similarly, heritabilities for 305-d milk, protein, and fat yield were 0.38, 0.33, and 0.31, respectively, aligning with earlier studies (Lidauer et al., 2003; Hinrichs et al., 2005; Bohloul et al., 2015; NAV, 2024). The economic implications are noteworthy, as Hietala and Juga (2017) demonstrated that breeding for carcass traits in dairy herds could increase profitability and sustainability through simultaneous beef and milk production. Consistent with this evidence, Ireland's Economic Breeding Index incorporates cow carcass weight and calf carcass traits to reflect their contribution to overall breeding objectives (Berry et al., 2007).

The high heritability estimates for stature (0.64) and MBW (0.66), combined with their positive genetic correlations with cow carcass traits (Table 3), indicate that body size has a positive genetic relationship with cow carcass value. The genetic correlation of 0.75 between stature and MBW indicates these traits are largely controlled by similar genetic mechanisms. However, the strength of these relationships with cow carcass traits varied. For MBW, we estimated a very strong correlation with carcass weight (0.90), which is consistent with earlier findings (Mehtiö et al., 2021). In contrast, the estimated genetic correlations of MBW with carcass conformation (0.51) and fat (0.39) were relatively weaker. This indicates that body size influences carcass weight more strongly than carcass quality. With genetic coefficients of variation of 18.4% for carcass conformation and 23.7% for carcass fatness, considerable genetic variation exists

in these carcass quality traits, independent of body size. This suggests that breeding strategies focused on carcass composition and conformation can improve carcass quality without necessarily increasing cow size.

Growth traits measured in bull calves showed lower heritability estimates (0.19–0.34) than cow traits, consistent with previous studies (Parkkonen et al., 2000; Schenkel et al., 2004; Johansson et al., 2009; Kelly et al., 2019). The lower heritabilities in bull carcass conformation and carcass fat compared with the same traits in cows likely reflect younger slaughter age in bulls, which also contributes to weaker genetic expression of these traits (Liinamo et al., 1999; Parkkonen et al., 2000). In NAV, daily carcass gain and carcass conformation in bull calves serve as primary indicators of growth performance, whereas carcass fatness provides information on body composition (NAV, 2024). Our study found positive genetic correlations between growth traits and cow carcass traits, but weak to nonsignificant correlations between growth traits and milk traits. This indicates that bull calf performance is relatively independent of maternal milk production, offering valuable flexibility for breeding strategies. Given that male calves represent a significant revenue stream through dairy-beef production, improving cow carcass traits can simultaneously enhance the beef value of male offspring. Furthermore, positive genetic correlations between daily carcass gain and both MBW and stature, as also found by Schenkel et al. (2004) and Mehrban et al. (2021), suggest that larger animals grow faster, which underlines the role of body size in overall carcass performance.

In the Nordics, the Saved Feed subindex of the NTM index aims to improve feed efficiency by selecting cows that require less energy for maintenance and utilize energy more efficiently for essential functions (NAV, 2024). Because maintenance energy requirements increase with body size, animals with larger body mass need more energy to sustain basic physiological functions compared with smaller animals (Ferrell and Jenkins, 1985; Evans et al., 2002). Consequently, selecting for improved Saved Feed may indirectly favor smaller-bodied animals. Our study has shown positive correlations between cow size traits and cow carcass traits. This could mean that selection against size traits will likely induce a corresponding directional response in cow carcass traits. Our results also showed negative genetic correlations between 305-d milk traits and all 3 carcass traits. This is particularly significant for the future of dairy-beef production, as it highlights a genetic antagonism between milk production traits and carcass quality. As selection pressure continues to favor high-yielding dairy cows, it becomes increasingly important to consider the broader implications on dairy-beef quality and overall sustainability of dairy breeding programs.

The integration of data from multiple sources introduced complexity in model specification, as animals belonged to different herds and traits were sex-linked, resulting in modeling of trait-specific fixed and random effects. Despite these challenges, our multivariate model converged successfully and produced biologically plausible estimates, suggesting that the model adequately captured the genetic and environmental variance structure. The slightly higher standard errors for correlations between cow and bull traits reflect this complexity but remain within acceptable ranges for parameter estimation.

CONCLUSIONS

In this study, we were able to estimate multivariate variance components for 11 traits in a single multivariate analysis using the MC-EM REML method. Although the estimated standard errors were higher for covariances between traits that were observed on different animals, we found significant positive genetic correlations between cow production traits (cow carcass and 305-d milk production) and bull calf daily carcass gain. This indicates a positive genetic relationship between both cow's meat and milk production, and progeny carcass growth. In addition to this, we also observed negative genetic correlations between 305-d milk production traits and cow carcass traits, suggesting an antagonistic relationship between milk production and cow meat production traits. These findings highlight the need to evaluate the influence of the current NTM index on carcass traits and body size of Nordic Red dairy cows, particularly carcass traits, which are currently not considered in the index.

NOTES

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Nonstandard abbreviations used: CarConf(B) = bull carcass conformation; CarConf(C) = cow carcass con-

formation; CarFat(B) = bull carcass fatness; CarFat(C) = cow carcass fatness; CarW = cow carcass weight; DCG = daily carcass gain; EUROP = 15-level European beef carcass conformation and fat class (E, U, R, O, P); Max = maximum; MBW = metabolic body weight; Min = minimum; NAV = Nordic Cattle Genetic Evaluation; NTM = Nordic Total Merit; MC-EM REML = Monte Carlo expectation maximization restricted maximum likelihood.

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