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Genetic relationship between the lifetime milk production, longevity and first lactation milk yield in Slovenian Brown cattle breed

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Janez Jenko[1], Tomaž Perpar[1], Milena Kovač[2]*

[1]Agricultural Institute of Slovenia, Hacquetova ulica 17, 1000 Ljubljana, Slovenia
[2]Department of Animal Science, Biotechnical Faculty, University of Ljubljana, Groblje 3, 1230 Domžale, Slovenia

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Abstract

To study the genetic relationship between the lifetime milk production (LMP), first lactation milk yield (MY305), and length of productive life (PL) in the Slovenian Brown cattle population, first lactation records from 14,389 cows and lifetime performance records (LMP and PL) from 12,416 cows were used. Records of LMP and PL were normalised using the square root transformation of the raw values. The fixed effect of the first calving year-season oscillated between different seasons within a year for all the traits. These changes followed a seasonal pattern in MY305, where cows with first calving in colder seasons of a year had the highest MY305 and cows with first calving in the warmer seasons of a year had the lowest. The estimated heritability was 0.12±0.017 for LMP, 0.09±0.015 for PL, and 0.15±0.001 for MY305. Genetic correlation between LMP and PL was very strong (0.96±0.008), while it was moderate (0.48±0.067) between LMP and MY305 and weak between PL and MY305 (0.23±0.085). The common herd environment correlation between PL and MY305 was moderate and negative (-0.41±0.052), whereas it was weak and positive between the LMP and MY305 (0.26±0.057) and strong and positive between LMP and PL (0.74±0.025). For the last 40 years, a positive genetic trend was observed for LMP and MY305, while the genetic trend for PL remained stable.

Key words: genetic evaluation, lifetime milk production, lactation milk yield, longevity, Brown cattle

Introduction

Lifetime milk production (LMP) is one of the traits of primary interest for dairy cattle breeders. It is important because the costs of rearing replacement cows represent a substantial part of the expenses in the dairy cattle production system. To decrease the costs, it is desirable that cows stay in a herd for a longer period of time and have a high level of milk production (Robertson and Rendel, 1950; Stott, 1994; Jenko et al., 2007). The combination of long productive life (PL) and high daily milk yield emerges in a high level of LMP and increase in the profitability. Although LMP is one of the most important traits, direct selection for a high LMP is usually not performed in dairy cattle breeding programmes. There are various reasons for this, but mainly they are related to the time elapse between the sire's birth and the time of selection for LMP. When the LMP data are available, bulls are already too old and the selection for LMP cannot be performed anymore. One of possible solutions to overcome the problem of time elapse between the sire's birth and selection would be the application of other genetic evaluation

*Corresponding author/Dopisni autor: E-mail: janez.jenko@kis.si

methods e.g. survival analysis techniques (Ducrocq and Casella, 1996). Here, the application of hazard function enables the inclusion of records from cows that are still in the herd. One of the difficulties when using this method is the non-linearity in the increase of LMP function due to the different level of milk production and dry periods during the herd life of a cow. In contrast, this method was successfully applied to predict the breeding values for the length of productive life, which is known to be a linearly increasing trait.

Selection for high LMP through the selection of genetically strongly correlated traits is another way to overcome the problem. Different traits can be used to perform selection for this purpose (Hoque and Hodges, 1980; Tsuruta et al., 2004). Since genetic evaluation for PL using survival analysis techniques was shown to be successful in Slovenian Brown cattle (Jenko et al., 2013a), it is of a great interest to investigate the genetic relationship between the LMP and PL.

There were four objectives of the current study: i) estimation of the fixed effect on LMP, PL, and the first standard lactation milk yield (MY305), ii) estimation of the variance components for LMP, PL, and MY305, iii) estimation of the genetic correlation between LMP, PL, and MY305, and iv) estimation of the genetic trend for these three traits in the Slovenian Brown cattle population. Results showed that the range of correlations between pairs of LMP, PL, and MY305 varies substantially. The genetic trend clearly illustrated an emphasis on selection for the Slovenian Brown cattle during the past 40 years.

Material and methods

LMP, PL, and MY305 data from Slovenian Brown cattle breed were used to study the genetic relationship between the LMP, MY305, and PL. The PL was defined as the time period between the date of first calving and the date of culling. When culling date was missing a maximum date from the dates of calving, milk recording, or drying off was used instead. Records from 36,663 cows involved in the milk-recording scheme that had the first calving between 1 January 1998 and 31 December 2008 were used. As the lifetime performance records (LMP and PL) were collected up until 31 August 2014, all the cows had the opportunity to stay in the herd for at least 68 months. Cows that were still alive on the last day of data collection (1,964 cows) were treated as culled on 31 August 2014. Cows younger than 20 months (104 cows) or older than 48 months (295 cows) at the day of first calving were excluded.

Because the study was performed on complete first standard lactation records, cows with first lactation shorter than 201 days were excluded (2,854 cows), as well as the records from cows that changed herds during the period of first lactation (1,137 cows). Due to the problems of model convergence only the records from herds with at least 20 cows that were progenies of sires with at least 30 daughters in the data records were kept. As small herds are typical for Brown cattle breed rearing systems in Slovenia, this restriction excluded 17,884 records.

After data filtering, there were 14,389 MY305 records included in the model to analyse MY305 variance components. As functional longevity was estimated, only cows with MY305 records were used to form the dataset for the analysis of LMP and PL. When the lifetime performance records of a single cow were collected from more than one herd, the records of a cow were excluded and the data were again updated for the minimum of 20 cows per herd and at least 30 daughters per sire. At the end, 12,416 cows were kept in the data set for the analysis of variance components for LMP and PL. For the purpose of genetic evaluation, the pedigree was prepared using the data from the last five generations. There were 25,468 animals in pedigree, from which 765 were sires and 165 of them were having progenies in the data.

A multivariate linear model was used for the estimation of variance components and the prediction of breeding values. A multivariate model overcomes the problem of the past selection for MY305, which is expected to be the problem in the data analysed. A single trait evaluation would not use all of the information to get good estimates, which may lead to biases in predicted breeding values, as well as an underestimation of the genetic trend when traits are correlated. Records for LMP and PL in which distribution was positively skewed were normalised using a square root transformation. Square root transformation is a proper solution for LMP and PL data, as all of the data are higher than 1 and no reranking within the data occurs. If data on the original scale were used, the convergence was not achieved.

Convergence was achieved with the normalised data used in the model. The fixed part of the model included the effect of region, calving-year season, age at first calving, first lactation length, and correction for the within herd first lactation milk yield. Cows were grouped into three regions (western, central, and eastern), based on the similarity in environmental conditions within each of the regions, as well as the presence of Brown cows in the territory of Slovenia.

The western region represents subpannonial Slovenia and part of Prealpine Hills, central Prealpine Hills with Dinaric Karst, and eastern sub-Mediterranean Slovenia. Due to the environmental factors, cattle breeding conditions are better in the central and western regions of Slovenia. The season in year-season interaction was formed through four seasons, with the periods from January to March, April to June, July to September, and October to December. To correct the model for the age at first calving, five classes were formed based on the age at first calving in months (≥ 20 < 22; ≥ 22 < 25; ≥ 25 < 28; ≥ 28 < 31; ≥ 31 ≤ 40). The effect of lactation length was included only for MY305, and was grouped in 14 classes, each covering 15 days between the period of 201 and 410 days of lactation and one class for lactations longer than 410 days. The corrected within herd rank lactation milk yield effect was included only for the estimation of PL to correct the model for the effect of voluntary culling. The MY305 records were corrected for the effect of calving year, and subsequently, the average values for each of the herds were calculated and subtracted from a single record of a cow. Based on the standard Z score, deviations were grouped into 10 deciles (1 - low milk production, 10 - high milk production) forming the classes to correct for the effect of voluntary culling.

The following multivariate linear model was used to estimate the variance components and to predict the genetic trend:

$$y_{ijklmno} = \mu + R_i + CYS_j + AFC_k + LL_{l[MY305]} + MY_{m[PL]} + h_{in} + a_{ijklmno} + e_{ijklmno}$$

where:

$y_{ijklmno}$ = trait (LMP, PL, and MY305); μ =general mean; R_i=fixed effect of region; CYS_j=fixed effect of year-season of first calving; AFC_k=fixed effect of age at first calving class; $LL_{l[MY305]}$=fixed effect of lactation length class (only for MY305); $MY_{m[PL]}$ = fixed effect of corrected within herd rank lactation yield (only for PL); h_{in}= random effect of herd; $a_{ijklmno}$= random effect of animal; $e_{ijklmno}$ = residual. Additive genetic variance (σ^2_a), common herd environment variance (σ^2_c), and residual variance (σ^2_e) were divided with phenotypic variance σ^2 to be expressed as heritability ($h^2 = \sigma^2_a / \sigma^2$), variance ratio for common herd environment ($c^2 = \sigma^2_c / \sigma^2$), and variance ratio for residual ($e^2 = \sigma^2_e / \sigma^2$).

To estimate the linear genetic trend, yearly averages of breeding values for sires born between 1970 and 2000 were standardised using the following equation:

$$SBV_{ty} = \frac{\overline{BV_{ty}}}{\sigma_{t1}} \quad where:$$

SBV_{ty} = standardised breeding value for trait t (LMP, PL, and MY305) and year y (1970-2000);

$\overline{BV_{ty}}$ = Average of predicted breeding values for trait t and year y; σ_{t1} = standard deviation of breeding values for trait t for sires born in year 1970.

Data were prepared using the R software (R Development Core Team, 2008), while the Wombat (Meyer, 2007) software package was used for the estimation of variance components and the prediction of breeding values.

Results and discussion

Descriptive statistics

Descriptive statistics for LMP, PL, and MY305 are presented in Table 1. On average, cows were producing 5,109 kg of milk in the first lactation and 24,376 kg total in 1,544 days. As records from the cows culled before 201 days of first lactation were excluded from the analysis, the lifetime performance records were higher than those from the yearly report for Slovenia (Sadar et al., 2014). The range of herd averages was wide for LMP and PL, where the maximum herd average was around four times the minimum herd average. For MY305, this range was smaller, with a maximum herd average of 2.3 times the minimum herd average.

Table 1. Descriptive statistics for lifetime milk production (LMP), length of productive life (PL), and first standard lactation milk yield (MY305)

Trait	N[1]	Mean	SD[2]	CV[3]	Herd Min[4]	Herd Max[5]
LMP (kg)	12,416	24,376	15,083	61.9	10,765	43,436
PL (days)	12,416	1,544	878	56.9	725	2,702
MY 305 (kg)	14,389	5,109	1,101	21.5	3,174	7,190

[1]Number of cows; [2]Standard deviation; [3]Coefficient of variation; [4]Minimum herd average; [5]Maximum herd average

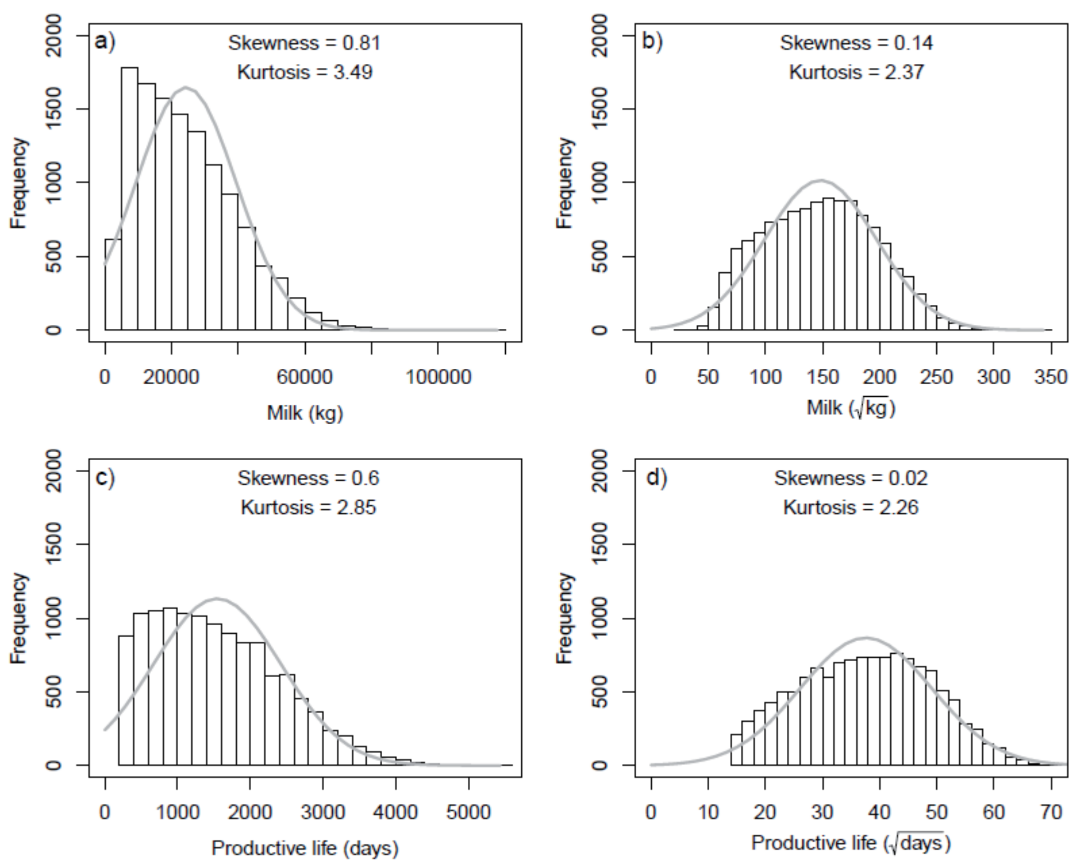

Figure 1. Distribution of lifetime milk yield a), square root of lifetime milk yield b), length of productive life c), and square root of length of productive life d) with curves of ideal normal distribution

Square root transformation decreased the skewness of distribution for both LMP and PL (Figure 1). With a skewness of 0.14 for LMP and 0.02 for PL, the transformation almost completely solved the problem of positive skewness in LMP and PL. The problem of kurtosis was not solved. Square root transformation changed the distribution of LMP from leptokurtic to platykurtic, and made the distribution of PL even more platykurtic. In the rest of the paper LMP and PL will be used as a square root transformed data.

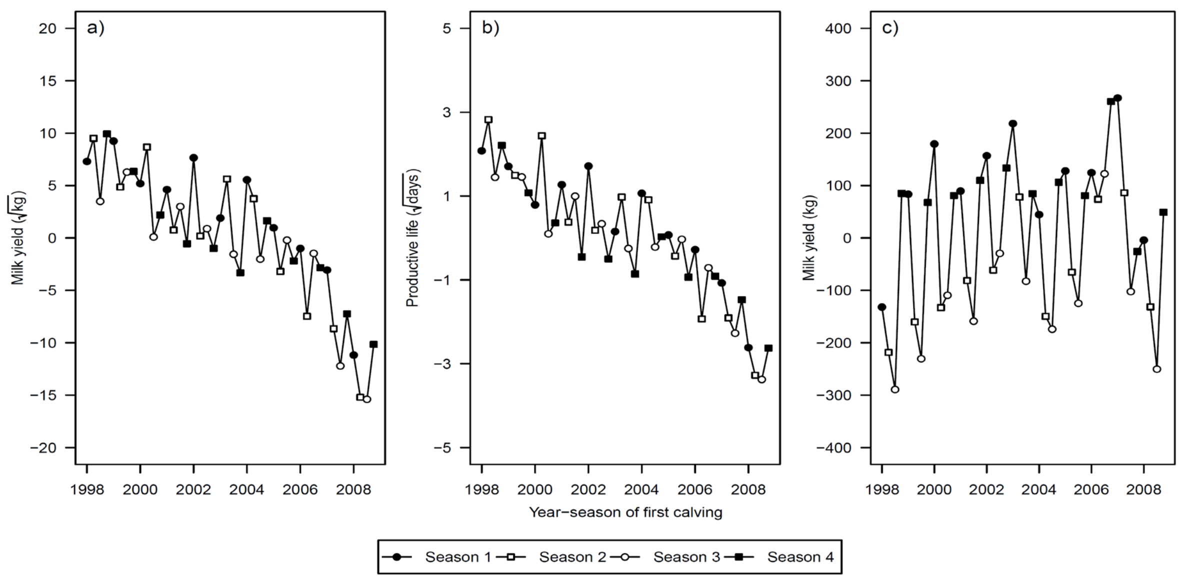

Figure 2. Estimates of year-season effect at first calving on the lifetime milk production a), length of productive life b), and first lactation milk yield c)

Table 2. Estimates of the effect of age at first calving on lifetime milk production (LMP), length of productive life (PL), and first lactation milk yield (MY305)

Age at first calving (months)	≥ 20 < 22	≥ 22 < 25	≥ 25 < 28	≥ 28 < 31	≥ 31 ≤40
LMP ($\sqrt{\text{kg}}$)	-1.48	0.08	-0.72	2.82	-0.71
PL ($\sqrt{\text{days}}$)	0.40	0.22	-0.28	0.39	-0.72
MY 305 (kg)	-658	-41	90	232	378

Fixed effects

The effect of year-season oscillated between different seasons. Yearly peaks and bottoms of seasonal effect are rather random in LMP (Figure 2a) and PL (Figure 2b). Oscillations followed a seasonal pattern in MY305 (Figure 2c) where cows with first calving in seasons one and four had the highest MY305 and cows with first calving in seasons two and three had the lowest. This might be the consequence of heat stress, which decreases the feed intake during the period of high temperatures and can occur during seasons two and three.

Increased temperatures have big influence on the feed intake of cows in the first stage of lactation (West et al., 2003). Between the years 1998 and 2007, the environmental conditions improved the MY305, while after the year 2007, there was a negative trend of environment effect on the MY305 observed. The general trend of the environmental effect on LMP and PL was negative throughout the whole observed period, which might be the consequence of a constant decrease of the population size in Brown cattle (Perpar et al., 2010). For this reason, cows did not have an opportunity to express their lifetime potential as they were culled for the reason of abandoned farming.

There was a stable trend observed for the effect of age at first calving on LMP and PL (Table 2). This is not surprising as the effect of age at first calving was found to be non-significant in a study of PL on the same breed (Jenko et al., 2013a). Older cows at first calving had a higher MY305. Differences between the extreme classes can be related to the differences in the maturity of first calving cows

Table 3. Estimates of the regional effect on the lifetime milk production (LMP) length of productive life (PL), and lactation milk yield (MY305)

	East	Central	West
LMP ($\sqrt{\text{kg}}$)	-0.7	-4.0	4.7
PL($\sqrt{\text{days}}$)	-1.0	-1.1	2.1
MY 305 (kg)	162	36	-198

Table 4. Estimates of variance components, heritability (h^2), variance ratio for common herd environment (c^2), and variance ratio for the residual (e^2) for lifetime milk production (LMP), length of productive life (PL), and first standard lactation milk yield (MY305)

Variance components / ratios	LMP $(\sqrt{\text{kg}})$	PL $(\sqrt{\text{days}})$	MY 305 (kg)
Additive genetic (σ_a^2)	299±43	12.4±2.0	139,178±955
Herd (σ_c^2)	204±21	12.7±1.2	373,442±2,854
Residual (σ_e^2)	1,908±39	106.7±2.0	441,152±6,356
Phenotipic (σ^2)	2,411±36	132.0±2.0	953,773±6,350
h^2	0.12±0.017	0.09±0.015	0.15±0.001
c^2	0.08±0.008	0.09±0.008	0.39±0.003
e^2	0.79±0.018	0.81±0.016	0.46±0.004

or the growth rate before puberty, which were both reported to cause differences in the milk yield (Sejrsen and Purup, 1997). Positive relationships between the age at first calving and the MY305 are in agreement with Moore et al. (1991).

Regional differences in the environmental conditions influenced management practices and culling reasons. Regional-specific characteristics are finally expressed as differences in LMP, PL, and MY305 (Table 3). In the eastern part of Slovenia, conditions were in favour of MY305, whereas in the western part, better conditions for LMP and PL existed. The longer life of Brown cows in the region with tougher conditions for cattle breeding was also confirmed by a study of functional traits (Jenko et al., 2013a).

Estimates of variance components

Estimated heritability for LMP was 0.12 (Table 2) and was practically the same as the estimates of 0.11 by Hoque and Hodges (1980) or 0.13 by Jairath et al. (1995) obtained in Canadian Holsteins. This shows that the selection of individuals for LMP is reasonable and can be performed. Heritability estimate for MY305 was 0.15 and was lower compared to the heritability estimate of 0.28 for the univariate repeatability model for Slovenian Brown cattle breed (Potočnik, 2001). The obtained heritability estimate was in the lower part of the reported heritabilities for milk yield, which can range from 0.13 to 0.48 (Hoekstra et al., 1994; Veerkamp and Goddard, 1998) and are usually higher for the higher milk production level (Hill et al., 1983). The estimated heritability for PL was 0.09 which is similar to the estimate obtained with the application of survival analysis techniques using a sire-maternal grand sire model for the same population (Jenko, et al., 2013b). Other studies reported heritability of PL in the interval of between 0.02 and 0.21

Table 5. Estimates of the phenotypic, genetic, common herd environment, and residual correlations between the lifetime milk production (LMP), length of productive life (PL), and first standard lactation milk yield (MY305)

Variance component	Trait	LMP $\left(\sqrt{\text{kg}}\right)$	PL $\left(\sqrt{\text{days}}\right)$
Phenotypic	PL $\left(\sqrt{\text{days}}\right)$	0.95±0.001	
	MY305 (kg)	0.27±0.013	0.05±0.013
Genetic	PL $\left(\sqrt{\text{days}}\right)$	0.96±0.008	
	MY305 (kg)	0.48±0.067	0.23±0.085
Common herd environments	PL $\left(\sqrt{\text{days}}\right)$	0.74±0.025	
	MY305 (kg)	0.26 ±0.057	-0.41±0.052
Residual	PL $\left(\sqrt{\text{days}}\right)$	0.98±0.001	
	MY305 (kg)	0.26 ±0.014	0.16±0.015

(Sasaki, 2013). This relatively wide range of heritability estimates depends on the data structure and the model applied (Jenko et al., 2013b; Ragu쬠et al., 2014).

The variance of MY305 explained with the common herd environment was 2.7 times bigger compared to the variance explained with additive genetic variance. This means that the management practices are more important compared to the genetic effect for MY305. For PL and LMP, the variances explained by the common herd environment and additive genetic variance were close to each other. According to heritability and the proportion of phenotypic variance explained by the common herd environment, herd management is less important for lifetime performance traits than for MY305, which is in agreement with Zavadilová and Zink (2013). Residual variance remained the main part of the estimated phenotypic variance for all the traits. The proportions of total phenotypic variances that remained unexplained were 79 % for LMP, 81 % for PL, and 46 % for MY305.

Both the phenotypic and genetic correlations between LMP and PL were very strong (Table 5). This shows that LMP and PL are near identical traits and performing selection on one measure will increase the genetic values of the other measure. The phenotypic correlation between LMP and MY305 was much weaker (0.27), and even weaker between PL and MY305 (0.05). However, genetic correlations between MY305 and LMP or PL were stronger than were the phenotypic correlations. The genetic correlation between LMP and MY305 was 0.48, which shows a moderate predictive ability of MY305 for LMP. A similar result of estimated genetic correlation between the LMP and MY305 (0.56) was obtained in the study of lifetime production traits in the Canadian Holstein population (Hoque and Hodges, 1980). A weak positive (0.23) genetic correlation between PL and MY305 indicates that cows with high potential for milk yield are also genetically superior for PL. Literature reports of genetic correlations between PL and MY305 or survival are in the range of between -0.53 and 0.84 (De Lorenzo and Everett, 1982; Jairath et al., 1995; Dematawewa and Berger, 1998; González-Recio and Alenda, 2007).

There are different reasons for the explanation of positive correlations obtained in the current study. One of them is the method used to analyse the longevity records, which can be analysed as continuous or as survival up to the specific point in time.

Another reason is the preferential treatment of cows with a higher milk yield that are receiving more health treatments compared to the cows with a lower milk yield.

The correlation between the common herd environment effect for PL and MY305 was moderately negative (-0.41). This shows that improvement in the herd environment for MY305 deteriorated the herd environment for PL (Table 5). Zavadilová and Zink (2013) also obtained a weak negative correlation (-0.28) for the common herd-year environment between PL and MY305. When looking at the residuals, there was a weak positive correlation of 0.16 between PL and MY305, meaning that the

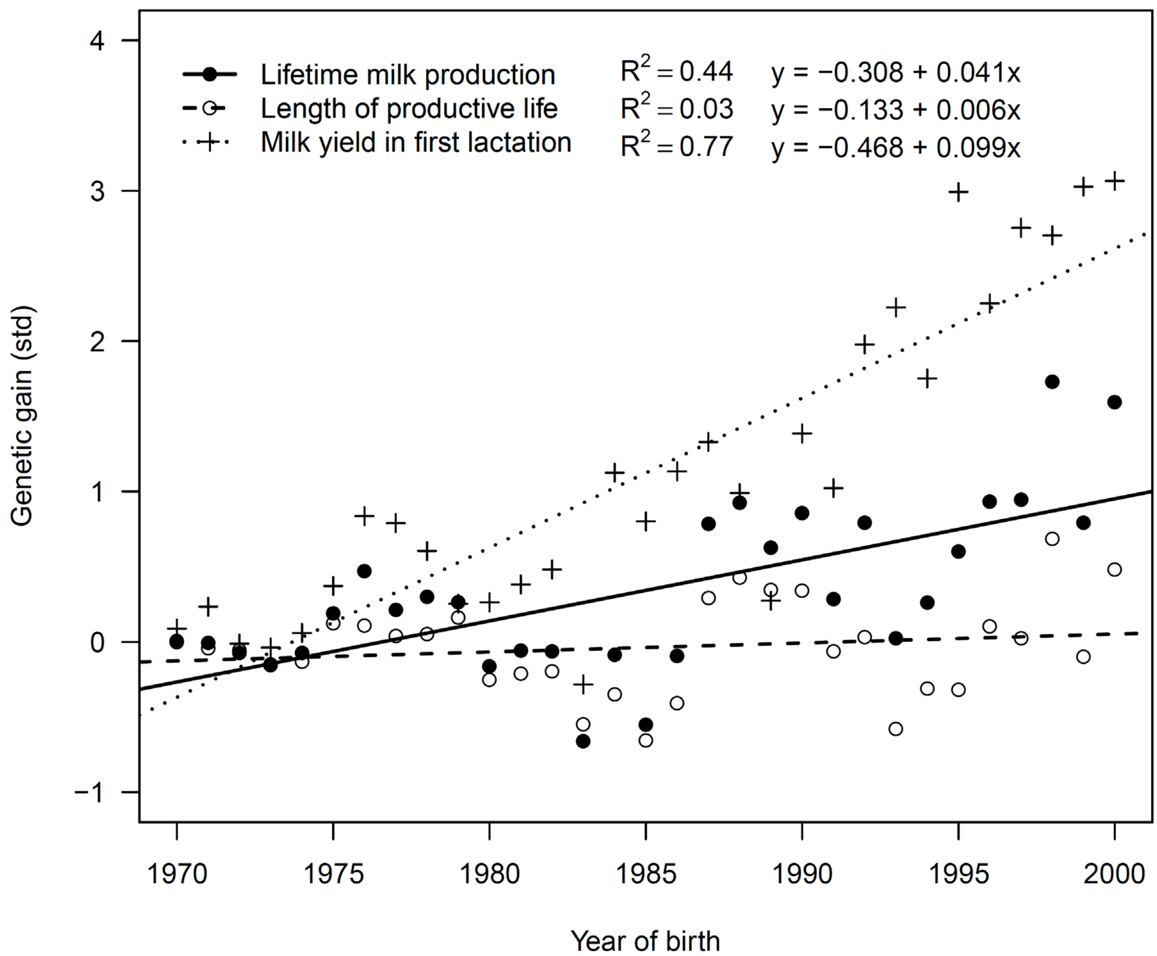

Figure 3. Genetic trend for lifetime milk production, length of productive life, and first lactation milk yield for sires born between 1970 and 2000

improvement in the cow microenvironment for one of the traits will also improve the cow's microenvironment for the other trait. Between the other trait combinations, the correlations in the common herd environments and residuals were always positive but of different strength. It was weak for the common herd environments and the residuals between LMP and MY305 (0.26), strong for the common herd environments between LMP and PL (0.74), and very strong for the residuals between LMP and PL (0.98).

Genetic trend

The linear regression coefficient of the standardised genetic trend for LMP was 0.041±0.009, whereas for MY305, it was more than two times steeper and was 0.099±0.011 (Figure 3). Genetic trend for PL remained stable as selection on longevity was recently implemented (Potočnik et al., 2011). The presented genetic trends confirm that in the past, the main emphasis in the selection of Brown cattle in Slovenia was on production traits. The first genetic evaluation on a smaller scale started in 1958 (Ferčej, 1965) and in 1974, two yearly breeding value estimation were introduced for milk and fat traits (Pogačar, 1978). Due to the moderate genetic correlation between MY305 and LMP, an improvement in genetic values for LMP was achieved indirectly with the selection for production traits.

Conclusions

It was shown that cows with first calving in a year's colder seasons had higher MY305 compared to the cows that had their first calving in the warmer seasons. This structured pattern of seasonal effect was not detected for LMP and PL. Very strong genetic correlation (0.96) was found between LMP and PL in Slovenian Brown cattle breeds. This shows that LMP and PL are near identical traits, and performing selection on one of the traits would also affect the change in genetic values for the other trait. The genetic correlation between LMP and MY305 was moderate (0.48) and weak between PL and MY305 (0.23). Herd and residual correlations were, except for the common herd environment between PL and MY305 (-0.41), always positive. The linear regression coefficient of the standardised genetic trend for the last four decades was positive for MY305 (0.099) and LMP (0.041), whereas it was stable for PL.

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Genetska povezanost između životne proizvodnje mlijeka, dugovječnosti i proizvodnje mlijeka u prvoj laktaciji smeđe pasmine goveda u Sloveniji

Sažetak

Za proučavanje genetske povezanosti između životne proizvodnje mlijeka (LMP), količine mlijeka u standardnoj laktaciji (MY305) i dužine produktivnog života (PL) slovenske populacije smeđe pasmine goveda, korišteni su podaci prvih laktacija 14.389 krava kao i životne proizvodnje (LMP i PL) za 12.416 krava. U svrhu dobivanja normalne distribucije, prvobitne vrijednosti za LMP i PL transformirane su pomoću kvadratnog korijena. Fiksni utjecaj interakcije između godine i sezone prvog teljenja razlikovao se između različitih sezona unutar godine za sva analizirana svojstva. Navedene promjene slijede sezonski uzorak proizvodnje mlijeka u standardnoj laktaciji (MY305) gdje krave koje se tele tijekom hladnijih sezona imaju najvišu MY305 proizvodnju, a krave koje se tele tijekom toplijih godišnjih razdoblja imaju najnižu MY305 proizvodnju. Procijenjeni heritabiliteti su iznosili 0,12±0,017 za LMP, 0,09±0,015 za PL i 0,15±0,001 za MY305. Genetska korelacija između LMP i PL je bila visoka i pozitivna (0,96±0,008), umjerena i pozitivna korelacija (0,48±0,067) između LMP i MY305, dok je slaba i pozitivna korelacija utvrđena između PL i MY305 (0,23±0,085). Korelacija za utjecaj stada između PL i MY305 bila je umjerena i negativna (-0,41±0,052), slaba i pozitivna između LMP i MY305 (0,26±0,057) te jaka i pozitivna između LMP i PL (0,74±0,025). Tijekom posljednjih 40 godina zabilježen je pozitivan genetski trend za LMP i MY305, dok genetski trend za PL nije moguće detektirati.

Ključne riječi: genetsko vrednovanje, životna proizvodnja mlijeka, količina mlijeka u standardnoj laktaciji, dužina produktivnog života, smeđa pasmina goveda

References

1. Dematawewa, C.M.B., Berger, P.J. (1998): Genetic and phenotypic parameters for 305-day yield, fertility, and survival in Holsteins, *Journal of Dairy Science 81*, 2700-2709.
   doi: dx.doi.org/10.3168/jds.S0022-0302(98)75827-8
2. Ducrocq, V., Casella, G. (1996): A Bayesian analysis of mixed survival models, *Genetics Selection Evolution 28*, 505-529.
   doi: dx.doi.org/10.1186/1297-9686-28-6-505
3. Ferčej, J. (1965): Vrednotenje bikov po mlečnosti hčera. RSS, Kmetijski inštitut Slovenije, Ljubljana.
4. González-Recio, O., Alenda, R. (2007): Genetic relationship of discrete-time survival with fertility and production in dairy cattle using bivariate models, *Genetics Selection Evolution 39*, 391.
   doi: dx.doi.org/10.1186/1297-9686-39-4-391
5. Hill, W.G., Edwards, M.R., Ahmed, M.-K.A., Thompson, R. (1983): Heritability of milk yield and composition at different levels and variability of production, *Animal Science 36* (1), 59-68.
   doi: 10.1017/S0003356100039933
6. Hoekstra, J., van der Lugt, A.W., van der Werf, J.H.J., Ouweltjes, W. (1994): Genetic and phenotypic parameters for milk production and fertility traits in upgraded dairy cattle, *Livestock Production Science 40* (3), 225-232.
   doi: dx.doi.org/10.1016/0301-6226(94)90090-6
7. Hoque, M., Hodges, J. (1980): Genetic and phenotypic parameters of lifetime production traits in Holstein cows, *Journal of Dairy Science 63*, 1900-1910.
   doi: dx.doi.org/10.3168/jds.S0022-0302(80)83157-2

8. Jairath, L.K., Hayes, J.F., Cue, R.I. (1995): Correlations between first lactation and lifetime performance traits of Canadian Holsteins, *Journal of Dairy Science 78*, 438-448.

   doi: dx.doi.org/10.3168/jds.S0022-0302(95)76653-X

9. Jenko, J., Moljk, B., Perpar, T. (2007): Analiza dolgoživosti krav molznic in njen vpliv na ekonomiko prireje mleka. Zbornik predavanj 16. mednarodno znanstveno posvetovanje o prehrani domačih živali "Zadravčevi-Erjavčevi dnevi". KGZS-Zavod MS, Murska Sobota, Radenci.

10. Jenko, J., Ducrocq, V., Kovač, M. (2013a): Comparison of piecewise Weibull baseline survival models for estimation of true and functional longevity in Brown cattle raised in small herds, *Animal: An International Journal of Animal Bioscience 7*, 1583-1591.

    doi: dx.doi.org/10.1017/S1751731113001055

11. Jenko, J., Gorjanc, G., Kovač, M., Ducrocq, V. (2013b): Comparison between sire-maternal grandsire and animal models for genetic evaluation of longevity in a dairy cattle population with small herds, *Journal of Dairy Science 96*, 8002-8013.

    doi: dx.doi.org/10.3168/jds.2013-6830

12. De Lorenzo, M.A., Everett, R.W. (1982): Relationship between milk and fat production, type, and stayability in Holstein sire evaluation, *Journal of Dairy Science* 65, 1277-1285.

    doi: dx.doi.org/10.3168/jds.S0022-0302(82)82341-2

13. Meyer, K. (2007): WOMBAT - A tool for mixed model analyses in quantitative genetics by restricted maximum likelihood (REML), *Journal of Zhejiang University. Science 8* (11), 815-821.

    doi: dx.doi.org/10.1631/jzus.2007.B0815

14. Moore, R.K., Kennedy, B.W., Schaeffer, L.R., Moxley, J.E. (1991): Relationships between age and body weight at calving and production in first lactation Ayrshires and Holsteins, *Journal of Dairy Science 74*, 269-278.

    doi: dx.doi.org/10.3168/jds.S0022-0302(91)78170-8

15. Perpar, T., Arlič, S., Babnik, D., Čandek Potokar, M., Glad, J., Jenko, J., Jeretina, J., Kramer, Z., Logar, B., Opara, A., Plesničar, P., Podgoršek, P., Prevolnik, M., Rigler, M., Sadar, M., Škrlep, M., Verbič, J., Žabjek, A., Žnidaršič, T. (2010): Brown cattle in Slovenia. Zbornik Evropske konference rejcev govedi rjave pasme, Novo mesto, Slovenija, 14-16 Oct. 2010, Ljubljana.

16. Pogačar, J. (1978): Metode testiranja plemenske vrednosti govedi. Projekt: Genetika in selekcija v živinoreji. RSS, Kmetijski inštitut Slovenije, Ljubljana.

17. Potočnik, K. (2001): Metode napovedovanja plemenskih vrednosti pri črnobeli, rjavi in lisasti pasmi govedi v letu 2001. Biotehniška fakulteta, Oddelek za zootehniko, Domžale.

18. Potočnik, K., Gantner, V., Krsnik, J., Štepec, M., Logar, B., Gorjanc, G. (2011): Analysis of longevity in Slovenian Holstein cattle, *Acta agriculturae Slovenica 98* (2), 93-100.

    doi: dx.doi.org/10.2478/v10014-011-0025-5.

19. Raguž, N., Jovanovac, S., Mészáros, G., Sölkner, J. (2014): Usporedba linearnog i "piecewise" modela po Weibullu u genetskom vrednovanju bikova za dugovječnost u populaciji simentalske pasmine goveda, *Mljekarstvo 64* (3), 141-149.

    doi: dx.doi.org/10.15567/mljekarstvo.2014.0301

20. R: Development Core Team (2008): R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria.

21. Robertson, A., Rendel, J. (1950): The use of progeny testing with artificial insemination in dairy cattle, *Journal of Genetics 50* (1), 21-31.

    doi: dx.doi.org/10.1007/BF02986791

22. Sadar, M., Jenko, J., Jeretina, J., Logar, B., Opara, A., Perpar, T., Podgoršek, P. (2014): Rezultati kontrole prireje mleka in mesa: Slovenija 2013, Kmetijski inštitut Slovenije, Ljubljana.

23. Sasaki, O. (2013): Estimation of genetic parameters for longevity traits in dairy cattle: A review with focus on the characteristics of analytical models, *Animal Science Journal 84* (6), 449-460.

    doi: dx.doi.org/10.1111/asj.12066

24. Sejrsen, K., Purup, S. (1997): Influence of prepubertal feeding level on milk yield potential of dairy heifers: A review, *Journal of Animal Science 75*, 828-835.

25. Stott, A.W. (1994): The economic advantage of longevity in the dairy cow, *Journal of Agricultural Economics 45* (1), 113-122.

    doi: dx.doi.org/10.1111/j.1477-9552.1994.tb00382.x

26. Tsuruta, S., Misztal, I., Lawlor, T.J. (2004): Genetic correlations among production, body size, udder, and productive life traits over time in Holsteins, *Journal of Dairy Science 87*, 1457-1468.

    doi: dx.doi.org/10.3168/jds.S0022-0302(04)73297-X

27. Veerkamp, R.F., Goddard, M.E. (1998): Covariance functions across herd production levels for test day records on milk, fat, and protein yields, *Journal of Dairy Science 81*, 1690-1701.

    doi: dx.doi.org/10.3168/jds.S0022-0302(98)75736-4

28. Zavadilová, L., Zink, V. (2013): Genetic relationship of functional longevity with female fertility and milk production traits in Czech Holsteins, Czech *Journal of Animal Science 58*, 554-565.