Original scientific paper - Izvorni znanstveni rad UDK: 636.23

Estimation of nonadditive genetic influences on standard lactation production (305 days) in upgrading of Serbian-Fleckvieh to Holstein-Friesian cattle breed

doi: 10.15567/mljekarstvo.2016.0409

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Received - Prispjelo: 25.01.2016.
Accepted - Prihvaćeno: 20.10.2016.

Abstract

The purpose of this paper is to estimate the effects of systematic factors, primarily the degree of crossing, on the standard lactation lengths of 305 days in 6 different genotypes of cows (F_1, R_1, R_2, R_3, R_4, R_5) obtained by the upgrading of the Serbian Fleckvieh (SF) to the Holstein-Friesian (HF) breed of cattle. The systematic effects included in the general linear model (GLM) exerted a significant ($P<0.05$) influence on the milk yield, as well as the fat yield and content. During the upgrading process, statistically significant ($P<0.05$) differences were recorded between the traits of the genotypes examined. With an increase in the share of HF genes, the milk yield increased from 5020 kg (F_1) to 5801 kg (R_5) and the fat yield from 176.2 kg to 201.6 kg, whereas the fat content simultaneously decreased from 3.55 % (F_1) to 3.49 % (R_5). The F_1 cows had the highest heterosis realized (h^R) regarding the milk yield (185.8 kg), while the R_1 and R_2 cows displayed negative heterosis effects (-21.0 and -205.7 kg) and negative recombination effects (r^I). The highest value of h^R (regarding the milk fat yield) was recorded in the F_1 cows (6.07 kg) in comparison with the R_2 cows, which had the negative h^R (-3.79 kg), whereas the negative r^I was recorded in the R_1 and R_2 genotypes. The positive r^I (regarding the milk fat content) was recorded in the R_1, R_2 and R_3 genotypes accompanied by the positive h^R.

Key words: upgrading, crossbreeding, recombination, heterosis, standard lactation length

Introduction

Over the last few decades, considerable changes have occurred in the European dairy cattle production. Breeding aims and therefore breeding programs have been altered. Crossings with the upgrading method have changed the genetic structure of most combined breeds (McAllister 2002; Swalve et al., 2008) in the European countries (Lederer, 2005). In breeding, the most used breed has been the intensive dairy Holstein-Friesian (HF) breed, which originated from the North American continent (Cunningham, 1983). The countries which were breeding the traditional spotted cattle such as Switzerland, Hungary and Serbia, had the national breeding programs dictating the direction of cattle production development, which meant the introduction of the HF breed and upgrading the indigenous breed population to this breed. The significance of crossing the HF breed with the indigenous breeds was discussed by Wolf et al. (2005) in the instance of

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Czech spotted cattle and Schichtl (2007) in the instance of Bavarian spotted cattle, namely "Fleckvieh". According to Kräusslich (2002), the average share of HF genes in the Hungarian cow population in 1999 was only 1.65 %, whereas the share of HF genes in the Austrian cow population was 6.4 % (Egger, 2005). According to Perišić (2008), the share of the Serbian Fleckvieh (SF) cattle breed amounts to around 70 % in Serbia. The same author argues that in the period from 1990 to 2006 the milk yield within the standard lactation length was slightly increased from 4540 kg to 4660 kg, which created a necessity for enhancing the breed.

Non-additive genetic effects (recombination and heterosis), which influence the productivity during the upgrading of dairy herds, are addressed in a limited number of studies. The primary reason lies in the data collection spanning over several decades. The very act of upgrading is very expensive and the end results cannot be reliably planned ahead. Moreover, the market treats the individuals of unknown genetic constitution and breeding value very indifferently, especially because each successive generation of crossed animals differ in body measures, productivity and technological requirements (Freyer et al., 2008). Lopez-Villalobos et al. (2000) state that the crossing and genetic variability may provide favorable advantages which substantially balance the production costs and market conditions.

The purpose of this paper is to assess the results of the upgrading of the SF to the HF breed of cattle according to the standard lactation features (such as milk yield, milk fat yield and content), to evaluate the non-additive genetic effects caused by crossing, and to determine the occurrence of gene recombination and heterosis.

Materials and methods

The population of animals studied consisted of 12,944 cows, sired by 390 HF bulls (originating from Vojvodina-Bečej, Yugoslavia-Serbia, USA and Canada) and 8 SF bulls (originating from Yugoslavia-Serbia and foreign countries), which were produced on seven farms in the same ownership in Vojvodina, Serbia, in the period from 1971 to 2008. The crossing, i.e. the upgrading of the SF breed to the HF breed started in 1971. The whole process lasted until 2008, wherein six cow genotypes (F_1, R_1, R_2, R_3, R_4 and R_5) with different proportions of the HF genes were obtained so that purebred HF cows could be produced eventually. The F_1 cows were created by crossing the SF cows with the HF bulls which possessed 50 % of HF genes. Each newer generation was produced by a consequent use of the HF semen. The crossbreeding process was conducted until receiving a cow generation with the HF blood proportion exceeding 99 %. As a result of many years of crossing, the following cow genotypes and HF gene proportions were obtained in order to produce the last generation of cows with 100 % HF genes: R_1 with 75 % HF genes, R_2 with 87.5 % HF genes, R_3 with 93.75 % HF genes, R_4 with 96.88 % HF genes, R_5 with 98.44 % HF genes.

After examining the records of each cow, the proportion of HF genes (or the HF gene share within each genotype), the degree of crossing, the number of generations, the total production of milk, the amount of milk fat and the percentage of milk fat were determined.

The production traits within the standard lactation length (305 days) were analyzed by means of the following multiple-trait nested linear model:

$$Y_{ijklmnopqrs} = \mu + K_i + B_j + S_k + E_l + I_m + T_n + P_o(K_i) + A_p(K_i) + Z_q + X_r + e_{ijklmnopqrs}$$

where: $Y_{ijklmnopqrs}$ = the mean value of the trait examined; μ = the overall mean value; K_i = the genotype (n = 8); B_j = the origin of the bull (n = 6); S_k = the number of parity (n = 7); E_l = the year of calving (n = 38); I_m = the period of calving (n = 2); T_n = the housing system (n = 2); P_o = the service period (nested in the degree of crossing); A_p = the age at first calving (nested in the degree of crossing); Z_q = the year of bull's birth (n = 48); X_r = the year of cow's birth (n = 39); $e_{ijklmnopqrs}$ = the error.

For the traits analyzed, the adjusted mean value (LSM - Least Square Means) was computed by the multiple-trait hierarchical linear model. The Duncan's post-hoc test for statistically significant differences among genotypes was applied (StatSoft, Inc. 2011). Moreover, the Dickerson-model (Dickerson 1969) was also applied for the estimate of the non-additive crossing effects (Nemes et al., 2014).

Results and discussion

Table 1 shows that all the systematic effects included in the model had a significant ($P<0.05$) influence on the milk yield, milk fat yield and fat content in the standard lactation length. The values of the coefficient of multiple correlation obtained during the data processing indicate a moderate correlation between the dependent variables (the milk yield = 0.61, the milk fat yield = 0.59 and the milk fat content = 0.61) and the independent variables (the systematic effects) included in the model. The values of the coefficient of determination ranged from 0.32 to 0.37. With regard to the milk yield and fat yield, slightly higher values (0.37 and 0.35) were obtained compared to Marković's (1999) previous findings, who reported the values between 0.31 and 0.26. However, the milk fat percentage results of this study were in accordance with his findings (0.32).

According to the F values obtained (Table 2), the most important influence was exerted by the housing system (F = 576.5) and the period of calving (F = 190.7). As in this study, other researchers (Vidović, 1990; Gáspárdy, 1995; Gaydarska et al., 2001; Petrović et al., 2012) confirmed the influence of systematic factors on dairy traits. White et al. (1981) reported that non-specific factors such as heard, year, season and their mutual interaction cause about 30 to 50 % of variability in milk production within the standard lactation length.

Tables 3, 4 and 5 show the adjusted least square means (LSM) and the adjusted standard error of the mean (SE_{LSM}) of the milk yield, fat yield and fat content within different cow genotypes. The results displayed in the tables indicate that the milk yield and milk fat increased with an increase in the share of HF genes in the cow's genotype, while the percentage of milk fat slightly decreased. Furthermore, it can be noticed that the standard error of the mean (SE_{LSM}) of the traits analyzed decreased with the increase of HF genes, which can be explained by the increased number of cows with a higher share of HF genes in the population. Moreover, a significant increase in the milk production within different degrees of crossing was recorded, with the lower milk and milk fat production in the purebred HF breed compared to the R_5 cows with the 98.45 % HF genes. Similar results were obtained by Kräusslich (1998), Heins et al. (2006), Dechow et al. (2007) and Perišić (2008).

Significant additive genetic differences in the milk amount (1834.9 kg) occurred between the HF and the SF breeds of cattle. Schmidlin (1979) has also confirmed the presence of significant additive genetic differences in the milk yield (1387.0 kg) between the Switzerland Simmental breed in comparison with the HF breed. Additive genetic differences of 1,383.0 kg in the milk yield of the German Spotted breed (GS) and the HF breed was reported by Schichtl (2007), and earlier Egger (2005) between the Austrian Spotted (AS) and the HF breed (of 1,232.0 kg).

Table 3 indicates that the F_1 cows had the positive and highest heterosis realized (h^R) regarding the total milk yield with an amount of 185.8 kg. Similar results were recorded by Schmidlin (1979) (282.0 kg), Egger (2005) (134.0 kg) and Schichtl (2007) (276.0 kg), respectively. The negative effect of recombination (r^I) was determined in the R_1 cows (-113.9 kg) and the R_2 cows (-252.2 kg). Schmidlin (1979) confirmed a relatively important recombination loss of 383 kg in the milk production for within the standard lactation length. Later results of Egger (2005) also show the recombination losses in the milk production of the R_1 (-86 kg) and R_2 (-64 kg) genotypes.

Table 1. Analysis of the sum of squares

Traits	R	R^2	SS	SS Res.	F	P
Milk yield, kg	0.61	0.37	2.534693E+10	4.270396E+10	206.59	0.000
Fat yield, kg	0.59	0.35	2.320413E+07	4.349862E+07	185.67	0.000
Fat content, %	0.57	0.32	6.373367E+02	1.325074E+03	167.41	0.000

R - the multiple correlation coefficient, R^2 - the multiple coefficient of determination, SS - the sum of squares of the model, SS Res. - the residual sum of squares

Table 4 shows the amounts of milk fat gained from cows of different genotypes. The milk fat yield increased from 139.4 kg (SF) to 201.0 kg (HF) with an increase in the share of HF genes in the cow's genotype. The value of heterosis realized h^I was the highest in the F_1 cows (6.07 kg). In the instance of the R_1 cows, a recombination loss (r^I) of -0.25 kg was lower than the expected heterosis (h^I = 3.04 kg), so the realized heterosis (h^R = 2.79 kg) was positive. The R_2 cows had a higher recombination loss (-5.31 kg) in the milk fat yield than the expected heterosis (1.52 kg), so the heterosis realized was negative (-3.79 kg). In contrast, Schmidlin (1979) obtained a positive heterosis of 13.8 kg for the milk fat yield, while later Schichtl (2007) also obtained a positive heterosis of 19.75 kg. We determined the recombination losses only in the R_2 cows, while the recombination losses in the milk fat yield within other genotypes were omitted. This is of great importance because milk fat yield is a primary parameter in milk price formation in many countries.

The results shown in Table 5 indicate a decrease in the milk fat content with an increase in the share of HF genes. Prior to the upgrading, the SF cows had 3.6 % of milk fat, whereas, after six generation of crossing, that percentage decreased to 3.51 % in the HF cows. In comparison with the HF genotype, the R_5 cows indicated the lowest milk fat content (3.49 %). In the R_1 and R_2 genotypes, positive recombination effects (r^I) were determined for the milk fat content (0.054; and 0.047 respectively) with the positive results of realized (h^R) and relative (h^r) heterosis. In the crossing of F_1 cows, Schmidlin (1979) recorded a positive heterosis realized of 0.06 %, whereas a higher heterosis realized of 2.7 % was established later by Schichtl (2007), which was really high according the author. Fuerst and Sölkner (1994) have shown that the values of non-additive components of variance for milk fat content and milk protein is almost the same, while the influence of dominance on variation of specific traits can be classified as constant provided more lactations are taken into account.

Table 2. Systematic effects on the milk traits

Systemic effects	Wilk values	F values
Genotypes	0.997	3.8***
Origin of the bull	0.992	23.1***
Number of parity	0.957	64.9***
Year of calving	0.707	86.5***
Period of calving	0.979	190.7***
Housing system	0.938	576.5***
Service period	0.936	72.7***
Age at first calving	0.998	2.6***
Bull's birth year	1.000	4.0*
Cow's birth year	0.997	28.0***

* P<0.05; *** P<0.001

Table 3. Milk yield within the standard lactation length of 305 days and non-additive genetic effects in different cow genotypes

Genotype	Share of HF gene, %	No. of lactation	Milk yield, kg LSM ± SE_{LSM}	Expected additive superiority of heterosis, kg (h^i)	Additive component of heterosis, kg (h^I)	Recombination, kg (r^I)	Realized heterosis, kg (h^R)	Relative heterosis, % (h^r)
SF	0.00	721	3917^a±108	-	-	-	-	-
F_1	50.00	785	5020^b±103	917.5	185.8	-	185.8	3.84***
R_1	75.00	825	5272^c±100	1376.2	92.9	-113.9	-21.0	-0.40^{NS}
R_2	87.50	649	5317^d±104	160.5	46.5	-252.2	-205.7	-3.73***
R_3	93.75	782	5712^e±102	1720.2	23.2	51.1	74.3	1.32*
R_4	96.87	2583	5760^f±91	1777.5	11.6	53.5	65.1	1.14^{NS}
R_5	98.45	5561	5801^g±89	1806.2	5.8	72.4	78.2	1.37*
HF	100.0	20116	5752^f±88	-	-	-	-	-

*, **, *** - number of subscribed stars show a significant difference from the Serbian Fleckvieh (*P<0.05; **P<0.01; ***P<0.001): ^{abcdefg} - different letters in upper script indicates significant differences (P<0.05)

According to Melchinger et al. (2007), the genetic basis of heterosis is not yet fully known, but the epistatic interactions of individual loci are most important components of heterosis in relation to parents. All the traits of the crossbred F_1 progeny are partly under the influence of non-additive genes, i.e. dominance (interaction among the alleles of a single gene) and epistasis (gene interaction between loci), which means that in the F_1 generation, heterosis is a result of domination (mostly positive) and epistasis (often negative), as confirmed by Sörensen et al. (2008). Fuerst and Sölkner (1994) argue that, due to non-additive genetic effects, the crossed population differs from the initial population (or the breed used for crossing) particularly in the amount of produced milk. The results of our research confirm these findings. Boichard et al. (1993) argue that the offspring of the breeds which have close phylogenetic origin in crosses have a low heterosis with the milk production which generally ranges from 2.0 to 2.5 %. The results of this study are in accordance with the general experience in as much as the property with a low degree of inheritance achieves a higher degree of heterosis. If crossbred animals are

Table 4. Fat yield in the lactation of 305 days and the heterosis realized within genotypes

Genotype	Share of HF gene, %	No. of lactation	Fat yield, kg LSM ± SE_{LSM}	Expected additive superiority of heterosis, kg (h^i)	Additive component of heterosis, kg (h^I)	Recombination, kg (r^I)	Realized heterosis, kg (h^R)	Relative heterosis, % (h^r)
SF	0.00	721	139.4^{a}±3.46	-	-	-	-	-
F_1	50.00	785	176.2^{b}±3.29	30.78	6.07	-	6.07	3.53***
R_1	75.00	825	188.4^{c}±3.22	46.18	3.04	-0.25	2.79	1.51*
R_2	87.50	649	189.5^{d}±3.31	53.88	1.52	-5.31	-3.79	-1.97**
R_3	93.75	782	200.2^{e}±3.25	57.73	0.76	2.33	3.06	1.55*
R_4	96.87	2583	201.3^{f}±2.92	59.68	0.38	1.89	2.27	1.12^{NS}
R_5	98.45	5561	201.6^{g}±2.85	60.62	0.19	1.37	1.56	0.78^{NS}
HF	100.0	20116	201.0^{f}±2.80	-	-	-	-	-

*, **, *** - number of subscribed stars show a significant difference from the Serbian Fleckvieh (*P<0.05; **P<0.01***P<0.001);
^{abcdefg} - different letters in upper script indicates significant differences (P<0.05)

Table 5. Fat content in the lactation of 305 days and the heterosis realized within genotypes

Genotype	Share of HF gene, %	No. of lactation	Fat content, % LSM ± SE_{LSM}	Expected additive superiority of heterosis, % (h^i)	Additive component of heterosis, % (h^I)	Recombination, % (r^I)	Realized heterosis, % (h^R)	Relative heterosis, % (h^r)
SF	0.00	721	3.60^{d}±0.019	-	-	-	-	-
F^1	50.00	785	3.55^{c}±0.018	-0.048	-0.0090	-	-0.009	-0.25^{NS}
R^1	75.00	825	3.58^{d}±0.018	-0.072	-0.0050	0.0540	0.049	1.39*
R^2	87.50	649	3.56^{c}±0.018	-0.084	-0.0030	0.0470	0.044	1.25^{NS}
R^3	93.75	782	3.52^{b}±0,018	-0.090	-0.0020	0.0020	0.000	0.00^{NS}
R^4	96.87	2583	3.51^{b}±0.016	-0.093	-0.0010	-0.0050	-0.006	-0.17^{NS}
R^5	98.45	5561	3.49^{a}±0.016	-0.095	-0.0005	-0.0195	-0.020	-0.27^{NS}
HF	100.0	20116	3.51^{b}±0.015	-	-	-	-	-

*, **, *** - number of subscribed stars show a significant difference from the Serbian Fleckvieh (*P<0.05; **P<0.01***P<0.001);
^{abcd} - different letters in upper script indicates significant diferences (p<0.05)

used for further breeding, recombination losses must be taken into account, i.e. significant non-additive effects of the opposite direction genes (which can be observed in the R_1 and R_2 genotypes).

Conclusions

The upgrading under conditions determined by certain systemic factors, based on the generally positive assessment of non-additive genetic effects (which affect the properties of the milk yield realized in the standard lactation length), can be justified. On the basis of the additive genetic effects (recombination and heterosis), the expected additive difference was increased during the upgrading. A positive heterosis was achieved owing to the fact that the actual realized production of crossed animals largely exceeded the expected additive superiority. With an increase in the share of Holstein-Friesian genes from generation to generation (accompanied by optimal zootechnical requirements and care), there was an increase in the total amount of milk within the standard lactation length of 305 days from 3917 kg in the SF breed to 5752 kg in the HF breed, the amount of milk fat from 139.4 kg to 201.0 kg, and a decrease in the milk fat content from 3.60 to 3.51 %, respectively. Judging from our experiences on the farms in Vojvodina and all the above mentioned facts, it can be concluded that the upgrading method is very successful (despite decreasing trends) and results in a significant improvement of dairy herd traits.

Procjena neaditivnih genetskih utjecaja na standardnu laktacijsku proizvodnju (305 dana) kroz poboljšanje domaćeg-šarenog goveda s holštajn-frizijskom pasminom goveda

Sažetak

Cilj ovog rada bio je ispitati procjenu sistematskih faktora, prvenstveno stupnja križanja na standardnu laktacijsku proizvodnju od 305 dana kod 6 genotipova krava (F_1, R_1, R_2, R_3, R_4 i R_5) dobivenih pretapanjem domaćeg šarenog goveda (SF) s holštajn-frizijskom (HF) pasminom goveda. Sistematski utjecaji uključeni u GLM model imali su značajan utjecaj ($P<0,05$) na količinu mlijeka, mliječne masti i postotak mliječne masti. Između dobivenih genotipova tijekom procesa pretapanja, zabilježene su statistički značajne razlike ($P<0,05$) u promatranim osobinama. S povećanjem udjela HF gena, povećavala se i količina mlijeka od 5020 kg kod F_1 generacije do 5801 kg kod R_5 generacije, mliječne masti od 176,2 do 201,6 kg, dok je istovremeno došlo do pada postotka mliječne masti (od 3,55 % kod F_1 do ,49 % kod R_5). Krave F_1 generacije su imale najveći realizirani heterozis (h^R) za količinu mlijeka od 185,8 kg, dok su krave genotipa R_1 i R_2 imale negativan realizirani heterozis (-21,0 odnosno -205,70 kg) pa samim tim i negativne rekombinacije (r^I). Najveća realizirana vrijednost heterozisa (h^R) za količinu mliječne masti je kod krava F_1 generacije (6,07 kg), u odnosu na krave R_2 generacije koje su imale negativan realizirani heterozis (-3,79 kg), a negativne rekombinacije su zabilježene kod krava R_1 i R_2 genotipa. Kod krava genotipa R_1, R_2 i R_3 ustanovljene su pozitivne rekombinacije (r^I) za postotak mliječne masti, uslijed čega su i realizirani heterozisi (h^R) bili pozitivni.

Ključne riječi: pretapanje, križanje, rekombinacija, heterozis, standardna laktacija

Acknowledgments

In memory of Zlatko Skalicki, PhD, Professor at the Faculty of Agriculture in Zemun-Belgrade.

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