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Effects of crossbreeding on milk production of sheep

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Abstract: The aim of this study was to estimate the effects of crossbreeding on milk production and milk components in crossbred Tsigai, Lacaune, and Improved Wallachian sheep used to create a synthetic Slovak dairy sheep population. The local breeds Tsigai and Improved Wallachian were crossed with the high-yielding breed Lacaune to increase milk yield. The effects of crossbreeding were evaluated based on breed and heterosis effects. The database used consisted of 23 018 lactations from 15 888 ewes. The effects of crossbreeding on milk production and fat and protein content were estimated using the restricted maximum likelihood method in REMLF90. Fixed effects on milk yield were also studied. In ewes with a 100% heterosis effect (ewes from purebred parents of different breeds), the heterosis effect increased milk production by 11.642 kg, milk fat production by 0.772 kg, and protein production by 0.565 kg per milking period. The effect of the Tsigai breed on milk production was –21.98 kg compared to Lacaune, while for the Improved Wallachian breed, the value was –38.58 kg. The Tsigai direct breed effect reduced fat production by 1.56 kg and protein production by 1.34 kg. The Improved Wallachian direct breed effect was –2.71 kg for fat production and –2.27 kg for protein production.

Keywords: Tsigai; Improved Wallachian; Lacaune; heterosis effect; effect of breed; crossing

Sheep breeding with cattle breeding ranks among the two most important sectors of Slovak agriculture (Krupova et al. 2014). Dairy sheep with commercial milk production make up most of the total number of sheep reared in Slovakia. The most numerous breeds are the local Tsigai and the Improved Wallachian breeds. These multipurpose breeds are of local importance and are bred for milk, meat, and wool (Oravcova et al. 2005; 2018). The Improved Wallachian breed originated from the native Slovak Wallachian coarse wool breed, where an intensive genetic improvement program was initiated in 1950. Crossbreeding with a wide range of breeds (Leicester, Lincoln, Texel, Cheviot, Kent, and East Friesian sheep) was carried out to improve wool, meat, and milk production. The Improved Valachian was recognized as a separate dual-purpose breed (wool-meat and meat-milk) in 1982. The Tsigai and the Improved Valachian have very similar production potential. Currently, Tsigai and Improved Valachian are being crossed to improve their milk yield, production, and fertility

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with specialized dairy breeds such as Lacaune and East Friesian (Makovicky et al. 2013). The high-yielding breed Lacaune was introduced in the 1990s. To increase the dairy performance of local breeds, two- and three-breed crossbred mixed populations have been created in the last two decades (Oravcova et al. 2018).

Crossbreeding has been used extensively for livestock genetic improvement, leading to improved performance traits (Stock et al. 2020). The use of crossbreeding can help livestock farmers increase the production of animal products while maintaining genetic diversity (Van Arendonk et al. 2011). It can lead to a combination of favorable breed traits based on the direct additive breed effect and heterosis effect (Freyer et al. 2008). Although crossbreeding was previously mainly used for meat performance, interest in crossbreeding dairy breeds to increase milk production has since increased (Sorensen et al. 2008). Crossbreeding schemes for genetic improvement of milk production are often too complex to implement, so breeders mainly choose simpler schemes that only involve the improvement of local breeds with high dairy breeds (Carta et al. 2009). Local breeds are well adapted to their production areas. The creation of synthetic lines by crossing local and imported breeds can be a successful strategy for increasing milk production (Barillet 2007) and reducing inbreeding depression by increasing the genetic diversity of low-performing breeds (Hartwig et al. 2014).

The positive effect of crossbreeding on milk quality and morphological traits of udders has been previously demonstrated in studies conducted on sheep in Slovakia (Makovicky et al. 2013; Oravcova et al. 2018). The aim of this study is to estimate the influence of crossbreeding effects on milk production and milk components in crossbred Tsigai, Lacaune, and Improved Wallachian sheep.

MATERIAL AND METHODS

The effect of nonadditive gene effects on milk yield was estimated in sheep reared in Slovakia. More precisely, in sheep involved in the creation of the new Slovak national breed Slovak Dairy Sheep. Thanks to many years of breeding work, there are many records on the performance of breeds and their crosses involved in creating this breed.

Database and data editing

The effect of crossbreeding on milk production and milk components was investigated using lactation records collected from Tsigai, Improved Wallachian, Lacaune, and their crossbred ewes. The Breeding Services of the Slovak Republic provided data and pedigree. The evaluation was carried out between 2012 and 2017. The effects of crossbreeding were evaluated based on breed and heterosis effects. The influence of these effects was estimated for milk production (kg), fat production (kg), and protein production (kg) per milking period.

The following adjustments were applied to the data. Records with milk production below 40 kg and above 600 kg were removed. Similarly, fat and protein content were omitted from 2 to 15% and 1 to 9%, respectively. The interval from lambing to the first measurement ranged from 5 to 95 days. The length of the days in milk ranged from day 100 to day 250. Ewes from a total of 102 flocks were included in the evaluation. The average number of ewes in the flock was 155.76. A total of 455 contemporary groups were formed from these flocks. Contemporary groups were created by combining flock, year, and season. Since most lambings took place from January to March, the lambing period was divided into winter (December–February) and spring lambing (March–May). Additional lambing was not included in the evaluation. The minimum number of animals in contemporary groups was seven, and ewes were from at least two rams. On average, there were 50.58 ewes per contemporary group. The flock and year effect is an important source of interrow variability in dairy sheep, especially in breeding systems with considerable variation in management techniques and environmental conditions. The month of lambing is another important source of variability. The magnitude of its effect is mainly due to the availability of grazing, which is directly related to milk yield in grazing systems (Carta et al. 2009). The litter size effect was created based on the number of lambs born in a litter. The first class contained ewes that had single litters (16 223 lactations). In the second class, some ewes had multiple litters – twin, triplet, or above (6 795 lactations). The lactation number was divided into three classes: first lactation (43.74% of lactations), second lactation (39.85% of lactations), and third and other lacta-

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tions (16.41% of lactations). The representation of the other lactations in the evaluated set was minimal. Therefore, they were assigned to the third lactation. Random effects were used to create an additive genetic effect of the individual required for linkage to the relationship matrix and a permanent environment effect due to the observation of multiple lactations in an individual.

The resulting dataset for estimating crossbreeding effects consisted of 23 018 lactations from 15 888 ewes. The frequency of lactations for the selected breeds and their crosses is shown in Table 1. The pedigree file was constructed by adding four generations of ancestors to the performance ewes. In total, 47 871 individuals were in the pedigree file.

Effects of crossbreeding

To evaluate the effects of crossbreeding on milk production, the following crossbreeding effects were created: effects of breed and heterosis effect. Two effects of the breed were created – Improved Wallachian and Tsigai – depending on the proportion of genes of a given breed in an individual.

Table 1. Frequency of lactations for the selected breeds and their crosses

Breed or crossbreed	Proportion of breed (%)			Frequency of lactations
	Tsigai (TS)	Improved Wallachian (IV)	Lacaune (LC)	
TS	100	0	0	8 491
IV	0	100	0	8 949
LC	0	0	100	2 332
TS × LC	87.5	0	12.5	67
	75	0	25	76
	62.5	0	37.5	219
	50	0	50	286
	37.5	0	62.5	329
	25	0	75	166
	12.5	0	87.5	65
IV × LC	0	87.5	12.5	77
	0	75	25	247
	0	62.5	37.5	360
	0	50	50	516
	0	37.5	62.5	457
	0	25	75	265
	0	12.5	87.5	116

For purebreds, the value was 0 or 100% (0% if the genes of the breed were not present in the individual, 100% if it was a purebred of the breed); for crossbreds, the value ranged from 0% to 100% (87.5%, 75%, 62.5%, ...), depending on the proportion of genes of the breed. The heterosis effect was determined as the degree of heterozygosity using the formula from Van der Werf and de Boer (1989):

$$\text{Heterozygosity} = Pd \times (1 - Ps) + Ps \times (1 - Pd) \qquad (1)$$

where:

Pd – proportion of the primary breed coming from the dam;

Ps – proportion of the primary breed coming from the sire.

The effect of breed and heterosis effect were entered into the model equation as regression coefficients.

Statistical models

SAS software v9.4 (SAS Institute, Inc., Cary, NC, USA) was used to adjust the database and determine the statistical significance of the fixed effects. The statistical significance of the model and fixed effects was tested using the GLM procedure. Statistically significant effects ($P < 0.05$) were included in the models. The effects of crossbreeding on milk production and fat and protein content were estimated using the restricted maximum likelihood method in REMLF90 (Misztal et al. 2014). Due to high correlations between milk production and milk components (Iniguez et al. 2009), estimates were determined for each trait using three univariate models, including the same fixed and random effects. The model equation for estimating crossbreeding effects was as follows:

$$y_{ijklmnopqr} = \mu + FYS_i + L_j + LS_k + LMP_l + I_m H_n + BT_o + BIV_p + ANI_q + PE_r + e_{ijklmnopqr} \qquad (2)$$

where:

$y_{ijklmnopqr}$ – value of dependent variable (milk production, fat and protein content);

μ – general value of dependent variable;

FYS_i – fixed effect of flock-year-season of lambing;

L_j – fixed effect of lactation number (j = 1, 2 and 3);

LS_k – fixed effect of litter size (k = 1 and 2);

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LMP_l – length of days in milk (100–250 days);
I_m – interval from lambing to the first measurement (5–95 days);
H_n – heterosis effect;
BT_o – effect of breed – Tsigai;
BIV_p – effect of breed – Improved Wallachian;
ANI_q – random direct animal effect;
PE_r – random permanent environmental effect;
$e_{ijklmnopqr}$ – random residual error.

RESULTS AND DISCUSSION

Descriptive statistics

The effect of crossbreeding was evaluated for the most important milk traits in Slovak sheep, which are considered milk yield, fat and protein production. Descriptive statistics of the evaluated traits, fixed effects, and crossbreeding effects are presented in Table 2. The average milk production was 122.39 kg. Rupp et al. (2003) reported that the average milk yield of French Lacaune ewes for the first lactation was 230 l. The lower value could be due to the higher representation of Tsigai and Improved Wallachian ewes, which have lower milk production than Lacaune ewes. However, a possible lower milk yield of the Lacaune breed bred in Slovakia is probably due to different feeding levels and insufficient adaptability to different management and environmental conditions that do not allow exceptional genetic potential (Oravcova et al. 2006). The average fat production was 8.64 kg, and the average protein yield was 7.02 kg. The average length of the days in milk was lower than the standardized period length (150 days) within the Slovak sheep breeding system (Oravcova et al. 2005). Its value was approximately 131.75 days. The first measurements were taken on average around Day 68.

Table 2. Descriptive statistics of evaluated traits and fixed effects

	Mean	SD	Min.	Max.
Evaluated traits				
Milk production (kg)	122.39	62.96	40.03	593.72
Fat content (kg)	8.64	4.03	1.72	42.60
Protein content (kg)	7.02	3.49	1.59	35.71
Fixed effects				
Lactation number	1.73	0.73	1	3
Days in milk	131.75	14.98	100	223
Litter size	1.30	0.46	1	2
Interval from lambing to the first measurement (days)	68.08	15.67	5	95

Fixed effects on milk yield

The results show that a higher lactation number increases milk production and milk components. The effects of lactation number and other factors on milk production and milk components are shown in Table 3. Compared to the first lactation, in the third and subsequent lactations, milk production increased per lactation by 6.44 kg, fat content increased by 0.44 kg, and protein content increased by 0.42 kg. Similar results were also reported by Oravcova et al. (2006) for the daily milk yield of ewes evaluated on the first three lactations. Lower milk yields were recorded for ewes in the first lactation than for ewes in the second. Lower milk yields were observed in ewes in the second lactation compared to ewes in the third. In contrast, Pollott and Gootwine (2004) reported the highest milk yield in the second lactation. Milk yield then declined as the ewes aged. The declining milk yield was partly due to the shortening of lactation length as ewes aged but was also due to the declining maximum secretory potential of ewes, which developed similarly to total milk yield. According to Kasap et al. (2019), ewes with multiple litters had higher lactation milk yield, fat and protein yield. During the milking phase of the lactation period, ewes with multiple litters produced higher milk yield (21 kg), fat (1.62 kg), and protein (1.15 kg). Many other authors have also reported higher milk production in multiple litters in their studies (Pollott and Gootwine 2004; Chay-Canul et al. 2019; Robles Jimenez et al. 2020). Extending days in milk by one day increased milk production by 1.02 kg, fat production by 0.07 kg, and protein production by 0.06 kg. Extending the interval from lambing to the first measurement by one day decreased milk production by 0.33 kg, fat production by 0.02 kg, and protein production by 0.01 kg.

Crossbreeding effects on milk yield

A positive effect of crossbreeding on milk yield has been demonstrated. In ewes with a 100% het-

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Table 3. Effect of fixed effects on milk yield

Fixed effects	Level	Milk production (kg)		Fat content (kg)		Protein content (kg)	
		solution	SE	solution	SE	solution	SE
Lactation number	2	5.31	0.461	0.35	0.032	0.33	0.026
Lactation number	3	6.44	0.712	0.44	0.050	0.42	0.040
Litter size	2	3.76	0.484	0.23	0.034	0.23	0.028
Days in milk	–	1.02	0.031	0.07	0.002	0.06	0.002
Interval from lambing to the first measurement (days)	–	–0.33	0.024	–0.02	0.002	–0.01	0.001

erosis effect (ewes from purebred parents of different breeds), the heterosis effect increased milk production by 11.642 kg, fat production by 0.772 kg, and protein production by 0.565 kg (Table 4). A greater influence of the heterosis effect was reported by Gootwine and Goot (1996), who evaluated this effect on total milk production per lactation in crossbred Awassi and East Friesian sheep bred in Israel. F1 ewes, due to the heterosis effect, produced 47 ± 7 l more milk than purebred ewes. Murphy et al. (2017) estimated intergenic and nonadditive gene effects on milk yield in crosses of Tarhee, Dorset, Finnish, and Romanov ewes with East Friesian and Lacaune rams bred in North America. For recalculated milk production, fat and protein content at 180 days, the effect of heterosis in F1 ewes was 41.7 kg, 2.6 kg, and 1.98 kg, respectively. A positive heterosis effect was also demonstrated in crossbred Syrian and Turkish Awassi sheep reared in Syria. The effect of direct heterosis on milk production was 18.28 l. Fat production increased by 1.22 kg, and protein production increased by 4.30 kg. Crossing these sheep resulted in desirable and statistically significant effects on milk production and reproduction (Haile et al. 2019). The heterosis effect was only evaluated within a single flock for all of the above studies.

Estimates of the effects of the Tsigai and Improved Wallachian breeds show the positive effect of crossbreeding these breeds with the Lacaune breed. The effect of the Tsigaia and Improved Wallachian breeds reduced milk production by 21.987 kg and 38.58 kg, respectively, compared to that in the Lacaune breed. In the case of F1 crosses, half the value is passed on from the parent. There was a negative effect of both breed effects on fat and protein content. The effect of the Tsigai breed reduced fat production by 1.56 kg and protein production by 1.34 kg. The effect of the Improved Wallachian breed reduced fat production by 2.71 kg and protein production by 2.27 kg. Although it has been proven that Tsigai and Improved Wallachian ewes have a higher percentage of fat and protein content (Macuhova et al. 2017), Lacaune ewes have higher milk production (Oravcova et al. 2006; Macuhova et al. 2008; Tancin et al. 2011; Ferro et al. 2017). The negative breed effect only illustrates that using a high-yielding Lacaune breed increases milk, fat and protein production. In studies by Oravcova et al. (2018), lower milk yields were shown for Tsigai and Improved Wallachian ewes not only compared to Lacaune ewes but also to crossbred ewes coming from "Tsigai × Lacaune" and "Improved Wallachian × Lacaune" parents. The effect of genotype (Tsigai, Improved Wallachian, and Lacaune) on milk production was also reported in a study by Tancin et al. (2011).

CONCLUSION

Crossbreeding effects were estimated using single-trait models for milk production, fat and

Table 4. Effects of crossbreeding on milk yield

Effects of crossbreeding	Milk production (kg)		Fat content (kg)		Protein content (kg)	
	estimations	SE	estimations	SE	estimations	SE
Direct heterosis effect	11.64	3.126	0.77	0.217	0.57	0.175
Breed additive effects – Tsigai	–21.98	5.622	–1.56	0.386	–1.34	0.314
Breed additive effects – Improved Wallachian	–38.58	6.590	–2.71	0.451	–2.27	0.368

protein content. The results of this study showed that the role of crossbreeding effects in increasing milk yield is important. Although the direct breed effects of Tsigai and Improved Wallachian were negative for all traits evaluated, this indicates the positive use of the Lacaune breed to increase milk yield. A positive heterosis effect has been demonstrated. Therefore, breeders should cross local breeds adapted to the local production area with high-yielding breeds to increase milk yield. The study also showed how fixed effects such as lactation number and litter size affect milk yield.

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Conflict of interest

The authors declare no conflict of interest.

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