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Inheritance of the birth weights in crosses between Istrian, Awassi, East-Friesian and Travnik Pramenka sheep in Croatia: a case study

Nasljeđivanje porodne mase kod križanaca istarske ovce, Awassi, istočnofrizijske ovce i travničke pramenke u Hrvatskoj: studija sa jedne farme

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ABSTRACT

The purpose of the study was to estimate the influence of the additive and non-additive genetic effects on the birth weight, using two different crossbreed models. Data on 1176 birth weights were collected. The animals were crosses, with different ratios of Awassi, East-Friesian, Istrian, and Travnik Pramenka sheep breed. The focal breed in this study was Istrian, which is an autochthonous breed in Croatia. In both models mixed procedure was used with random effect of sire and fixed effects of sex, year and month of birth, litter size, and direct inbreeding. The first model contained the additive breed effects, while the second model additionally included non-additive effects of heterosis and recombination loss. Sex, litter size, year and month of birth significantly affected birth weight in both models. Effect of direct inbreeding was negative and significant only in second model. Significant positive additive breed effect was estimated for Awassi breed in both models. The East-Friesian additive breed effect was positive in both models, but it was significant for the first one only. The positive and significant heterosis effect for the birth weight was estimated for the crosses between East-Friesian and Travnik Pramenka, as well as between Travnik Pramenka and Istrian breed. Same crosses showed significant and positive effect of recombination loss. The negative effect of recombination loss was estimated for the crosses of Awassi breed.

Keywords: crossbreeding effects, birth weight, sheep, inbreeding, heterosis

SAŽETAK

Cilj rada je bila procjena utjecaja genetskih efekata na porodnu masu koristeći dva različita modela. Prikupljeni su podaci o 1176 porodnih masa janjadi sa jedne farme. Životinje su bile križanci, različitog pasminskog omjera Awassi ovce, istočnofrizijske ovce, istarske ovce i travničke pramenke. Oba modela su bila bazirana na mješovitom modelu sa slučajnim efektom ovna te fiksnim efektima spola, godine rođenja, mjeseca rođenja, veličine legla i uzgoja u srodstvu jedinke. Prvi model bio je aditivni model koji uz navedene slučajne i fiksne efekte sadrži i aditivni efekt pasmine. Drugi model uz sve navedeno u prvom modelu sadrži i neaditivne efekte heterozisa i rekombinacijskog gubitka. Rezultati su pokazali da spol, veličina legla, godina i mjesec rođenja značajno utječu na porodnu masu u oba modela. Utjecaj uzgoja u srodstvu jedinke bio je negativan i značajan samo u drugom modelu. Značajan i pozitivan aditivni efekt pasmine dobiven je za Awassi pasminu u oba modela. Aditivni efekt istočnofrizijske pasmine pokazao je pozitivan utjecaj u oba modela, ali samo je u prvom bio značajan. Pozitivan i značajan utjecaj heterozisa pokazali su križanci istočnofrizijske ovce i travničke pramenke, te križanci travničke pramenke i istarske ovce. Isti križanci pokazali su značajan i pozitivan efekt rekombinacijskog gubitka. Negativan utjecaj rekombinacijskog efekta su pokazali križanci Awassi ovce.

Ključne riječi: utjecaj križanja, porodna masa, uzgoj u srodstvu, heterozis

INTRODUCTION

In the Mediterranean part of Croatia, as in the other Mediterranean regions, sheep breeding is traditional activity and foundation of the livestock production. The sheep breeding in those regions is usually described as a low-input and extensive with dual-purpose production goals (milk and meat). With the continuous growth of the tourism, market demand for specific sheep products increased and the economical precondition for further development of sheep breeding was established. Birth weight is economically important trait connected with both neonatal and adult survival and health. There is an optimal range for the birth weight, as lambs with extremely low birth weight have increased mortality while the heavier extremes can exhibit dystocia (Alexander, 1974). It was found that increasing the birth weight of lighter lambs and reducing the variation in birth weight increases overall lamb survival in a study on twins (Morel et al., 2009). The most importantly, lambs with higher birth weights have greater average daily gain (Greenwood et al., 1998), reach slaughter weights sooner, and therefore can be on the market earlier (Thomson et al., 2004). Crossbreeding is considered to be fast, efficient, and cost-effective breeding method for increasing the production by mating animals from different breeds, that relies mainly on exploiting the heterosis or hybrid vigor and breed complementarity (Leymaster, 2002). Heterosis effect is opposite of the inbreeding depression, and it is manifesting when a crossbred animal outperforms the average of the parental purebreds. In practical terms for the farmer, desirable outcome of crossbreeding should be higher performance of the crossbreed animal relative to the locally adapted purebred animal. Drawbacks of these systems are heterosis retention in the future generations and recombination loss. Therefore, the long-term strategies should be developed to maintain the positive effects of crossbreeding. With the lack of the official crossbreeding systems that would follow up sheep breeding development, farmers have begun with their own breeding schemes. Their aim was to mate locally adapted autochthonous sheep (Istrian) with highly productive imported breeds, such as Awassi, East-Friesian, and Sarda sheep. Similar crossbreeding systems were utilized in the other Mediterranean regions (Boyazoglu et al., 1979, Sanna et al., 2001, Ugarte et al., 2001). Choice of the breeds that will result in the best performing crossbred and at the same time be suitable for production in the given environment is crucial, and therefore it would be desirable if the farmer could be supplied with the optimal crossbreeding scheme. The objective of this study was to estimate and evaluate the genetic effects influencing birth weight in crosses between Istrian, Awassi, East-Friesian, and Travnik Pramenka sheep, and to possibly ease the farmers decision on which crosses to utilize to increase the birth weight. Our goal is to use this research as a case study which will increase the farmers interest in planned crossbreeding systems, and more importantly, to provide a basis for more extensive project in the future.

MATERIAL AND METHODS

Data

Data on 1176 birth weights, spanning over 12 years (2000 - 2011), were collected from the family farm Radosevic in Brtonigla (Istria region of Croatia). Animals were crosses, with different ratios of Awassi (A), East-Friesian (F), Istrian (I), and Travnik Pramenka (P) breed. Lambs were of almost perfectly equal sex ratio, with 596 females and 580 males. More than 90% of the lambs (1072) were born in first three months of the year, with February being the dominant month with almost 60% (681) of the births. Most of the lambs were twins (659), there were 430 singles, and 87 triplets. All the examined lambs had the information on recent ancestors (28 sires, 284 dams, and 29 maternal grandsires). However, the sires overlapped across the generations, which means that 23 of the registered grandsires also sired the lambs under consideration. Breed proportions for each lamb were calculated from information about sire and dam breed proportions. Only 75% of breed proportion for every animal could be assessed (50% from sire and 25% from dam, i.e. dam's sire). We supposed that contribution coming from the maternal grandmothers is equal for all breeds. Breed composition of all the 28 rams that were used as the sires, together with the number of records and the mean birth weight of their progeny is presented in Table 1. Furthermore, we included in the Appendix distribution of records and mean birth weights by all the breed groups we could find among our 1176 lambs.

Statistical analyses

Two different genetic models were used to estimate genetic effects that influence birth weight of crosses. Similar methodology was used by Hirooka et al. (1998). Dickerson's model (1969, 1973) was used for calculation of crossbreeding parameters as defined by Wolf et al. (1995). First model (Model M1) was an additive breed model in which additive breed effects (a) were expressed as deviation from Istrian (I) breed:

$$y_{klmnop} = \mu + VL_k + GR_l + MR_m + SEX_n + F_o + \alpha_A a_A + \alpha_F a_F + \alpha_P a_P + sire_p + e_{klmnop} \quad \text{(M1)}$$

where y is the birth weight, μ is the overall mean, VL is the class fixed effect of litter size k (k = 1 to 3), GR is the class fixed effect of birth year l (l = 2000 to 2011), MR is the class fixed effect of month of birth m (m = November, December, January, February, March, April, May, and June), SEX is the class fixed effect of sex n (n = female or male), F is the class fixed effect of direct inbreeding o (o = 0, 0.0078, 0.0156, 0.0469, 0.1250, 0.1875, 0.1953, and 0.25). Coefficient of additive breed effect (αi) is gene proportion of breed i (i = I, A, F, and P)

Table 1. Breed composition (%) of 28 rams used as the sires

Breed composition (%)				Number of sires	Number of lambs sired	Mean birth weight of lambs sired (kg)
Awassi	Istrian	East-Friesian	Travnik Pramenka			
40	0	30	30	1	4	5.18
37.5	12.5	50	0	2	15	5.07
0	70	30	0	1	3	4.87
20	40	40	0	1	29	4.72
75	25	0	0	2	18	4.58
0	100	0	0	4	175	4.46
0	0	100	0	7	428	4.45
25	25	50	0	3	102	4.40
18.75	6.25	75	0	2	243	4.40
0	40	0	60	1	78	4.38
0	30	70	0	1	29	4.37
0	0	70	30	1	18	4.29
20	50	0	30	1	9	4.21
50	25	25	0	1	25	4.18
			Total:	**28**	**1176**	

in animal, $\alpha_i = ½ (\alpha_i^S + \alpha_i^D)$, where S stands for sire and D for dam gene proportion. Since in our case study breed composition of maternal grandmother (dam's dam) was unknown, formula for coefficient of additive breed effect becomes $\alpha_i = ½ (\alpha_i^S + ½\alpha_i^D)$. Those coefficients are fitted into the model as covariates (linear regressions), and a are additive breed effects for Awassi (a_A), East-Friesian (a_F) and Travnik Pramenka (a_P). Sire is the random effect of sire p (p = 1 to 28) distributed as sire ~ N(0,Iσ^2_{sire}), and e is random residual distributed as e ~ N(0,Iσ_e^2). The second model (Model M2), in addition, contained heterosis and recombination loss effects:

$$y_{klmnop} = \mu + VL_k + GR_l + MR_m + SEX_n + F_o + \alpha_A a_A + \alpha_F a_F + \alpha_P a_P + \delta_{FA} h_{FA} + \delta_{FI} h_{FI} + \delta_{FP} h_{FP} + \delta_{AI} h_{AI} + \delta_{AP} h_{AP} + \delta_{PI} h_{PI} + \varepsilon_{FA} r_{FA} + \varepsilon_{FI} r_{FI} + \varepsilon_{FP} r_{FP} + \varepsilon_{AI} r_{AI} + \varepsilon_{AP} r_{AP} + \varepsilon_{PI} r_{PI} + sire_p + e_{klmnop} \quad (M2)$$

where h and r are heterosis and recombination loss effects between combination of breeds, respectively, and δ and ε are their coefficients, respectively. Coefficients of heterosis (δ) and recombination loss effects (ε) are calculated by formulas; $\delta_{ij} = \alpha_i^S \alpha_j^D + \alpha_j^S \alpha_i^D$ (for i ≠ j) and $\varepsilon_{ij} = 4\alpha_i\alpha_j - \delta_{ij}$, respectively. As in the M1, those are fitted as covariates (linear regressions) in the model.

The statistical analyses of the models were performed using the MIXED (REML) procedure of SAS (SAS Institute Inc., 2008). Coefficients of direct inbreeding were calculated using the INBREED procedure of SAS.

RESULTS

The estimates of additive breed effects (expressed as deviation from the Istrian breed), heterosis and recombination loss for birth weight trait are presented in Table 2.

Table 2. Estimates of crossbreeding effects for the birth weight (kg) using different genetic models

	Model (M1)	Model (M2)
Effect[a]	EV (SE)[b]	EV (SE)[b]
a_A	2.50 (0.55) ***	4.51 (1.33) ***
a_F	0.75 (0.32) *	0.01 (0.33)
a_P	0.39 (0.54)	-5.77 (2.35) *
h_{FA}	-	-1.25 (0.69)
h_{FI}	-	-0.07 (0.49)
h_{FP}	-	2.84 (1.30) *
h_{AI}	-	-5.35 (1.66) **
h_{AP}	-	2.37 (1.32)
h_{PI}	-	3.79 (1.72) *
r_{FA}	-	-2.45 (1.12) *
r_{FI}	-	0.31 (0.94)
r_{FP}	-	4.56 (2.14) *
r_{AI}	-	-10.18 (2.84) ***
r_{AP}	-	2.97 (2.46)
r_{PI}	-	6.99 (2.69) **

[a] a = additive breed effects as deviation from Istrian breed, h = heterosis effect, r = effect of recombination loss,
[b] EV = estimated value, SE = standard error, *** = P<0.001, ** = P<0.01, * = P<0.05

In the additive model (M1), all three breeds (A, F, and P) had positive effect on birth weight, but only Awassi and East-Friesian had significant effect. These estimates can be interpreted as the effect of the breed proportion (%) of Awassi, East-Friesian, and Travnik Pramenka relative to a purebred Istrian. Therefore, the significant effect of breed on birth weight for Awassi and East-Friesian, equaled to increase of 2.50 (0.55) and 0.75 (0.32) kg compared to purebred Istrian. Sire effect accounted for about 13% of the total variance in the model. In the second model (M2) Awassi and East-Friesian had positive, and Travnik Pramenka negative additive effect on birth weight, while it was significant for Awassi and Travnik Pramenka only. Direct interpretation of magnitude of the estimates from M2 is not straightforward, due to possible confounding between additive and non-additive effects and data limitations in our study, as we explain in the discussion section. However, those estimates can still be useful for informing about the relative impact of various breed combinations on birth weight of crossbreed lambs, and to generate interest for systematic crossbreeding programs. Significant positive and favorable heterosis effects were estimated for combinations of East-Friesian and Travnik Pramenka breeds, as well as between Travnik Pramenka and Istrian breeds. Significant and unfavorable heterosis effect was estimated for combination of Awassi and Istrian breed. Crosses FxP and PxI had significant positive effect of recombination loss, while FxA and AxI had significant negative effect of recombination loss.

Average birth weight in our case study was 4.44 kg (SD = 0.86), highest recorded birth weight was 7.60 kg, and the lowest was 1.50 kg. Average birth weight (number of records) for singles was 4.99 kg (430), for twins was 4.20 kg (659), and for the triplets was 3.55 kg (87). Males (580) were born on average with 4.62 kg and females (596) with 4.27 kg. The estimated values of the direct inbreeding effects were mainly negative and significant only for the second model ($P < 0.05$). Based on our case study data, most animals (1023) showed no inbreeding, while only 153 showed certain degree of the inbreeding. From those exhibiting the inbreeding, most of animals (76) had $f = 0.125$, further 67 animals had $f = 0.25$, while all the other levels had 10 animals altogether (not reported). When accounting for the inbreeding, average birth weight (number of records) for singles with $f = 0$ was 5.02 kg (362), with $f = 0.125$ was 4.99 kg (21), and with $f = 0.25$ was 4.87 kg (43). For the twins, average birth weight (number of records) with $f = 0$ was 4.20 kg (583), with $f = 0.125$ was 4.28 kg (46), and with $f = 0.25$ was 4.10 kg (24). Same averages for the triplets were 3.52 kg (78) with $f = 0$, and 3.83 (9) with $f = 0.125$. We have to point out, that due to the small number of animals that showed inbreeding, and especially due to the limited pedigree information coming from single case study farm, these findings must be taken with caution and the real impact of direct inbreeding might be different.

DISCUSSION

Awassi had the highest positive breed effect on birth weight in both models. Because additive breed effects are shown as deviation from the Istrian breed, we could conclude that Awassi and East-Friesian breeds are superior to Istrian breed for the birth weight. Based on our estimates for the additive breed effects, the breed differences between Awassi and Istrian were larger than those between East-Friesian and Istrian. To the best of our knowledge, there were no studies analyzing birth weight performance of crossbreed Istrian animals. Therefore, in the following discussion, we provide examples from similar analyses, that were not based on the Istrian breed itself. Mavrogenis (1981) showed that from all the purebred sheep included in his study, Awassi breed produced lambs with the highest birth weight with estimate of 4.12 (0.06) kg. In the same study, F1 crosses between East-Friesian and Chios breed produced lambs with estimated birth weight of 4.47 (0.06) kg and F1 crosses between Awassi and Chios of 4.19 (0.08) kg. In Mavrogenis (1981), East-Friesian breed contributed more to increasing the birth weight of crosses with Chios than the Awassi breed, while in this work Awassi contributed more than East-Friesian in raising birth weight of crosses with Istrian breed. Boyazoglu (1979) showed that crosses with 75% East-Friesian breed and 25 % Sarda breed had higher birth weights than crosses with less percent of East-Friesian breed. Positive effect of East-Friesian breed on birth weight of crosses with Sarda breed was also shown in work by Sanna et al. (2001). Positive heterosis effect for birth weight is recorded for crosses between Awassi and Chios breeds, and was 5% (Mavrogenis, 1981). Due to the lack of phenotypic averages of the parental purebreds, we could not express the heterosis as percentage relative to them. In our work we did not detect positive (favourable) heterosis for crosses with Awassi breed. Exceptions were crosses between Awassi and Travnik Pramenka breed, which were favorable but non-significant. Similar findings of negative and non-significant effect of heterosis for crosses of Booroola merino and Assaf breed were reported by Gootwine et al. (1993). Mugambi et al. (2007) stated that low estimated values of heterosis effect for birth weight could be due to loss of co-adaptive gene combinations in crosses between divergent breeds or due to the environmental conditions in which animals were held. Cunningham (1981) stated that production in better environment is more influenced by the additive breed effects while the production in poor environment by heterosis effects. Effect of recombination loss tells us whether the crossbreeds have efficiently utilized heterosis and additive breed effects. Dickerson (1969, 1973) stated that recombination loss is due to the breakup of favorable epistatic effects during meiosis in parental population. Thus, if parents are crosses, as they are largely in our study, favorable epistatic effects which existed in purebred animals broken up and recombination loss occurred. In our study, significant negative values of recombination loss in crosses AxI and FxA, may denote that some favorable epistatic combinations that were present in original Awassi population were lost. Therefore, the negative estimates for the heterosis and recombination loss in our study are indicating that crossing Awassi and Istrian breeds might have unfavorable impact on the birth weight, but the magnitude could not be assessed due to the lack of records for purebred Awassi animals or actual F1 crosses between them. The Awassi breed in original production environment had developed specific epistasis of co-adaptive genes, especially for fitness and adaptation traits, due to long-term natural selection (Koch et al., 1985). Loss of such positive combinations in parental populations during recombination could be cause of negative heterosis effect of Awassi breed on the birth weight. Mugambi et al. (2007) offered similar explanation in their work on Kenya Dual Purpose Goat composites. This shows importance of inclusion of the non-additive effects in crossbred evaluations, as animals can show high additive value, but that positive additive value can be completely overrun by the negative non-additive effect values. Nevertheless, this is usually overlooked in typical animal breeding plans due to the small percentage of variance explained by those effects, lack of the large datasets to estimate them, and the lack of proper statistical modeling, especially in the era of genomics (Varona et al., 2018).

Due to the limited size of this case study data, our second model (M2) is most likely overparameterized, and therefore we would advise use of simpler model (M1) in similar circumstances. Our study's negative side were large standard errors and low significance for some of the effects, which introduces uncertainty in the interpretation of results of the second model (M2). Aforesaid is most prominently result of limited data in our study, but an estimation of non-additive effects was proven difficult even with larger datasets, and estimates could also be confounded with the additive effects (Hill, 2010; Lee et al. 2010; Varona et al., 2018). Estimated values of crossbreeding effects for birth weight were mainly statistically non-significant in Gootwine et al. (1993). Additionally, this is a field data from a single farm, unbalanced in the terms of number of animals for each breed composition group, and with many animals that are three-breed crosses from both paternal and maternal side. In ideal situation, phenotypic records for the purebred performances should be available to estimate the extra gain the farmer could expect from using the crossbreed animal compared to the each of the parental purebreds. In this study purebred performances for given environment were limited (21 purebred Istrian and 123 purebred East-Friesian records), especially as we could not infer 100 % of the breed composition of dams. Lack of purebred records was reported as potential source of underestimation of the crossbreeding effects in the study on Indian crossbreed sheep (Malik and Singh, 2006). Therefore, future studies that will include the data from more farms and herds are needed to fully grasp the crossbreed effects and provide reasonable guidelines for all the farmers. Furthermore, with the arrival of new data, we could compare additional crossbreed models (e.g., Hill, 1982; Kinghorn, 1982). The Istrian breed is under the national evaluation in Croatia for dairy traits (e.g., Kasap et al., 2019), and as such is likely candidate to be genotyped in agreement with the current trends to shift from the traditional (BLUP) to genomic selection. Availability of such genomic data will open the door for many supporting analyses that will have the power to improve crossbreed studies like this one, especially with proper breed and parentage assignment, genetic structure and admixture analyses, and most importantly missing pedigree reconstruction.

Alsheikh (2005) showed that there is a linear relationship between the direct inbreeding and the birth weight. Same study showed that every increase of direct inbreeding by 0.01 lowers the birth weight for 6 g. While we observed slight inbreeding depression, unbalanced data prohibits us from being conclusive and from establishing a proper relationship between the inbreeding and decrease of the birth weight in crossbred lambs. Significant negative effect of direct inbreeding on the birth weight was confirmed in a study by Ceyhan et al. (2011). Similar findings that indicate negative effect of inbreeding on birth weight and other traits in various sheep breeds were shown in Rzewuska et al. (2005), Pedrosa et al. (2010), and Drobnik & Martyniuk (2016). Since the effect of inbreeding was found to have negative effect on the birth weight across the studies and the breeds, planned mating should be proposed to the farmers to keep the inbreeding at the optimal level.

CONCLUSIONS

Birth weight is variable trait influenced by many genetic effects. Positive additive breed effects that were detected for the Awassi and East-Friesian sheep indicate their superiority compared to the Istrian breed in the terms of birth weights. The significant positive heterosis effect for birth weight was estimated for crosses between East-Friesian and Travnik Pramenka, as well as Travnik Pramenka and Istrian breed. The negative effect of the recombination loss of crosses with Awassi could be due to the loss of favorable epistatic combinations of adaptation genes. The crossbreed model that included non-additive effects of heterosis and recombination loss might not be of superior fit compared to the simple additive model. Therefore, the results of such a model should be interpreted with caution, especially in situations of limited data like in our study. Crossbreeding between locally adapted and the imported breeds can be used to increase birth weight of crossbreed lambs, but to provide the best recommendations for the farmers, long-term strategies should be developed, and analyses should be extended on more herds across the region. In general, farmers should consider planned breeding schemes that will utilize the best combination of the breeds for their specific production system, herd structure and environment, so they could maximize the heterosis and at the same time control the level of the inbreeding.

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Appendix

Distribution of records and mean birth weights by breed groups

Breed group[a] (sire x dam)[b]	Number of records	Mean birth weight (kg)	SD[c]
AFP x AIF	2	5.35	0.21
AFP x F	2	5.00	0.14
AIF x AI	118	4.69	0.87
AIF x AIF	151	4.32	0.91
AIF x AIP	4	3.95	0.24
AIF x AP	13	4.67	1.08
AIF x F	128	4.31	0.80
AIP x AIF	4	3.80	0.14
AIP x AIP	2	4.40	0.57
AIP x F	3	4.63	0.38
AI x AI	15	4.69	0.46
AAI x AIF	3	4.00	0.96
FP x AIF	1	4.70	-
FP x F	6	4.5	0.13
FP x I	1	4.9	-
FP x IP	10	4.07	0.28
F x AFP	3	4.17	0.64
F x AI	74	4.68	0.78
F x AIF	166	4.55	0.98
F x AIP	12	4.36	0.58
F x AP	9	5.29	0.69
F x F	123	4.21	0.89
F x I	1	3.00	-
F x IF	1	6.60	-
F x IP	39	4.25	0.82
IF x AIF	8	4.03	0.51
IF x AIP	2	4.40	0.14
IF x F	10	4.91	0.94
IF x IP	12	4.23	0.41
IP x AI	9	4.97	0.80

Continued

Breed group[a] (sire x dam)[b]	Number of records	Mean birth weight (kg)	SD[c]
IP x AIF	29	4.44	1.26
IP x F	31	4.19	0.85
IP x IP	9	4.20	0.89
I x AFP	1	5.30	-
I x AIF	13	4.53	0.72
I x AIP	8	4.66	0.63
I x F	72	4.34	0.59
I x I	21	5.09	0.72
I x IP	60	4.32	0.62
Total	1176		

[a] Breed composition was defined based on the sire (50 %) and the maternal grandsire (25 %) of the animal; dam's dam breed composition was unknown

[b] Differences between the sire and dam's sire breed were considered; A = Awassi, F = East-Friesian, I = Istrian , P = Travnik Pramenka

[c] SD = standard deviation