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Conventional and Mixed Model Approach to Estimate Heterosis of the Growth Traits in Boer Goat's Crossbred Offspring Populations

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Abstract

Heterosis is often utilized as a success indicator in a crossbreeding program. It is defined as the deviation of the crossbred means relative to their parental breeds. Heterosis mechanism is highly dependent on the genetic factors and thus, we incorporated genetic information in its estimation. The objective of this article was to compare heterosis estimated with conventional and mixed model approaches. In total, phenotypes of 3804 individuals were recorded. Data were obtained from a crossbreeding experiment involving Boer bucks and Jawarandu does. Observed traits were birth weight, weaning weight and average daily gain. Conventional and mixed model methods were used to estimate the heterosis. The heterosis values (%) between B×B vs B×J, estimated with conventional method were -11.38, -10.51 and -10.39; with mixed model were -6.23, -9.27 and -9.68 for BW, WW and ADG respectively. Heterosis values in B×(B×J) relative to B×B, estimated with conventional method were -6.16, -10.35 and -11.69; whereas with mixed model were -8.01, -10.82 and -9.14 for BW, WW and ADG respectively. Conventional method tends to underestimate the means phenotype with lower standard errors compared to mixed model analysis results in all traits. Conventional method also introduces biased heterosis estimates compared to the mixed model. Conventional method ignores any potential effects in the estimation procedures; whereas mixed model approach incorporates all the systematic and random effect including family relationship information. Thus, mixed model produced more reliable results in genetic parameters estimation. We recommend employing mixed model analysis in estimating heterosis.

Keywords: Boer goat, crossbreeding, genetic parameters, heterosis, Jawarandu goat, mixed model

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INTRODUCTION

In a country like Indonesia, where the livestock genetic diversity is abundant (Sutarno and Setyawan, 2015) but the local species' were lacking in production aspects, attempts to optimize the available resources are necessary (Hiemstra et al., 2006; Oldenbroek, 2007). Among the programs implied by the government, crossbreeding program is currently proven to be the most promising (Widi, 2015; Agus and Widi, 2018). Crossbreeding system is widely implemented to obtain commercial stocks; where the breeder choose the desired breeds and individuals within breed through selection procedures (Bourdon, 2014). Considerations in selecting the breeds depend on the traits in breeding goal. Local breeds were mostly used as the dams for their reproductive and adaptability traits whereas exotic breeds were chosen as the male genetic resources for their productive performance.

The adoption of crossbreeding program means to introduce new genetic resources and their respective interactions which will affect

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livestock's productivity (Wodzicka-Tomaszewska et al., 1993). Crossbreeding is able to improve livestock's productivity by utilizing the heterosis feature through the increase in heterozygosity (Hartl and Clark, 1997) which in turn, introduce new variation to the gene pool (Crow, 2001). Heterosis as a parameter contained information about the merit of the crossbred when compared to their respective purebred parent(s) and frequently utilized to assess a crossbreeding program.

Genetically, the effect of crossbreeding can be differentiated into additive and non-additive manners. The genetic basis of heterosis is very complicated; but researchers hypothesized that it is highly related with non-additive genetic effects such as dominance and epistasis which affect the interactions between alleles and/or genes (Crow, 2001; Williams et al., 2007). The effect of heterosis, however, depends on the genetic constitutions of the traits of interest. This fact is related to the number of loci involved in a trait and the differences of the allele frequencies of each locus with respect to the two parental populations.

Heterosis is normally estimated as the deviance of the crossbred relative to the purebred group (Bourdon, 2014). Since heterosis is highly genetics, the inclusion of genetic information in estimating heterosis is considered a proper thing. Komender and Hoeschele (1989) recommended mixed model analysis to be employed in the estimation of crossbreeding parameters including heterosis. In mixed model analysis all systematic and random effects were incorporated to give the estimated values. This model can also take into account the pedigree information through additive genetic relationship matrix (Henderson, 1984; Falconer and Mackay, 1996; Lynch and Walsh, 1998; Bourdon, 2014).

Currently, crossbreeding programs involving Boer and local goats are common in Indonesia. Boer goat is a meat-type African-origin goat with high growth rate and adaptable to tropical environment (Casey and van Niekerk, 1988). Whereas Jawarandu is an Indonesian local breed which is the descendant of Etawah and Kacang goats (Pandjono et al. 2014). This breed is known to be robust to humid-tropical environment and highly prolific (Wodzicka-Tomaszewska et al., 1993). The crossbreeding product between Boer bucks and Jawarandu does is potential as an improved meat-type goat breed. This research aimed to estimate and analyse the heterosis values through conventional and mixed model approaches in Boer goats pure and crossbred populations. The traits of interest in this study inclusive birth weight, weaning weight and average daily gain (ADG) traits.

MATERIALS AND METHOD

Data collection

Data was obtained from CV. Kambing Burja farm, Malang district, East Java, Indonesia. The records comprised of 3804 individuals with phenotypes and 4744 individuals in the pedigree. The individuals with phenotype records were born between 2012 to 2015. Three different populations involved: B×B (offspring of Boer bucks and Boer does, 461 records); B×J (offspring of Boer bucks and Jawarandu does, 2164 record) and B×(B×J) which is the offspring of Boer bucks and B×J does (1179 records). There were three types of litter size observed (1, 2 or 3 offspring per litter). The study populations were the descendants of 26 service bucks and 1288 does. Phenotype data of birth weight (BW), weaning weight adjusted for 77 days (WW) according to the farm's management practice and average daily gain until wean (ADG) were collected.

Heterosis estimation

The heterosis values were estimated with two different methods which were the conservative and mixed model. In the conventional approach, heterosis value was simply the differences between the means of phenotypes between pure and crossbred presented in both absolute value and relative to the purebred mean (percentage).

$$H \quad = \bar{P}_c - \bar{P}_p$$

$$H\% = \frac{(\bar{P}_c - \bar{P}_p)}{\bar{P}_p} \times 100\%$$

where $\boldsymbol{H}$ was the absolute heterosis value and $\boldsymbol{H}\%$ was the relative heterosis value presented in percentage relative to the purebred phenotype means. Further, $\overline{\boldsymbol{P}_c}$ was the mean phenotype value of crossbred individuals whereas $\overline{\boldsymbol{P}_p}$ was the mean phenotype of the purebred.

The second heterosis estimation was performed with mixed model approach considering that this model is recommended to estimate genetic parameters inclusive the pedigree relationship information. The model we built was as followed:

$$\boldsymbol{Y} = \boldsymbol{Xb} + \boldsymbol{Z_1 s} + \boldsymbol{Z_2 d} + \boldsymbol{Z_3 u} + \boldsymbol{e}$$

where **Y** is a vector of observed variables (BW, WW, ADG), **b** is a vector of fixed effects including sex, birth year, litter size and breed with **X** is the design matrix corresponded to the fixed effects. There were three random effects in the model: **s** is a vector of random service bucks, **d** is random doe effect whilst **u** is random additive genetic effect where **u** ~N(μ, $A\sigma_u^2$) with Z_1, Z_2 and Z_3 were their respective incidence matrices (Wright, 1922; Henderson, 1984; Quaas, 2012). A vector of random residual is represented as **e** ~N(0, $I\sigma_e^2$). The mixed model equations were solved with *Restricted Maximum Likelihood* (REML) methods (Kaps and Lamberson, 2004; Ott and Longnecker, 2010; Harville, 2012) using breedR package (Munoz and Sanchez, 2018) in R programming language (R Core Team, 2015). We later derived $\widehat{P_p}$ and $\widehat{P_c}$ as the conditional means from REML solutions. Heterosis estimation employing mixed model approach was then formulated as:

$$H = \widehat{P_c} - \widehat{P_p}$$

$$H\% = \frac{(\widehat{P_c} - \widehat{P_p})}{\widehat{P_p}} \times 100\%$$

RESULTS AND DISCUSSION

Purebred (B×B) performed best compared to the two crosses in all three observed traits. However, the rank order between the two crossbreds differed between the conventional and mixed model estimates (Table 1).

Table 1. Descriptive statistics of observed traits

Traits	Breed	N*	Mean±se**(Kg)	
			Conventional	Mixed model
Birth weight	B×B	461	3.20±0.03	3.69±0.06
	B×J	2164	2.84±0.01	3.46±0.05
	B×(B×J)	1179	3.00±0.02	3.38±0.06
Weaning weight	B×B	461	15.08±0.17	18.01±0.26
	B×J	2164	13.49±0.08	16.34±0.21
	B×(B×J)	1179	13.52±0.12	16.06±0.21
Average daily gain	B×B	461	0.15±0.002	0.19±0.03
	B×J	2164	0.14±0.001	0.17±0.02
	B×(B×J)	1179	0.14±0.002	0.17±0.03

Note: * Number of observations; ** standard error of the means

Data on Boer goat BW was around 3.20±0.03 - 3.69±0.06 in our study which is in agreement with previous information of 3.2±0.13 (Browning and Leite-Browning, 2011), 3.5±0.48 (Schoeman et al., 1997) and 3.6±0.54 kg (Zhang et al., 2008). BW of crossbred offspring (B×J) were 2.84±0.01 - 3.46±0.05; whereas between Boer × Spanish goat, BW were reported to be 2.79±0.05 (Rhone et al., 2013), 3.38±0.13 kg and 3.34±0.13 kg for crossbred kids between Boer and Kiko (Browning and Leite-Browning, 2011). Our results on Boer goats' WW were 15.08±0.17 - 18.01±0.26 kg and from previous studies were 13.50±0.62 (Browning and Leite-Browning, 2011) and varied between 13.0±0.14 to 16.5±0.23 kg (Zhang et al., 2009). Reports from the preceding studies showed that WW for Boer × Spanish were 15.20±0.34 kg (Rhone et al., 2013) and 14.19± 0.60 while for Boer × Kiko was 16.10±0.61 kg (Browning and Leite-Browning, 2011) within the range of our findings which were 13.49±0.08 - 16.34±0.21.

Results of BW traits showed that in conventional methods, B×(B×J) was superior compared to B×J with estimated values of 3.00±0.62 and 2.84±0.58 kg respectively. Whereas in mixed model method, the BW trend was reversed; B×J had the higher birth weight compared to B×(B×J) with 3.46±0.05 versus 3.38±0.06 kg, respectively. Similar trends were observed in WW traits. Overall, it was shown that conventional procedure tends to underestimate the means obtained from mixed model equations. In conventional method, the means were estimated for each breed regardless any other potential effects. On the other hand, means obtained through mixed model were corrected for systematic effects of sex, litter size and birth year (as contemporary group) as well as random effects of service bucks, random does effects and random additive genetic effects. Hence, conventional estimation results were biased (under- and/or overestimated) accompanied with lower standard errors compared to the mixed model (Komender and Hoeschele, 1989). It is proven that sex have significant effect on an animal's weight so this factor was included in the systematic part of the mixed model. Male kids grew faster and weigh heavier that female kids (van Niekerk and Casey, 1988; Zhang et al., 2009; Nugroho et al., 2018). Zhang et al. (2009) also explain that litter size was highly affecting birth weight and weaning weight. Bigger litter size means more fetuses competing for resources and space and thus yielding in smaller individual kids at birth.

In this study, heterosis was estimated as the difference between the mean purebred phenotype and the mean of the respective crossbred. Hence, the minus (-) sign indicated that purebred means were higher than the crossbred for all traits both as absolute and percentage values (Table 2). In the comparison between B×B and B×J crossbred, heterosis values were underestimated in the conventional procedure compared to the mixed model results. However, when the B×B was compared against B×(B×J), heterosis values obtained by the conventional procedure seemed to overestimate the results from mixed model. We proposed that these different trends were due to different genetic architectures of each trait and also the difference in allelic frequencies in each population (Hartl and Clark, 1997).

Table 2. The estimated heterosis values

Traits	Conventional		Mixed model	
	Absolute	Percentage	Absolute	Percentage
B×B vs B×J[1]				
Birth weight	-0.30	-11.38	-0.23	-6.23
Weaning weight	-1.58	-10.51	-1.67	-9.27
ADG*	-0.02	-10.39	-0.02	-9.68
B×B vs B×(B×J)[2]				
Birth weight	-0.20	-6.16	-0.31	-8.01
Weaning weight	-1.56	-10.35	-1.95	-10.82
ADG*	-0.02	-11.69	-0.02	-9.14

Note: 1) heterosis between purebred and B×J crossbred; 2) heterosis between purebred and B×(B×J) crossbred; *Average daily gain

The mixed model analysis was able to correct the bias for the confounding information and thus recommended for the estimation of crossbreeding parameters (Komender and Hoeschele, 1989). Based on this statement, we will hence focus our discussions on the results obtained through mixed model analysis. When we compared B×B and B×J crossbred, crossbreeding decreased the BW in B×B by 6.27%, WW by 9.27% and ADG by 9.68%. In the comparison between B×B and B×(B×J), BW of the purebred was lowered by 8.01%, WW by 10.82% and ADG by 9.14%.

One must recall that the genetics of a trait comprised of additive and non-additive effects (Falconer and Mackay, 1996). To be able to get the more thorough assessments, both factors should be estimated. Regardless the genetic effects, heterosis values respective to both crosses were considerably low for all traits. However, the development of B×(B×J) crossbred require more efforts compared to B×J in term of time, financial and other related resources. Based on these findings only, we can postulate that B×J crossbred was relatively better than its counterpart B×(B×J) crossbred.

Heterosis is a genetic phenomenon; its occurrence is very much affected especially by the non-additive genetic effects in the form of within and/or between genes interactions (Crow, 1986; Hartl and Clark, 1997; Williams et al., 2010). We can therefore explain the mechanisms of heterosis at the trait level and at the population level. The variables of interest in this study (BW, WW, ADG) were three distinct traits. Although these traits were moderate to highly correlated among each other, these traits were the expression of different (though some overlapped) sets of genes and thus, undergone different interactions and pathways. The effect of heterosis was also depend on the genetics of the populations in crossbreeding program. It is related to the number of genes and which genes involved in a trait. This information corresponded to the differences in allele frequencies at each locus with respect to the two purebred populations (Hartl and Clark, 1997).

CONCLUSIONS

Conventional method resulted in biased heterosis estimates compared to the mixed model approach. Conventional method ignores any potential effects; whereas mixed model approach incorporates all the systematic and random effect including family relationship information. Thus, we recommend employing mixed model analysis in estimating crossbreeding parameters including heterosis.

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