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Genetic (co)variance components for ratio of lamb weight to ewe metabolic weight as an indicator of ewe efficiency

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ABSTRACT

Data from a multibreed commercial flock located at Mid-West of Brazil, supported by Programa de Melhoramento Genético de Caprinos e Ovinos de Corte (GENECOC), were used to estimate genetic parameters of traits related to ewe productivity by Average Information Restricted Maximum Likelihood method applied to an animal model. The analyzed traits were litter weight at birth (LWB) and at weaning (LWW), ewe weight at weaning (EW) and ewe production efficiency, estimated by $WEE = LWW/EW^{0.75}$. The heritabilities were 0.26 ± 0.05, 0.32 ± 0.06, 0.37 ± 0.03 and 0.10 ± 0.02 for LWB, LWW, EW and WEE, respectively. Significant effects for direct heterosis were observed for LWW and EW. Recombination losses were important for EW and WEE. Genetic correlations of LWB with LWW, EW and WEE were 0.68, 0.37 and 0.15, respectively; of LWW with EW and WEE were 0.30 and 0.34, respectively; and between EW and WEE was −0.25. Even though it is a low heritability trait, WEE can be indicated as a selection criteria for improving the ewe productivity without increasing the mature weight of animals due to its genetic correlations with LWW and other traits.

1. Introduction

Sheep meat production is the principal product of sheep industries in many regions of the world (Morris, 2009). Productive efficiency or productivity of meat sheep production is as important as the total volume produced. This efficiency depends mainly on the potential of ewes to wean lambs.

The improvement in productivity per ewe is a major goal of the sheep industry and can be achieved by increasing the number of lambs weaned and weight of lambs weaned per ewe per year (Duguma et al., 2002). This trait is often used as a measure of the overall production of lamb (Bromley et al., 2001) to be indicative of fertility, prolificacy and survival. One way to evaluate the efficiency of a ewe is to relate its weight with the weight of its lambs at weaning (Iñiguez and Hilali, 2009). A variation of this would be to consider the metabolic weight of the ewe instead of its absolute weight (Bedier et al., 1992), making it more fair to compare animals of different sizes and weights. Several studies used the ratio of litter weight on ewe weight or ewe metabolic weight as a measure of ewe efficiency or ewe productivity (Annett et al., 2011; Galal et al., 1996; Vatankhah and Salehi, 2010).

The fasting heat production and the metabolic rate of an animal are related with its weight applying the exponent 0.75, i.e. $weight^{0.75}$, in a way that this formula represents the metabolic weight of the animal (Brody, 1945). According to Owen (1981) the maintenance requirements represent up to 80% of the total feed requirements and these maintenance

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requirements are a function of metabolic weight of the animal.

Thus, ewes with high adult weight and/or with high milk production, which tend to produce heavier lambs at the time of weaning or slaughter, may not be the most efficient. Schoeman (1996) observed that smaller ewes were slightly more efficient than the larger ewes. This would have a practical implication in animal breeding, since the selection for weaning weight may increase the adult weight of replacement females and thus increase the costs of maintaining the flock. Actually, results from earlier studies have shown that the relative economic value of ewe body weight is not important or in some cases negative (Lôbo et al., 2011; Morais and Madalena, 2006).

Estimates of genetic parameters are essential for implementation of breeding programs (Vanimisetti et al., 2007). Moreover, the evaluation of sheep breeds and their crosses can be based on ewe productivity indexes (Shrestha et al., 2002), since the genetic potential of the ewes has a direct influence on the offtake rate of the flock, being decisive in its technical and economic feasibility. Thus, the aim of this study was to estimate the (co)variance for traits related to productivity of ewe in a multibreed commercial flock in Brazil.

2. Material and methods

The data bank analyzed contained 14 years (1996–2009) of information from a flock maintained by Gaasa Agropecuária Ltda. and supported by the Programa de Melhoramento Genético de Caprinos e Ovinos de Corte (GENECOC) of Embrapa Caprinos e Ovinos. This flock is located at Inhumas in the state of Goiás in Brazil (altitude 770 m, 16° 21′ 28″ S, 49° 29′ 45″ W) with a tropical semi-humid climate.

The sheep underwent standard sanitary care and were vaccinated with Poli-Star® (against botulism, enterotoxemia, gangrene and symptomatic carbuncle) at 50 and 80 days of age. Annually in March all adult animals were revaccinated. Treatment for eimeriosis was done twice a year (March and October). Fecal egg counts and the Famacha® method were used to control gastrointestinal nematodes. Footbaths (50 g of copper sulfate in 60 mL of 40% formaldehyde) were used during the rainy season.

The breeding season was year round with animals grouped by lots of 300 ewes according to availability and oestrus cycle. The lambs were weaned at 60 days, confined, and fed with maize silage and corn and soy bran meal containing 21% crude protein (CP); they were slaughtered at 120–150 days. After weaning the lambs, the ewes underwent a 30-day breeding season in the presence of vasectomized rams for detecting those in oestrus. Then these ewes were submitted to mating with breeding rams. Ewes and rams were fed with Tifton 85 pasture, silage and meal containing 15% CP.

The flock was initially established by acquiring seven sire breeds (purebred Santa Inês, Poll Dorset, Hampshire Down, Suffolk, Ile de France, Brazilian Somali and Texel) and six dam breeds (Santa Inês, Poll Dorset, Morada Nova, Brazilian Somali, Santa Inês × Morada Nova and Santa Inês × Brazilian Somali). Later, purebred Dorper, Primera and East Friesian rams were acquired. The matings were controlled (hand mated) but not technically designed. Due to the great quantity of available ewes, all rams of all breeds had the same opportunity to mate ewes of all genetic groups (purebred and crossbred). As a result, within a few years the flock was a mixture of crossbred dams with a varied contribution from the different breeds. Only the rams and some Santa Inês, Poll Dorset and Brazilian Somali dams were purebred.

Data used in this study contained all the breeds indicated above. However, many genetic groups were excluded from analysis because of insufficient information. The rams used included purebred Santa Inês (36), Poll Dorset (16), Hampshire Down (5), East Friesian (4), Dorper (4), Suffolk (3), Île de France (2), Brazilian Somali (2), Texel (1), Samm (1), White Dorper (1), Lacaune (1), and Primera (1). The dams used included purebred Santa Inês, Poll Dorset, Brazilian Somali and crossbreeds involving all of the breeds indicated above. Table 1 shows the genetic groups analyzed.

The analyzed traits were litter weight at birth (LWB) and at weaning (LWW), ewe weight at weaning (EW) and ewe production efficiency, estimated by $WEE = LWW/EW^{0.75}$.

The MIXED procedure of SAS (SAS Institute Inc, 1996) was used to define fixed effects in the analysis. For each trait, many linear models were evaluated, with the use of contemporary groups or effects being analyzed individually. The logarithm of the Restricted Maximum Likelihood, Aikaikes's Information Criteria and Schwarz's Bayesian Information Criteria were the criteria for choice of the best fit.

After preliminary analysis and based on criteria used to determine the best fit, the fixed model used in analysis had the contemporary group for all trait. The contemporary groups (CGs) consisted of animals of the same genetic group, with lambing in the same year-season, the same birth type (1 — one male lamb, 2 — one female lamb, 3 — two male lambs, 4 — two females lambs, 5 — one male lamb and one female lamb or 6 — more than two lambs, independent of sex) and the same lambing order. The seasons were: season 1 — January, February and March, season 2 — April, May and June, season 3 — July, August and September, and season 4 — October, November and December. Only CGs with a minimum of six animals were considered.

The effects of age of dam as covariable also was considered for EW and WEE. The additive genetic difference among breeds (expected proportion of genes from Santa Inês breed), direct heterosis effect and individual recombination loss effect were included in model too. In this study this crossbreeding parameters were fitted as covariates in the models, following Hirooka et al. (1998). The crossbreeding in this population was completely random, i.e., there was no specific design in the breeding pattern used.

The (co)variances and genetic parameters were estimated by the Average Information Restricted Maximum Likelihood method (AI-REML) using the software WOMBAT (Meyer, 2007), with single or multiple trait animal models. WOMBAT assesses whether an analysis has converged, based on the following criteria: 1) a change in log L of $<5\times10^{-4}$, 2) a change in parameters of $<10^{-8}$ and 3) a gradient vector norm $<10^{-3}$.

The relationship matrix included 24,590 animals. Of these, 77 were rams and 2590 were dams with progeny in the data, 23,441 animals had a complete pedigree (sire and dam known) and 1035 were from the basal flock; 1130 animals had an unknown sire.

Table 1
Genetic groups analyzed in this work with their respective number of observations and performance for litter weight at birth (LWB), litter weight at weaning (LWW), weight of dam at weaning of lambs (EW) and ewe productivity (WEE).

Genetic groups	N	LWB (kg)	LWW (kg)	EW (kg)	WEE (kg/kg$^{0.75}$)
Dorper	13	5.09 ± 1.76	22.23 ± 6.49	52.00 ± 12.56	1.22 ± 0.37
1/2 Dorper × 1/2 Santa Inês	960	5.18 ± 1.77	19.98 ± 8.61	47.28 ± 9.04	1.22 ± 0.39
3/4 Dorper × 1/4 Santa Inês	166	5.02 ± 1.75	19.53 ± 10.81	48.62 ± 7.34	1.11 ± 0.35
East Friesian	71	5.25 ± 1.61	17.65 ± 10.70	47.34 ± 6.93	1.21 ± 0.51
1/2 East Friesian × 1/2 Santa Inês	79	5.62 ± 1.71	18.85 ± 9.20	45.20 ± 6.25	1.16 ± 0.37
1/2 Hampshire Down × 1/2 Santa Inês	176	5.39 ± 1.79	20.13 ± 8.59	52.19 ± 9.11	1.14 ± 0.39
Ile de France	6	4.97 ± 2.01	24.25 ± 8.70	56.50 ± 8.31	1.16 ± 0.32
1/2 Ile de France × 1/2 Santa Inês	297	5.25 ± 1.59	20.45 ± 8.28	50.09 ± 8.86	1.18 ± 0.36
1/2 Lacaune × 1/2 Santa Inês	16	3.88 ± 0.94	12.73 ± 6.66	36.45 ± 8.92	1.08 ± 0.17
Poll Dorset	227	4.54 ± 1.51	16.72 ± 9.76	48.39 ± 8.30	1.12 ± 0.40
1/2 Poll Dorset × 1/2 Santa Inês	1307	5.24 ± 1.71	18.57 ± 8.64	46.99 ± 8.55	1.20 ± 0.40
3/4 Poll Dorset × 1/4 Santa Inês	304	4.92 ± 1.74	17.00 ± 9.99	48.37 ± 8.58	1.10 ± 0.41
1/2 Primera × 1/2 Santa Inês	50	4.24 ± 1.73	15.33 ± 9.39	51.06 ± 7.25	0.93 ± 0.23
1/2 Samm × 1/2 Santa Inês	6	5.67 ± 1.81	16.85 ± 9.21	49.90 ± 4.89	1.03 ± 0.33
Santa Inês	7342	5.12 ± 1.58	16.56 ± 8.07	45.72 ± 7.40	1.08 ± 0.36
1/2 Santa Inês × 1/2 Poll Dorset	206	4.94 ± 1.60	18.18 ± 8.32	42.48 ± 8.65	1.22 ± 0.38
3/4 Santa Inês × 1/4 Poll Dorset	702	5.01 ± 1.55	17.17 ± 8.09	46.59 ± 7.84	1.09 ± 0.35
Brazilian Somali	199	3.67 ± 1.10	12.80 ± 6.71	29.09 ± 5.90	1.17 ± 0.23
1/2 Brazilian Somali × 1/2 Santa Inês	62	4.68 ± 1.18	17.06 ± 7.30	32.53 ± 6.52	1.39 ± 0.43
3/4 Brazilian Somali × 1/4 Santa Inês	6	4.90 ± 1.56	17.64 ± 5.37	32.25 ± 1.71	1.71 ± 0.35
Suffolk	10	6.30 ± 2.37	14.71 ± 9.57	75.75 ± 16.14	0.93 ± 0.48
1/2 Suffolk × 1/2 Santa Inês	180	5.67 ± 1.78	22.09 ± 9.96	55.01 ± 8.61	1.18 ± 0.40
1/2 Texel × 1/2 Santa Inês	358	5.63 ± 1.90	20.43 ± 8.35	46.77 ± 8.40	1.30 ± 0.43
White Dorper	6	5.28 ± 1.87	21.60 ± 11.46	58.00 ± 4.36	1.07 ± 0.35
1/2 White Dorper × 1/2 Santa Inês	779	4.96 ± 1.74	20.09 ± 8.47	47.61 ± 8.96	1.19 ± 0.38
3/4 White Dorper × 1/4 Santa Inês	80	3.95 ± 1.35	13.38 ± 9.05	45.32 ± 9.25	1.00 ± 0.33

LWB and LWW were analyzed in a two-trait model while EW and WEE were analyzed in a single-trait model. The general model was:

$$Y = X\beta + Z_1 a + Z_2 pe + b_1 id + b_2 ad + b_3 d + b_4 r + e;$$

where Y is a (N × 1) vector of observations; β, the vector of fixed effects of contemporary groups, related to incidence matrix X; a, the vector of direct genetic effects, related to incidence matrix Z_1; pe, the vector of permanent environmental individual effects, related to incidence matrix Z_2; id, the age of ewe (for EW and WEE); ad, expected proportion of genes from Santa Inês breed; d, direct heterosis effect calculated as $p_r(1-p_e)+p_e(1-p_r)$ according to Dickerson et al. (1973); r, individual recombination loss effect, estimated as $p_r(1-p_r)+p_e(1-p_e)$, where p_r and p_e are the proportion of genes of Santa Inês breed in the rams and ewes, respectively; b_1 to b_4 are the regression coefficients; and e, the vector of random residuals.

According to Van Vleck et al. (1987), correlations among breeding values may be considered as the proper definition of genetic correlations. Thus, genetic correlations involving EW and WEE were estimated as Pearson's correlation between ewes breeding values.

3. Results

The number of observations, observed averages and crossbreeding parameters for the traits analyzed are presented in Table 2. The numbers of observations for EW and WEE were lowest as recording of EW has started only in recent years. The averages of 5.07 kg and 19.11 kg for LWB and LWW, respectively, and of 1.15 for WEE, indicate a good potential for ewe productivity under the feeding conditions of this flock compared to productivity of other flocks supported by GENECOC (data unpublished).

Additive effects of Santa Inês breed were significant for LWB (0.94), LWW (1.76) and EW (15.67), with positive contributions. However the negative contribution for WEE (−0.17) must be emphasized as this breed is considered the principal maternal lineage for sheep production in Brazil. Genetic breed differences were evaluated in deviation of this breed due to its major participation in the flock (almost 85% of ewes have Santa Inês genes). Direct heterosis was significant only for LWW (4.34) and EW (8.17). Recombination loss was important for EW (12.01) and WEE (−0.19).

Estimates of (co)variances, Log L value, heritabilities and genetic correlations are shown in Table 3. The heritabilities for LWB (0.26), LWW (0.32) and EW (0.37) were moderated while the heritability for WEE was low (0.02). As expected,

Table 2
Number of observations (N), averages and standard deviation (A ± SD), additive direct effect of Santa Inês breed (SI), direct heterosis (H) and recombination loss (R) for traits related to ewe efficiency in a commercial multibreed flock.

Traits	N	A ± SD	SI	H	R
LWB (kg)	13,614	5.07 ± 1.63	0.94*	0.04	−0.17
LWW (kg)	12,456	19.11 ± 6.80	1.76*	4.34*	0.39
EW (kg)	8156	44.91 ± 8.15	15.67*	8.17*	12.01*
WEE (kg/kg$^{0.75}$)	7848	1.15 ± 0.37	−0.17*	0.05	−0.19*

LWB = litter weight at birth; LWW = litter weight at weaning; EW = weight of dam at weaning of lambs; WEE = ewe productivity.
* $P<0.05$.

Table 3
Estimates of genetic parameters for traits related to ewe efficiency in a commercial multibreed flock.

	Additive genetic (co)variances				Permanent environmental (co)variances				Phenotypic (co)variances			
	LWB	LWW	EW	WEE	LWB	LWW	EW	WEE	LWB	LWW	EW	WEE
LWB	0.2186				0.05240				0.8284			
LWW	1.0341	10.6656			−0.00034	0.00001			1.0338	32.8847		
EW			18.1814				7.9466				48.9352	
WEE				0.0127								0.1302
Log L	LWB and LWW		−31546.19	EWE	−18759.8	WEE	3920.7					

Heritabilities (along diagonal) and genetic correlations (off diagonal)

Traits	LWB	LWW	EW	WEE
LWB	0.26 ± 0.05			
LWW	0.68 ± 0.05	0.32 ± 0.06		
EW	0.37[a]	0.30[a]	0.37 ± 0.03	
WEE	0.15[a]	0.34[a]	−0.25[a]	0.10 ± 0.02

LWB = litter weight at birth; LWW = litter weight at weaning; EW = weight of dam at weaning of lambs; WEE = ewe productivity.
[a] Estimated as Pearson's correlation between breeding values

WEE was correlated positively with LWB (0.15) and LWW (0.34), but negatively with EW (−0.25).

4. Discussion

Duguma et al. (2002) reported an average of 24.3 kg for LWW in first lambing of Merino. This value is greater than that presented in this study. Matika et al. (2003) observed averages of 19.6 kg and 35.9 kg for LWW and EW, respectively, in Sabi sheep. Iñiguez and Hilali (2009) estimated values ranging from 19.8 to 23.1 kg for LWW, from 47.3 to 49.1 kg for EW and from 0.42 to 0.48 kg for kg of lambs weaned per ewe body weight, in Awassi genotypes. Using the averages of their study the WEE will range from 1.07 to 1.28. The differences between the values observed in this study and in literature are expected, due to the differences in breeds and environments considered. Galal et al. (1996) estimated an average of 1.62 for WEE of ewes raised under the Egyptian small-holder sheep production system.

Annett et al. (2011) reported averages for WEE of 2.00, 2.15, 2.04, 2.26 and 2.10 in Scottish Blackface (BF), Swaledade × Blackface (SW × BF), Cheviot × Blackface (CH × BF), Lleyn × Blackface (LL × BF) and Texel × Blackface (T × BF) ewes considering the body weight of ewe at mating (W) instead of body weight of ewe at weaning as in this study. The authors highlighted that LL × BF produced 13% more lamb per unit W$^{0.75}$ than BF due to their greater prolificacy and higher lamb growth rates. They observed that the replacement of purebred ewes (BF) with LL × BF ewes will improve the production efficiency enabling lamb output of the hill sector while reducing methane emissions.

Vatankhah and Salehi (2010) also used the ratio of litter weight on metabolic weight of ewe at mating and considered that this trait is the most conclusive measurement of total ewe's productivity since it combines conception rate, lambing rate, prolificacy, survival rate from birth to weaning, weaning weight, mothering ability and feed requirements for maintenance of ewes in the flock into one value. These authors observed an average for WEE of 1294 g/kg$^{0.75}$ (1.29 in dimensionless value — kg/kg$^{0.75}$) in Lori-Bakhtiari ewes.

According to Robinson et al. (1981), the use of models involving different genetic groups can account for all genetic influences, including non-linear and epistatic effects. However, additive genetic variance and heritability have been shown to be overestimated in an additive model with progeny groups in multibreed population. So the main purpose of inclusion of crossbreeding parameters in this study was remove biases in the estimates of additive genetic parameters since the number of observations of many genetic groups is quite small to estimate crossbreeding parameters separately for the different genetic groups.

Estimates for crossbreeding parameters are scarce in literature for sheep. Bittante et al. (1996) also observed important effect of heterosis in LWW in crossbreeding between Finnsheep and an Alpine sheep breed. In this study, the effect of direct heterosis observed for the traits LWW and EW was not verified in WEE. But, we observed negative contributions of additive direct effect of Santa Ines, as well as losses by recombination in WEE. This may partly explain the low coefficient of heritability found for this trait. The averages of heterosis observed here reinforce the use of crossbred animals for the efficiency of the production system. The additive effects of Santa Inês promoted highest averages for LWB, LWW and EW being favorable for the first two traits. However its effect on increasing the EW probably affected negatively the ewe productivity.

With data of this same population Barbosa Neto et al. (2010) observed that greater proportion of Brazilian Somali genes in relation to Santa Inês genes will reduce LWB and LWW. The greater proportion of Poll Dorset genes in relation to Santa Inês genes will reduce LWB. These authors reported significant heterosis of 0.66 kg between Poll Dorset and Brazilian Somali, 0.41 kg between Poll Dorset and Santa Inês and 0.42 kg between Santa Inês and Brazilian Somali for LWB. For LWW, the significant heterosis was 2.38 kg between Poll Dorset and Brazilian Somali and 3.11 kg between Poll Dorset and Santa Inês.

Rosati et al. (2002) reported heritability of 0.40 and 0.17 for LWB and LWW for purebred, composite and crossbred sheep. These values were higher and lower, respectively, than observed here. Duguma et al. (2002) also estimated a lower heritability (0.20) for LWW over four lambing. In Sabi sheep, Matika et al. (2003) reported heritability values of 0.12 and 0.67 for LWW and EW, respectively. The value for this last trait was higher than estimated here. In a review done by Safari et al. (2005), the average value of heritability for LWW was 0.11 ± 0.02, being lower than that found in this study. According to Ercanbrack and Knight (1998) the selection for LWW affects other traits as fertility, prolificacy, lamb growth, lamb survival to weaning, and ewe viability from mating to weaning.

Vatankhah and Salehi (2010) reported that heritability of ewe body weight at different stages of production as various traits was high (0.40–0.49). The value for the ewe weight after weaning was 0.40. This estimate was close to observed (0.37) in the present study.

The heritability for WEE was low, however this trait presented high variability (coefficient of variation of 32%). It is possible that this high CV is due to the data structure with different genetic groups although the data was adjusted for breed differences. However, this CV was estimated ranging from 22 to 24% in purebred flocks (of Santa Inês, Morada Nova and Brazilian Somali breeds) supported by GENECOC (unpublished data). Vanimisetti et al. (2007) considered the possibility of genetic improvement for trait as WEE, even with low heritability, because of its high phenotypic variability since genetic gain can be expressed by selection intensity × heritability × phenotypic variation. Despite being low, the heritability of WEE found in this study was higher than reported by Abegaz and Van Wyk (2002), the only reference found in the literature. These authors reported the value 0.03 ± 0.016.

The genetic correlations among the traits were as expected. The values found indicate that selection for WEE also improve LWB and LWW without increasing the adult weight of ewes. This is consistent with the ideas of Dickerson (1970) in which the objective is to seek more efficient lean growth and earlier sexual maturity with minimum increase in mature size, at least for breeds used as female parents in crossbreeding.

Michels et al. (2000) observed that a clear cut relationship between the litter weight components and ewe weight can probably not be considered as general but may vary among differentially selected breeds and lines within them. The genetic correlations of EW with LWB (0.37) and LWW (0.30) indicate that heaviest ewes produced heaviest litter at birth and weaning, similar to that reported by Ray and Smith (1966) who observed that an increase in the ewes' body weight of 1 kg resulted in a 0.1 kg increase in weaning weight of lambs. However this does not indicate a better efficiency of production. The negative correlation between EW and WEE (−0.25) argues that heaviest ewes produced slightest litter at weaning in relation to its metabolic weight. In fact, the selection for heaviest animals in weaning can produce heaviest ewes due to the positive correlations among weights in different ages. In this flock the aim is to produce highest kg of lambs at weaning without increase in the mature weight of ewes which can explain this negative genetic correlation.

The high positive genetic correlation between LWB and LWW is found according to Bromley et al. (2001), and Lôbo et al. (2009), that suggested the possibility of improving productivity through the selection for LWW due to its genetic association with other important traits.

The holder and the technical staff of this flock intended to experiment several available genetic groups in Brazil with the aim to find the bests. They were aware of the impossibility of establishing appropriate breeding strategies with an unstable population with multiple and not delineated matings. Today, with the experience gained they are driving the flock to produce with 1/2 Poll Dorset × 1/2 Santa Inês and the use of terminal rams of Dorper and Suffolk breeds. Actually, the results of this and previous studies pointed out that the use of crossbred ewes presents better efficiency of production for this system. In despite of the negative effect of additive genes of Santa Inês for WEE this is the major dam breed in Brazil and it is practically impossible to produce lamb meat in great part of Brazilian territory without participation of this breed as maternal lineage. The country does not have other maternal breeds in sufficient number to attain highest production scale.

5. Conclusion

These results show the possibility of selection of commercial flocks for ewe productivity. The selection for LWW can improve the weaning efficiency of ewes but can increase the weight of adult animals due to genetic correlations among weights in different ages. The inclusion of WEE as selection criteria, even though it is a low heritability trait, will improve the ewe productivity without increasing the mature weight of animals.

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