



Direct and maternal effects models for variance components and genetic parameters estimation of growth traits in prolific Garole sheep

VED PRAKASH¹, L L L PRINCE², G R GOWANE³, R C SHARMA⁴ and ARUN KUMAR⁵

ICAR-Central Sheep and Wool Research Institute, Avikanagar, Rajasthan 304 501 India

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ABSTRACT

The objective of the study was to identify the most suitable model for estimation of (co) variance components and genetic parameters of different growth traits in prolific Garole sheep. Growth data of 1,058 Garole lambs born to 49 sires and 208 ewe was collected from ICAR-Central Sheep and Wool Research Institute (ICAR-CSWRI), Avikanagar, India. The traits studied were birth weight (BWT), 3 month weight (3WT), 6 month weight (6WT), 9 month weight (9WT), 12 month weight (12 WT), average daily gain from birth to 3 month age (ADG1), average daily gain from 3 month to 6 month age (ADG2). Twelve different animal models were fitted to account for different direct genetic and maternal effects. Model including maternal permanent environmental effect, maternal temporary environmental effect and direct genetic effects (Model 8) was most appropriate model for BWT. For other traits model with direct genetic effect and common litter effect (Model 7) was found most suitable. From best model direct heritability estimates of 0.037 ± 0.054 , 0.148 ± 0.075 , 0.104 ± 0.077 , 0.079 ± 0.083 , 0.103 ± 0.116 , 0.137 ± 0.072 and 0.045 ± 0.071 were obtained for BWT, 3WT, 6WT, 9WT, 12WT, ADG1 and ADG2, respectively. Maternal temporary environmental effect variance contributed highest to total phenotypic variance. It ranged from 0.347 ± 0.040 for BWT to 0.451 ± 0.083 for 9WT. Estimates of direct genetic correlation ranged from -0.047 for BWT-ADG1 to 1.00 for BWT-12WT, 6WT-12WT and 9WT-12WT. Phenotypic correlations were positive and varied from 0.119 for ADG1-ADG2 to 0.982 for 3WT-ADG1. The growth traits of Garole sheep have low to moderate heritability and were influenced by maternal temporary environmental effect due to sharing of common litter environment.

Key words: Average Daily Gain, Body Weight, Garole Sheep, Heritability, Maternal effects, Variance

Garole is a prolific sheep breed found in the Sundarban region of West Bengal of India. The Garole sheep has been utilized in various breeding experiments to improve the prolificacy of non-prolific Indian sheep breeds (Prakash *et al.* 2017). Limited attempt has been made to study genetic parameter of growth traits in Garole sheep (Karmakar *et al.* 2018; Mandal *et al.* 2017). The genotype of mother, uterine capacity, influence of dam on the litter mates or progenies of a dam born in different years, ewe role in survival and growth of lambs are some of the maternal sources of variation. These maternal sources of variation are more relevant for the prolific sheep breeds. Inclusion of maternal effects in animal models has an important effect on the estimates of variance components and heritability (Gowane *et al.* 2010; Prakash *et al.* 2012). These maternal effects can be partitioned into permanent and temporary

components (Boujenane *et al.* 2015). Among the maternal effects similarity arising among common litter mates contributes to maternal temporary environmental effects and similarities between lambs born to the same ewe in different lambings contributes to maternal permanent environmental effects. For prolific Garole sheep maternal temporary effects arising due to sharing of common litter environment should be accounted along with other effects. However, information on genetic parameters estimates for body weight and growth rates in Garole sheep accounting for direct and maternal effects is limited. Therefore, the aim of the present study was to identify most appropriate genetic model and estimate the genetic parameters for body weight and average daily gain in Garole sheep raised under semi-arid tropics.

MATERIALS AND METHODS

Data: The body weight records of 1,058 Garole lambs born to 49 sires and 208 ewe collected over a span of 19 years between 1997 to 2015 at the ICAR-Central Sheep and Wool Research Institute (CSWRI), Avikanagar were analyzed. The details of Garole sheep flock development at ICAR-CSWRI, Avikanagar and its rearing, breeding and management in semi-arid conditions of Rajasthan has been

Present address: ¹Scientist (drvedagb@gmail.com), National Research Centre on Camel, Bikaner, Rajasthan. ²Principal Scientist (drleslie@gmail.com) Directorate of Poultry Research, Hyderabad, Telangana. ³Senior Scientist (gopalgowane@gmail.com), ⁴Principal Scientist (rcsagb@gmail.com), ⁵Principal Scientist and Head (karunt04@yahoo.com), Division of Animal Genetics and Breeding.

reported by (Prakash *et al.* 2017). The different economic traits used for analysis were birth weight (BWT), 3 month weight (3WT), 6 month weight (6WT), 9 month weight (9WT), 12 month weight (12 WT), average daily gain from birth to 3 month (ADG1) and average daily gain from 3 month to 6 month (ADG2). A description of data used in analyses is presented in Table 1.

Statistical methods: (Co) variance components were estimated by restricted maximum likelihood (REML) using an average information (AI) algorithm WOMBAT (Meyer, 2007) fitting an animal model. Data were first analyzed by least squares analysis of variance (SPSS, 2011) to identify the fixed effects to be included in the model. The fixed effect considered in the model were sex of lamb (2 levels), type of birth (3 levels), parity of dam (5 levels), season of lambing (3 levels) and period of lambing (5 levels). The data was classified into four periods, Period I (1997–2000), Period II (2001–2004), Period III (2005–2009) and Period IV (2010–2015). Classification of sex of lamb, season of lambing, type of birth and parity of dam was similar to classification of Prakash *et al.* (2017). Only significant effects ($P \geq 0.05$) were included in the models used for the genetic analyses. Convergence was assumed when change of value of the natural logarithm of the restricted likelihood function in two consecutive iterations was lower than 5×10^{-4} . Twelve models which accounted for the direct genetic, maternal genetic, maternal temporary environmental effects and maternal permanent environmental effects were as follows:

$$y = X\beta + Z_a\alpha + \varepsilon \text{ (Model 1)}$$

$$y = X\beta + Z_a\alpha + Z_c c + \varepsilon \text{ (Model 2)}$$

$$y = X\beta + Z_a\alpha + Z_m m + \varepsilon \text{ with Cov}(a_m, m_o) = 0 \text{ (Model 3)}$$

$$y = X\beta + Z_a\alpha + Z_m m + Z_c c + \varepsilon \text{ with Cov}(a_m, m_o) = 0 \text{ (Model 4)}$$

$$y = X\beta + Z_a\alpha + Z_m m + \varepsilon \text{ with Cov}(a_m, m_o) = A\sigma_m \text{ (Model 5)}$$

$$y = X\beta + Z_a\alpha + Z_m m + Z_c c + \varepsilon \text{ with Cov}(a_m, m_o) = A\sigma_m \text{ (Model 6)}$$

$$y = X\beta + Z_a\alpha + Z_l l + \varepsilon \text{ (Model 7)}$$

$$y = X\beta + Z_a\alpha + Z_c c + Z_l l + \varepsilon \text{ (Model 8)}$$

$$y = X\beta + Z_a\alpha + Z_m m + Z_c c + Z_l l + \varepsilon \text{ with Cov}(a_m, m_o) = 0 \text{ (Model 9)}$$

$$y = X\beta + Z_a\alpha + Z_m m + Z_c c + Z_l l + \varepsilon \text{ with Cov}(a_m, m_o) = A\sigma_m \text{ (Model 10)}$$

$$y = X\beta + Z_a\alpha + Z_m m + Z_l l + \varepsilon \text{ with Cov}(a_m, m_o) = 0 \text{ (Model 11)}$$

$$y = X\beta + Z_a\alpha + Z_m m + Z_l l + \varepsilon \text{ with Cov}(a_m, m_o) = A\sigma_m \text{ (Model 12)}$$

where, y is the vector of records; β , a , m , c , l and ε are vectors of fixed, additive direct genetic, maternal additive genetic, maternal permanent environmental effects, maternal temporary environmental effects and residual

effects, respectively; X , Z^a , Z^m , Z^c and Z^l are incidence matrices that relate these effects to the records. A is the numerator relationship matrix between animals; and σ^{am} is the covariance between additive direct and maternal genetic effects. Assumptions for variance (V) and covariance (Cov) matrices involving random effects were $V(a) = A\sigma_a^2$, $V(m) = A\sigma_m^2$, $V(c) = I^n \sigma_c^2$, $V(l) = I_l \sigma_l^2$, $V(e) = I_n \sigma_e^2$ and $\text{Cov}(a, m) = A\sigma^{am}$ where I^{nd} , I^l and I^n are identity matrices of order equal to the number of dams, number of litters and number of records, respectively and σ_a^2 , σ_m^2 , σ_c^2 , and are additive direct, additive maternal, maternal permanent environmental, maternal temporary environmental effect and residual variances, respectively. The total phenotypic variance (σ_p^2), direct heritability (h^2), maternal heritability (m^2), permanent environmental effect (c^2), maternal temporary environmental effect (l^2), additive direct-maternal covariance (σ_{am}) and correlation (r_{am}), total heritability, repeatability of ewe effects across years (t_m) for each model was calculated as reported by prakash *et al.* 2012, Ngere *et al.* 2017. The correlation between full-sib lambs was estimated as reported by Ngere *et al.* 2017.

Model comparison: The genetic models were compared using Schwarz's Bayesian information criteria (BIC) value (Schwarz, 1978). The most appropriate model for each trait was subsequently used in bivariate analyses to estimate different co-variances and correlations among traits. Bivariate models included the fixed effects and random effects used for corresponding univariate analyses.

RESULTS AND DISCUSSION

Model selection and comparison of estimates across model: Estimates of log likelihood values and BIC values obtained from fitting 12 different animal models are given in Table 2. The most appropriate model for each trait, based on lowest BIC value is given in asterisk. Based on the BIC values the animal model with maternal permanent environmental effects, maternal temporary environmental effect and direct genetic effects was most appropriate model (Model 8) for BWT. For 3WT, 6WT, 9WT, 12WT, ADG1 and ADG2 model with direct genetic effect and maternal temporary environmental effect due to common litter effect was found most suitable (Model 7). The estimates were influenced by model used. The results showed that fitting either maternal genetic, maternal permanent environmental or maternal temporary environmental effect in model results in decrease in $-2 \log L$ and BIC values in comparison with model 1 for BWT. For 3WT, 6WT, 9WT, 12 WT, ADG1 and ADG2 model with maternal temporary environmental

Table 1. Characteristics of the data and model structure for growth traits in Garole sheep

Trait	BWT	3WT	6WT	9WT	12WT	ADG1	ADG2
No. of records	1058	619	489	401	313	619	479
No of sire	49	41	40	39	36	41	40
No of dams	208	164	152	133	118	164	152
Mean $\pm$ SD	1.16 $\pm$ 0.46 kg	6.34 $\pm$ 2.32 kg	9.67 $\pm$ 3.35 kg	11.55 $\pm$ 4.25 kg	13.58 $\pm$ 4.0 kg	56.02 $\pm$ 23.15 gm	37.31 $\pm$ 22.15
CV (%)	39.65	36.59	34.64	34.72	31.30	41.32	59.38

Table 2. Log likelihood and BIC values from different model for different growth traits in Garole sheep

Particulars	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11	Model 12
<i>Birth weight (BWT)</i>												
-2logL	-1125.49	-1179.32	-1170.99	-1179.90	-1171.47	-1179.99	-1210.82	-1243.81	-1244.12	-1244.14	-1237.43	-1237.49
BIC	-1111.58	-1158.47	-1150.12	-1152.08	-1143.66	-1145.22	-1189.96	-1215.99*	-1209.35	-1202.41	-1209.62	-1202.72
<i>3 Month weight (3WT)</i>												
-2logL	1389.39	1387.99	1389.15	1387.99	1386.37	1384.81	1371.85	1371.83	1371.83	1369.74	1371.85	1370.00
BIC	1402.52	1407.58	1408.76	1413.99	1412.14	1416.97	1391.24*	1397.64	1404.05	1408.20	1397.65	1402.04
<i>6 Month weight (6WT)</i>												
-2logL	1428.91	1428.91	1428.91	1428.91	1426.82	1426.82	1410.67	1410.67	1410.67	1409.018	1410.67	1409.02
BIC	1441.25	1447.42	1447.42	1453.59	1451.49	1457.66	1429.18*	1435.35	1441.52	1446.036	1435.35	1439.87
<i>9 month weight (9WT)</i>												
-2logL	1342.46	1342.46	1342.46	1342.46	1335.86	1335.81	1320.77	1320.77	1320.77	1316.70	1320.77	1318.40
BIC	1354.39	1360.36	1360.36	1359.73	1366.32	1365.65	1338.67*	1344.63	1350.60	1352.50	1344.63	1346.23
<i>12 month weight (12WT)</i>												
-2logL	1075.73	1075.73	1075.73	1075.73	1073.90	1073.81	1066.55	1066.55	1066.55	1079.45	1066.55	1065.30
BIC	1091.13	1092.84	1092.84	1098.54	1096.72	1102.33	1083.66*	1089.36	1095.07	1113.67	1089.36	1093.82
<i>Average daily gain from birth to 3 month (ADG1)</i>												
-2logL	4239.52	4238.48	4239.52	4238.48	4234.51	4232.41	4226.20	4226.20	4226.20	4222.13	4226.20	4222.37
BIC	4252.34	4257.70	4258.74	4264.11	4260.14	4264.45	4245.42*	4251.83	4258.24	4260.57	4251.83	4254.40
<i>Average daily gain from 3 month to 6 month (ADG2)</i>												
-2logL	3320.78	3320.64	3319.88	3319.88	3316.28	3316.28	3294.65	3294.65	3294.65	3293.04	3294.65	3293.04
BIC	3333.06	3339.06	3338.30	3344.44	3340.84	3346.98	3313.07*	3319.21	3325.35	3329.88	3319.21	3323.74

*BIC Values indicate best identified model.

resulted in substantial decrease in -2logL value and BIC value compared to model1. However, the inclusion of maternal genetic effect or maternal permanent environmental effect alone or in combination did not affect the -2logL and BIC value much. Furthermore, model 1 which ignored maternal effects, overestimated direct genetic variance and resulted in highest estimates for h_d^2 compared with the other models. Boujenane *et al.* (2015); Ngere *et al.* (2017), Mandal *et al.* (2017), Karmakar *et al.* (2018) showed that models not accounting for maternal effects result in substantially higher estimates of direct genetic variance and higher h_d^2 estimates.

For the BWT m^2 accounted for 4 to 26% of total phenotypic variance and c^2 accounted for 17 to 22% of phenotypic variance from different model applied. For 3WT, 6WT, 9WT, 12WT, ADG1 and ADG2 m^2 contributed 0 to 17% of the phenotypic variance, while c^2 contributed 0 to 12% of the phenotypic variance across the model applied. Thus from three month age onward the maternal influence in terms of m^2 and c^2 declined. This indicated important influence of maternal effects on birth weight which diminishes as age advances. According to Karmakar *et al.* (2018) maternal genetic effects contributed 6–16% and maternal permanent environmental effects (c^2) accounted for 5–11% of the total variance for birth weight under different models in Garole sheep. The maternal temporary environmental effect was significant source of variation for all body weight and daily gain traits. It contributed 29 to 45% of the phenotypic variance across the models. The current estimate of temporary maternal effect is similar to estimates of Ekiz (2005) but higher than the reports of Abassi *et al.* (2012), Boujenane *et al.* (2015).

Genetic parameters from best model: The variance components and genetic parameters estimates from best model is given in Table 3. Estimates of direct heritability for BWT (0.037 ± 0.054) was higher than reports of Mohammadi *et al.* (2013), similar to reports of Mokhtari *et al.* (2013), Boujenane *et al.* (2015) but lower than the estimates of Abassi *et al.* (2012); Ngere *et al.* (2017). Estimates of direct heritability for 3WT (0.148 ± 0.075) was higher than reports of Abassi *et al.* (2012); Boujenane *et al.* (2015); similar to reports of Mokhtari *et al.* (2013) and lower than the estimates of Mohammadi *et al.* (2013); Ngere *et al.* (2017). Estimates of direct heritability for 6WT (0.104 ± 0.077) was higher than reports of Abassi *et al.* (2012) but lower than the estimates of Mokhtari *et al.* (2013); Mohammadi *et al.* (2013). Estimates of direct heritability for 9WT (0.079 ± 0.083) from best model was similar to reports of Mokhtari *et al.* (2013) but lower than the estimates of Mohammadi *et al.* (2013). Estimates of direct heritability for 12WT (0.103 ± 0.118) was lower than the reports of Mohammadi *et al.* (2013); Mokhtari *et al.* (2013). Estimates of direct heritability for ADG1 (0.137 ± 0.072) was higher than the reports of Abassi *et al.* (2012) but lower than the estimates of Mokhtari *et al.* (2013); Mohammadi *et al.* (2013). Estimates of direct heritability for ADG2 (0.045 ± 0.071) was similar to reports of Abegaz *et al.* (2005) but lower than the estimates of Ekiz (2005). Fractions of variance due to maternal temporary environmental effect of the total phenotypic variance ranged from 0.317 ± 0.071 (ADG1) to 0.451 ± 0.083 (9WT). Importance of maternal temporary environmental effects due to sharing of common litter environment was also reported for different growth traits by (ApDewi *et al.* 2002; Abegaz *et al.* 2005;

Table 3. (Co) variance components and genetic parameter estimates from best model for different growth traits in Garole sheep

Particulars	BWT	3WT	6WT	9WT	12WT	ADG1	ADG2
Best Model	Model 8	Model 7	Model 7	Model 7	Model 7	Model 7	Model 7
σ^2_a	0.0049± 0.007	0.509±0.267	0.692±0.519	0.798±0.850	1.141±1.307	50.93±27.83	16.73±26.34
σ^2_c	0.026± 0.006						
σ^2_l	0.045± 0.006	1.193±0.259	2.540±0.570	4.52±0.960	4.421±1.314	117.94±28.76	154.45±31.37
σ^2_e	0.054± 0.005	1.734±0.254	3.390±0.53	4.734±0.860	5.534±1.234	203.53±28.49	199.11±29.70
σ^2_p	0.130±0.007	3.437±0.213	6.628±0.46	10.049±0.76	11.096±0.959	372.40±22.99	370.24±25.75
h^2_d	0.037±0.054	0.148±0.075	0.104±0.077	0.079±0.083	0.103±0.116	0.137±0.072	0.045±0.071
c^2	0.199±0.040						
l^2	0.347±0.040	0.347±0.068	0.384±0.076	0.451±0.083	0.398±0.107	0.317±0.071	0.417±0.073
-2 logL	-1243.81	1371.85	1410.67	1320.77	1066.55	4226.20	3294.65
BIC	-1215.99	1391.24	1429.18	1338.67	1083.66	4245.42	3313.07
h^2_t	0.038	0.148	0.104	0.080	0.103	0.137	0.045
t_{fs}	0.560	0.421	0.435	0.490	0.450	0.385	0.440
t_m	0.203	0.037	0.026	0.020	0.026	0.034	0.011

σ^2_a , direct genetic variance; σ^2_c , maternal permanent environmental variance; σ^2_l , maternal temporary environmental variance; σ^2_e , residual variance; σ^2_p , phenotypic variance; h^2_d , direct heritability; σ^2 , ratio of maternal permanent environmental variance to phenotypic variance; l^2 : ratio of maternal temporary environmental variance to phenotypic variance; h^2_t : total heritability; t_m : repeatability of ewe performance; t_{fs} , correlation between full-sib lambs.

Table 4. Estimate of genetic (r_g), maternal temporary environment (r_l), residual (r_e) and phenotypic (r_p) correlations for growth traits in Garole sheep

Trait combination	r_g	r_l	r_e	r_p
BWT-3WT	0.321± 0.152	0.345± 0.122	0.441±0.080	0.350± 0.037
BWT-6WT	0.660± 0.543	0.200± 0.135	0.432±0.086	0.321± 0.042
BWT-9WT	0.999± 0.473	0.331± 0.128	0.388±0.097	0.377± 0.044
BWT-12WT	1.000± 0.376	0.359± 0.157	0.332±0.119	0.395± 0.050
BWT-ADG1	-0.047± 0.605	0.125± 0.140	0.307±0.088	0.185± 0.041
BWT-ADG2	0.999± 0.707	0.178± 0.134	0.032±0.105	0.145± 0.047
3WT-6WT	0.926± 0.113	0.780± 0.061	0.712±0.051	0.766± 0.020
3WT-9WT	0.823± 0.228	0.539± 0.102	0.644±0.071	0.619± 0.033
3WT-12WT	0.858± 0.301	0.368± 0.129	0.663±0.085	0.555± 0.041
3WT-ADG1	0.965± 0.023	0.969± 0.008	0.995±0.002	0.982± 0.002
3WT-ADG2	0.396± 0.535	0.202± 0.156	0.058±0.110	0.143± 0.051
6WT-9WT	0.941± 0.156	0.829± 0.046	0.863±0.032	0.854± 0.014
6WT-12WT	1.000± 0.322	0.622± 0.087	0.806±0.051	0.737± 0.027
6WT-ADG1	0.862± 0.155	0.770± 0.071	0.689±0.054	0.737± 0.022
6WT-ADG2	0.661± 0.347	0.627± 0.087	0.716±0.054	0.675± 0.027
9WT-12WT	1.000± 0.231	0.845± 0.040	0.911±0.025	0.881± 0.013
9WT-ADG1	0.716± 0.303	0.493± 0.116	0.632±0.072	0.581± 0.035
9WT-ADG2	0.951± 0.315	0.643± 0.101	0.586±0.081	0.638± 0.032
12WT-ADG1	0.740± 0.322	0.286± 0.154	0.658±0.090	0.513± 0.045
12WT-ADG2	0.689± 0.552	0.509± 0.160	0.510±0.160	0.509±0.047
ADG1-ADG2	0.238± 0.589	0.208± 0.165	0.043±0.107	0.119± 0.051

BWT, Birth weight; 3WT, 3-month weight; 6WT, 6 month weight; 9WT, 9 month weight; 12WT, 12 month weight; ADG1, average daily gain from birth to 3 month; ADG2, average daily gain from 3 month to 6 month.

Boujenane *et al.* 2015; Ekiz, 2005; Mohammadi *et al.* 2013; Ngere *et al.* 2017). For BWT best model had small contribution of maternal permanent environmental effect ($c^2 = 0.005 \pm 0.007$). The influence of c^2 on BWT was also reported by (Abassi *et al.* 2012, Mokhtari *et al.* 2013; Ngere *et al.* 2017).

The estimate of h^2_t was low to moderate. It ranged from 0.038 to 0.148 for different traits. Estimates of h^2_t by Abegaz *et al.* (2005) was similar for ADG1 and ADG2,

higher for BWT, 6WT and 12WT and lower for 3WT compared to present study. Ekiz (2005) reported lower estimates for ADG1 but higher estimate for ADG2. The estimates were lower than the estimates of Mohammadi *et al.* 2013; Mokhtari *et al.* 2013; Ngere *et al.* 2017 for different growth traits. Boujenane *et al.* (2015) reported higher h^2_t value for BWT but lower values for 3WT compared to present findings. The repeatability of ewe effects across years (t_m) was high for BWT (0.203) but

low of all other traits. Mohammadi *et al.* (2013); Mokhtari *et al.* (2013); Ngere *et al.* (2017) reported higher t_m estimates compared to present study for different growth traits. The correlation between full-sib (t_{fs}) lambs ranged from (0.385–0.560) in Garole sheep. The t_{fs} value reported for BWT and 3WT by Ngere *et al.* (2017) was lower than the present estimates.

Bivariate analysis: Correlation estimates among various growth traits are presented in Table 4. The genetic (r_g), phenotypic (r_p), maternal temporary environmental (r_t) and residual (r_e) correlations were positive for all the trait combinations except BWT-ADG1. Estimates of direct genetic correlation varied from –0.047 to 1.00 for different traits. Estimates of maternal temporary environmental correlations were low to high in magnitude and ranged from 0.125 to 0.969. Phenotypic correlations were low to high in magnitude which varied from 0.119 to 0.982. The positive correlation reported in present study were in agreement with those reported by Mokhtari *et al.* 2013, Mohammadi *et al.* 2013, Boujenane *et al.* 2015, Negre *et al.* 2017 for different trait combinations. Positive genetic correlation estimates for most of the traits indicated no genetic antagonism between the traits. High genetic (0.926 ± 0.113) and moderate maternal temporary (0.780 ± 0.061), environmental (0.712 ± 0.051) and phenotypic (0.766 ± 0.020) correlation between 3WT–6WT show that performance of the lamb at 3 month age can be considered as a suitable indicator of 6 month growth performance and early selection of the lambs can be done in Garole sheep.

Maternal effects especially maternal temporary environmental effect arising due to sharing of common litter environment by lambs should be considered for the estimation of genetic parameters. Low to moderate estimate of direct heritability for body weight and growth rate suggests that studied population of Garole sheep has limited scope of improvement through selection for economic mutton production. Early selection of lamb after weaning can be done as high genetic correlation exists between three month weight and six month weight.

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