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Direct and maternal (Co) variance components, genetic parameters and trends for reproduction traits in Muzaffarnagari sheep of India

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Abstract
The aim of present investigation was to estimate variance and covariance components, genetic parameters and genetic, phenotypic and environmental trends for reproduction traits of Muzaffarnagari sheep for a period of 27 years (1991-2017). Phenotypic data was collected from Central Institute for Research on Goats, Makhdoom. The traits analyzed under present study were age at first service (AFS), age at first lambing (AFL) and litter size (LS). Season, year of lambing, parity and type of birth were included as fixed effects for mixed model analysis of AFS and AFL. Season, year of lambing and parity were included as fixed effects for mixed model analysis of LS. Six animal models with different combinations of direct and maternal genetic effects were fitted by restricted maximum likelihood method using wombat software. Bayesian information criterion was utilized for determining best model for all traits. Model 1, 2 and 6 were obtained as the best model for AFS, AFL and LS respectively. The direct heritability estimates from best models were 0.004±0.04, 0.36±0.1 and 0.59±0.24 respectively for AFS, AFL and LS. The respective maternal heritability estimates for AFL and LS from best models were 0.34±0.1 and 0.16±0.01 respectively. Negative covariance was observed between direct and maternal effects for all traits. The genetic and phenotypic correlation among the traits ranged from .82 (AFS-LS) to 0.99 (AFS-AFL); 0.03 (AFS-LS) to 0.99 (AFS-AFL) respectively. Overall genetic and phenotypic trends for all the traits were in favourable direction. Negative estimates were observed for environmental trends. Desired genetic improvement obtained through selection is hampered by environmental interaction. Importance of maternal effect in influencing the traits was found in the investigation.

Keywords: Animal model, (Co) variance, maternal effects, muzaffarnagari sheep, reproduction traits, trends

Introduction
India, with rich biodiversity, being endowed with 43 registered sheep breeds (NBAGR 2018) comprising of about 12.71% (http://dahd.nic.in/sites) of total livestock population stands in an important place in the income generation for shepherd community, small and marginal farmers. The Muzaffarnagari, sometimes referred as Bulandshahri, is one of the heaviest and largest mutton breeds of India and is widely distributed in the semi-arid region of western Uttar Pradesh, comprising districts of Meerut, Muzaffarnagar, Saharanpur, Bijnor and in some parts of Delhi and Haryana. With a population of about 0.18 million, it accounts for about 0.30% of India's total sheep population (DAHD, 2013) [13]. The breed has a better potential for meat and carpet wool production than other Indian sheep breeds (Mandal *et al*. 2003) [23].
Reproduction parameters have been identified as main factors affecting the profitability and improvement of sheep breeding systems (Matos *et al.* 1997) [28]. In comparison with the faster growth rate, increase in reproductive performance is far more effective in reduction of economic costs of meat production which is because of increase in the number lambs per ewe due to the increase of rate of conception, number of lambs per lambing and their survival and growth (Fogarty 1995) [8]. Accurate estimation of genetic parameters are substantial in developing efficient breeding strategies for economically important traits of sheep such as reproductive traits (Safari *et al.* 2005) [39].

Sheep farming cannot be successful without including the reproduction traits in selection. To determine the effectiveness of genetic selection, genetic trends in the population under consideration must be monitored. Follow-up and the interpretation of genetic trend estimates allow monitoring the efficiency of improvement strategies and assure that the selection pressure is directed towards traits of economic importance (Hudson and Kennedy, 1985) [14].

Some works have been carried out on genetic analysis of Muzaffarnagari sheep for various parameters for production traits (Mandal 2002, 2003, 2007, 2015) [23-26] but there is no information regarding the genetic analysis of this breed for reproduction traits. The aim of present study was to evaluate and analyse the genetic parameters and trends for reproduction traits in Muzaffarnagari sheep.

Materials and Methods

Source of Data

Phenotypic data was collected from the Muzaffarnagari flock maintained at the Genetics and Breeding Division of the Central Institute for Research on Goats (CIRG), Makhdoom, Mathura, Uttar Pradesh, India. The records on reproduction traits for Muzaffarganari sheep spread over a period of 27 years (1991-2017) were collected for the present investigation.

Study area

The Institute occupies an area of about 300 ha and maintains purebred Muzaffarnagari flock. It is situated between Agra and Mathura at 27º10'N and 78º02'E, 169 m above sea level. It is located in the south-western plains, categorized under agro climatic zone-V of the country. The land is undulating, with a difference of about 5-6 m between the lower and higher levels, and forms part of the Jamuna alluvial soil. The climate is almost semi-arid. The temperature ranges from 0 °C to over 45 °C, with annual precipitation of about 750mm, mainly during the monsoon from July to September.

Managemental Practises

At CIRG the animals were maintained under two systems of feeding management i.e. intensive and semi-intensive at farm condition. The sheep at different stages of production viz. pregnant, dry and lactating were kept in separate sheds. Newly born lambs were kept with their dams in lactating pens for 4-5 days and then shifted to lamb nursery.

All the lambs were weaned at 3 months age. In order to study growth potential and carcass characteristics of the breed, each year 15-20 male lambs were put under the intensive system of feeding and reared up to 6 months of age. During this period, lambs were given *ad libitum* growth ration, which consists of about 72% TDN and 16% DCP. Ration formulation consists of maize/rice polish (15%), barley (20%), groundnut cake (35%), wheat bran (20%), molasses (7%), mineral mixture (1.5%) and salt (1.5%). Lambs were also given dry and green fodders *ad libitum* and were not allowed to graze. The remaining animals were maintained under the semi-intensive system of feeding under which they were provided 100-400 g of growth ration at various ages, dry and green fodders, and allowed for 6 hrs of grazing. Ewes at 100 days of their pregnancy and during lactation were provided supplementary feeding, whereas dry ewes were fed only on maintenance ration. Green fodder was supplied by the farm section of the institute throughout the year as per availability in different seasons. The dry fodder like gram or pigeon pea straw was also fed to the animals. The grazing area of the institute is undulating ravine of sandy land with low organic C and available N and dominated with K. Controlled breeding was practiced wherein which breeding seasons were restricted in such a way that the lambing takes place in an optimum environmental period of the year. As such two breeding seasons namely (1) May-June and (2) October-November, were practiced with lambing in October-November and March-April months of the year respectively. Moreover, most of the ewes (70-80%) exhibited estrous in the above mentioned seasons.

Statistical Analysis

Traits studied under present investigation were age of ewe at first service (AFS), age of ewe at first lambing (AFL) and litter size (LS). Initially, data was analyzed for finding the fixed effects for including in the model by least-square analysis of variance (SPSS 2010). Fixed effects namely season of lambing (two levels), period of lambing (7 levels) with 4 years in each period, parity of dam (5 levels) and type of birth of lambs (2 levels) were included in the analysis for AFS and AFL. While season of lambing (two levels), period of lambing (7 levels) with 4 years in each period and parity of dam (5 levels) were included in the analysis of LS. Dam's weight at lambing was taken as a covariate. (Co) variance components and genetic parameters were estimated by restricted maximum likelihood (REML) procedure using wombat software (Meyer, 2013) [29]. Only significant effects ($p \leq 0.05$) were included in the models which were subsequently used for genetic analysis. The convergence of the REML solutions was assumed when the variance of function values ($-2 \log L$) in the simplex was less than 10^{-8}. This analysis was repeated until a global maximum was reached. When estimates did not change up to two decimals, convergence was confirmed. Six models which accounted for the direct and maternal effects were fitted and are as follows:

$$Y = X\beta + Z_a a + \varepsilon$$
$$Y = X\beta + Z_a a + Z_m m + \varepsilon, \text{ with } Cov(a_m, m_o) = 0$$
$$Y = X\beta + Z_a a + Z_m m + \varepsilon, \text{ with } Cov(a_m, m_o) = A\sigma_{am}$$
$$Y = X\beta + Z_a a + Z_c c + \varepsilon$$
$$Y = X\beta + Z_a a + Z_m m + Z_c c + \varepsilon, \text{ with } Cov(a_m, m_o) = 0$$
$$Y = X\beta + Z_a a + Z_m m + Z_c c + \varepsilon, \text{ with } Cov(a_m, m_o) = A\sigma_{am}$$

Where Y is the vector of record, β, a, m, c, and ε are the vectors of fixed, direct additive genetic, maternal genetic, permanent environmental effects of the dam and residual effects, respectively. X, Z_a, Z_m, and Z_c are the incidence matrices that relate these effects to 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

$$V(a) = A\,\sigma^2_a,\ V(m) = A\,\sigma^2_m,\ V(c) = I\,\sigma^2_c,\ V(\varepsilon) = I\,\sigma^2_e \text{ and } Cov(a,m) = A\sigma_{am}$$

Where I represents identity matrix; σ^2_a, σ^2_m, σ^2_c, and σ^2_e are additive genetic, additive maternal, maternal permanent environmental and residual variances respectively. The direct-maternal correlation (r_{am}) was calculated for all the traits under study. Bayesian information criterion (BIC) was used to choose the best fit model among all the models (Schwarz, 1978) [43]. The model yielding lowest BIC, best explains the variation in the trait and was considered as the best one.

The phenotypic trend can be estimated as the regression of population performance on time. The genetic trend was estimated by Henderson's principle (Henderson 1973) according to which, trend estimation was done as, regression of the weighted average transmitting abilities of the sires for each period on time (period). The Expected Breeding Values (EBV) of each sire was obtained by the formula given by Lush (1935) [22].

$$EBV = \frac{0.5nh^2}{1+(n-1)t}\ (LSC)$$

Where EBV indicates the expected breeding value, h^2 is heritability, t is intra class correlation (0.25 h2 for the half sib progeny), n is number of half sib progeny and LSC is the least squares constant which were obtained from the wombat analysis. The expected transmitting abilities were obtained by dividing the respective EBVs by 2. Then the weighted transmitting abilities of sires for period, were then regressed on period. The regression value, thus obtained, was multiplied by 7 (as there were 7 periods) to get the total genetic change and then divided by 27 (as there were 27 years in 7 periods) in order to get the annual genetic change. The environmental trends were obtained by subtracting the genetic trend from the phenotypic trend. (Balasubramaniam *et al.*, 2013) [44].

Results

The characteristics of data structure of studied traits are mentioned in table 1. The entire pedigree information was spread over the period of 27 years and intensity of distribution was fair enough to obtain reliable estimates of genetic parameters for the traits under study. The least square means along with standard error for reproduction traits were specified in the table 2. Statistical analysis revealed that season has significant effect ($p<0.05$) on litter size alone. Year of lambing has highly significant ($p<0.01$) effect on AFS and AFL. LS was not influenced by year of lambing.

Estimates of (co)variance components and genetic parameters obtained from different models are presented in table 3 highlighting the best model for different traits. Generally, model 1 by includes only animal additive genetic effects alone, whereas model 2 consists of both animal and maternal genetic effects and model 3 includes both animal and dam genetic effects along with the covariance between the effects. Model 4 includes only maternal permanent environment, model 5 includes both dam genetic and environmental effects and model 6 provides all the effects along with the covariance between the effects. In our study we found that model 1, 2 and 6 were best model for AFS, AFL and LS respectively based on BIC values. The direct heritability estimates from best models were 0.004±0.04, 0.36±0.1 and 0.59±0.24 respectively for AFS, AFL and LS. The respective maternal heritability estimates for AFL and LS from best models were 0.34±0.1 and 0.16±0.01 respectively. Clear negative correlation (-1) exists between additive genetic and maternal effects in all the studied traits. Estimates of genetic and phenotypic correlations among all the considered traits from the bivariate analysis were mentioned in the table 4. Genetic correlations among all the studied traits were highly positive, and the magnitude were high ranging from 0.82 (AFS-LS) to 0.99 (AFS-AFL) and the phenotypic correlations were also positive and varied from low to high in magnitude from 0.03 (AFS-LS) to 0.99 (AFS-AFL). The genetic, phenotypic and environmental trends for all the studied parameters are given in the table 5 and graphical representations of trends for all the traits were represented from fig 1 to 3. The genetic trends was positive for AFL, negative for AFS and LS. The genetic trends for the traits varied from -0.04 (LS) to 0.09 (AFL).

Discussion

Coefficient of variation for the present study ranged from 17 to 34.53. This is in agreement with the findings of Jafari *et al*. (2014) [17] and Aguirre *et al*. (2017) [1]. Lesser value than the present study was reported by Babar (2008) [3]. The overall least square means of AFS, AFL and LS were 599.54 days, 698.87 days and 1.07 respectively. Lesser value for AFS were reported by Babar (2008) [3] in lohi sheep and the estimate was comparable with the value of Babar and Javad (2009) [3] in lohi sheep. Higher value than the present estimate for AFL were observed by Lalit *et al*. (2017) [20] in Harnali sheep and Saghi and Shahdadi (2017) [40] in Kordi sheep and lower estimates for AFL obtained by Shoeman and Burger (1992) [42] in Dorper sheep, in multibreed meat sheep of Brazil, Aguirre *et al*. (2017) [1] in Santa Ines sheep, and Marufa *et al*. (2017) [27] in Abera sheep. Least square mean of LS is lesser than the estimates obtained by various authors in different breeds of sheep. Shoeman and Burger 1992 [42]; Hagger 2002 [9]; Hanford *et al*. 2002 [10]; Khalili *et al*. 2002 [18]; Rosati *et al*. 2002 [36]; Wyk *et al*. 2003 [47]; Ekiz *et al*. 2005 [5]; Hanford *et al*. 2006 [11]; Vatankhah *et al*. 2008 [48]; Rashidi *et al*. 2011 [35]; Mohammadi *et al*. 2012, 2013 [30, 32]; Boujenane *et al*. 2013 [4]; Posht-e-Masari *et al*. 2013 [34]; Mohammadi and Abollahi-Arpanahi 2015 [38]; Roshanfekr *et al*. 2015 [37]; Yavarifard *et al*. 2015 [49]; Aguirre *et al*. 2017 [1]; Marufa *et al*. 2017 [27]; Saghi and Shahdadi 2017 [40] and Roudbar *et al*. 2018 [38]. Lower least square means than the present study for LS was reported by Eteqadi *et al*. (2002) in Guilan sheep, Mokhtari *et al*. (2010) [33] in Kermani sheep and Jafari *et al*. (2014) [17] in Makuie sheep. Year of lambing had significant effect on AFS and AFL and this is in conformity with the report of Lalit *et al*. (2017) [20] and Saghi and Shahdadi (2017) [40]. But Shoeman and Burger (1992) [42] and Aguirre *et al*. (2017) [1] reported that year of lambing shows non-significant effect on AFL. Differences that prevailed in different periods could be due to changes in nutrition, management, agro climatic variations and breeding strategies followed during different periods. Year of lambing had no significant effect on LS and this is in agreement with the findings of Shoeman and Burger (1992) [42] and Rosati *et al*. (2002) [36]. In contrary many workers reported that year of lambing produces significant effect on LS (Ekiz *et al*. 2005 [5]; Mokhtari *et al*. 2010 [33]; Mohammadi *et al*. 2013; Fogarty and Mulholland 2014 [7]; Jafari *et al*. 2014 [17] and Roshanfekr *et al*. 2015) [37]. Season had significant effect on LS and same was reported by Fogarty and Mulholland (2014) [7].

The direct heritability estimates of AFS, AFL and LS in the present study were higher than the estimates reported by many workers, Khalili *et al*. 2002 [18]; Rosati *et al*. 2002 [36]; Wyk *et al*. 2003 [47]; Ekiz *et al*. 2005 [5]; Mokhtari *et al*. 2010 [33]; Boujenane *et al*. 2013 [4]; Posht-e-Masari *et al*. 2013 [34]; Mohammadi *et al*. 2013 [32]; Jafari *et al*. 2014 [17]; Roshanfekr *et al*. 2015 [37]; Yavarifard *et al*. 2015 [49]; Aguirre *et al*. 2017 [1]; Eteqadi *et al*. 2017 [6]; Khan *et al*. 2017; Saghi and Shahdadi 2017 [40] and Roudbar *et al*. 2018 [38]. Higher direct heritability estimate than the present study for AFS was reported by Babar 2008 [3] in Lohi sheep. Moderate heritability estimates observed in the present study shows that little improvement can be made by selecting these reproduction traits. The maternal heritability estimates of present investigation is higher than the reports of Rosati *et al*. (2002) [36], Rashidi *et al*. (2011) [35] and Saghi and Shahdadi (2017) [40]. Higher heritability estimates shows the importance of maternal effect in influencing the reproduction traits without measuring it, heritability may produce biased results. High and positive genetic and phenotypic correlation among the studied traits shows that selection for any of these traits will improve others spontaneously. Similarly, positive genetic and phenotypic correlation between AFS and AFL were reported by Khan *et al*. (2017) [19] and Saghi and Shahdadi (2017) [40]. In contrary negative estimates for LS with other traits was reported by Khan *et al*. (2017) [19]. Literature for genetic, phenotypic and environmental trends estimates for reproduction traits in sheep is very meagre. Present study shows positive genetic trends for AFL but negative for AFS and LS indicating that selection had not been done based on AFS and LS. Similar findings were reported by Mohammadi and Abollahi-Arpanahi (2015) [38] in Zandi sheep and Aguirre *et al*. (2017) [1] in Santa Ines sheep. Favourable genetic trend for LS was reported by Roshanfekr *et al*. (2015) [37] in Arabi sheep. High negative trend estimates for the traits indicate that the environmental interaction provides not much hinderance for genetic improvement in case of reproduction traits.

Table 1: Characteristics of the data structure of Muzaffarnagari sheep

Trait	AFS	AFL	LS
Number of records	1079	1039	1094
Mean	575.99	821.34	1.07
Standard deviation	198.86	384.55	0.18
(CV%)	34.53	46.8	17
Number of sires with progeny record	175	179	171
Number of dams with progeny records	765	783	770

AFS age at first service; AFL age at first lambing; LS litter size; CV coefficient of variation

Table 2: Least square means with Standard error for reproduction traits of Muzaffarnagari sheep

	AFS		AFL		LS	
	N	**MEAN ±SE (days)**	**N**	**MEAN ±SE (days)**	**N**	**MEAN ±SE (days)**
Overall mean	1079	599.54±8.54	1039	698.87±73.94	1094	1.07±0.02
Season	NS		NS		*	
1	507	620.13±10.83	493	724.56±74.21	511	1.08^a±0.02
2	572	578.96± 9.89	546	673.19±74.23	583	1.06^b±0.02
Period	**		**		**NS**	
1(1991-94)	191	656.64^c±15.73	175	785.04^d±75.47	209	1.04±0.03
2(1995-98)	69	781.45^d±23.33	96	912.69^e±76.61	136	1.03±0.03
3(1999-02)	202	521.35^a±14.68	187	603.88^a±75.75	203	1.03±0.02
4(2003-06)	141	587.03^b±17.08	145	653.62^{bc}±75.70	153	1.06±0.03
5(2007-10)	110	600.86^b±18.31	117	689.70^c±74.49	115	1.1±0.03
6(2011-14)	255	541.77^a±12.76	239	632.99^{ab}±74.86	227	1.08±0.02
7(2015-17)	111	507.70^a±17.84	80	614.19^{ab}±76.89	41	1.05±0.04
Parity	**NS**		**NS**		**NS**	
1	358	604.49±12.19	358	703.86±93.87	380	1.07±0.01
2	265	596.76±13.03	249	694.02±94.02	268	1.07±0.01
3	198	617.82±14.52	185	714.64±94.33	193	1.10±0.02
4	117	579.96±17.93	112	679.59±94.98	116	1.08±0.02
5	141	598.67±17.02	133	698.86±94.72	135	1.09±0.02
Type of birth	**NS**		**NS**			
1	920	588.87±7.23	899	750.89±33.60		
2	159	610.22±15.08	139	774.65±37.03		

AFS age at first service; AFL age at first lambing; LS litter size
***p*<0.01; **p*<0.05; NS non-significant (*p*>0.05); N number of observations; TOB type of birth; Means without superscript do not differ significantly.

Table 3: Variance components and genetic parameters for reproduction traits of Muzaffarnagari sheep from best models

Trait	AFS	AFL	LS
Best model	1	2	6
σ^2_a	0.66	2576670	219994
σ^2_m	-	2603910	31463.4
σ_{am}	-	-	-83197
σ^2_c	-	-	1252.8
σ^2_e	34139.1	2482030	27068.3
σ^2_p	34139.8	7662610	196581
h^2	0.004±0.04	0.36±0.1	0.59±0.24
m^2	-	0.34±0.1	0.16±0.01
r_{am}	-	-	-1
c^2	-	-	0.006±0.0
BIC	12338.9	8602.02	7091.35

σ^2_a, σ^2_m, σ^2_c, σ^2_e and σ^2_p are additive genetic, additive maternal, maternal permanent environmental residual and phenotypic variances respectively; σ_{am} is the covariance between additive direct and maternal genetic effects; h^2 direct heritability; m^2 maternal heritability; r_{am} direct-maternal genetic correlation; c^2 maternal permanent environment variance as a proportion of phenotypic variance; BIC bayesian information criteria, AFS age at first service; AFL age at first lambing; LS litter size.

Table 4: Genetic Correlation (above diagonal) and phenotypic correlation (below diagonal) among traits from bivariate analysis of Muzaffarnagari sheep

	AFS	AFL	LS
AFS		0.99±0.07	0.82±0.00
AFL	0.99±0.08		0.87±0.00
LS	0.03±0.03	0.04±0.03	

AFS age at first service; AFL age at first lambing; LS litter size

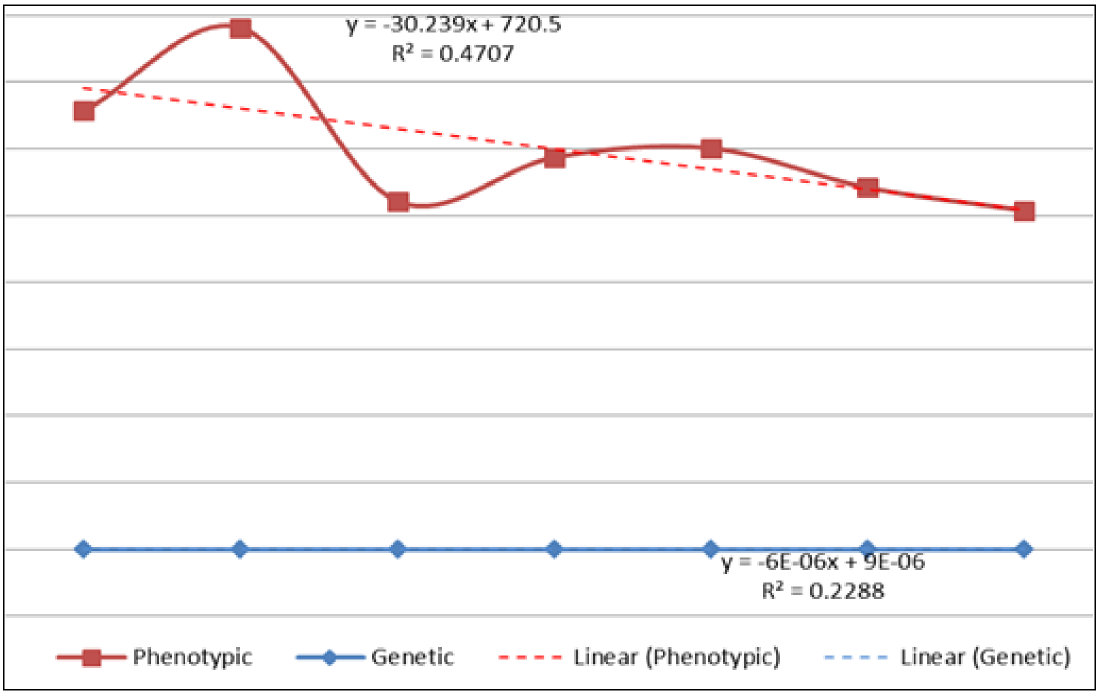

Fig 1: Period wise genetic and phenotypic trends of age of ewe at first service, R^2 coefficient of determination; y dependent variable; x independent variable

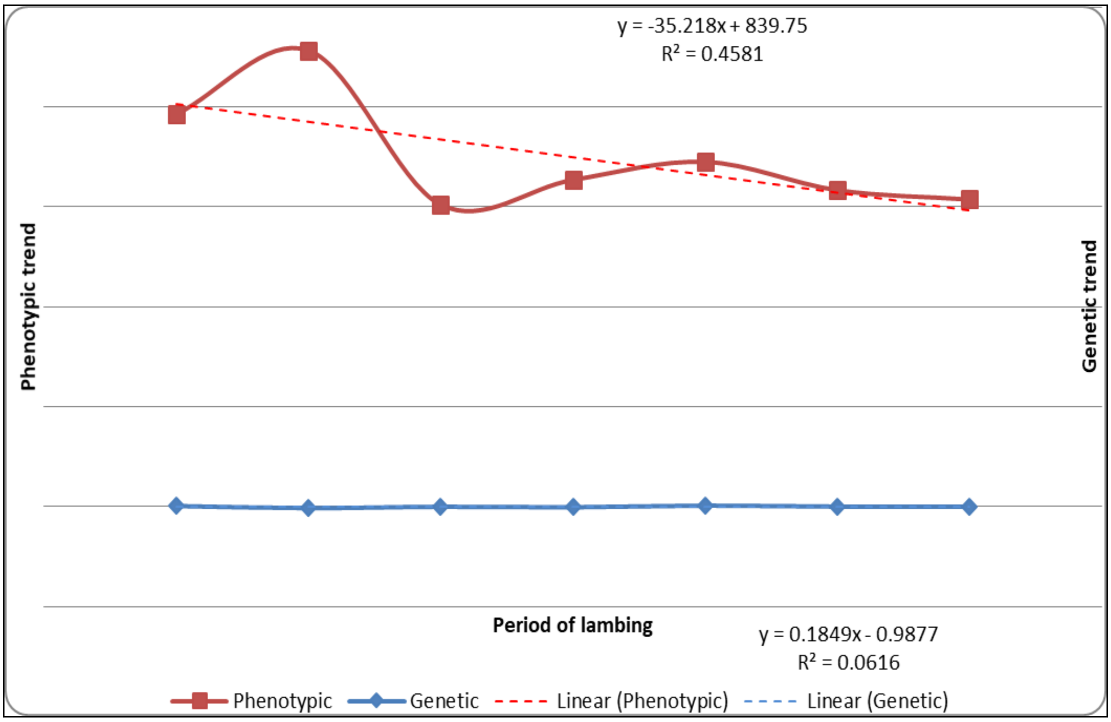

Fig 2: Period wise genetic and phenotypic trends of age of ewe at first lambing, R^2 coefficient of determination; y dependent variable; x independent variable

Table 5: Genetic, phenotypic and environmental trends per year for reproduction traits of Muzaffarnagari sheep

Traits	Genetic trend	Phenotypic trend	Environmental trend
AFS	-0.000002	-7.84	-7.84
AFL	0.09	-9.13	-9.22
LS	-0.04	0.002	0.04

AFS age at first service; AFL age at first lambing; LS litter size

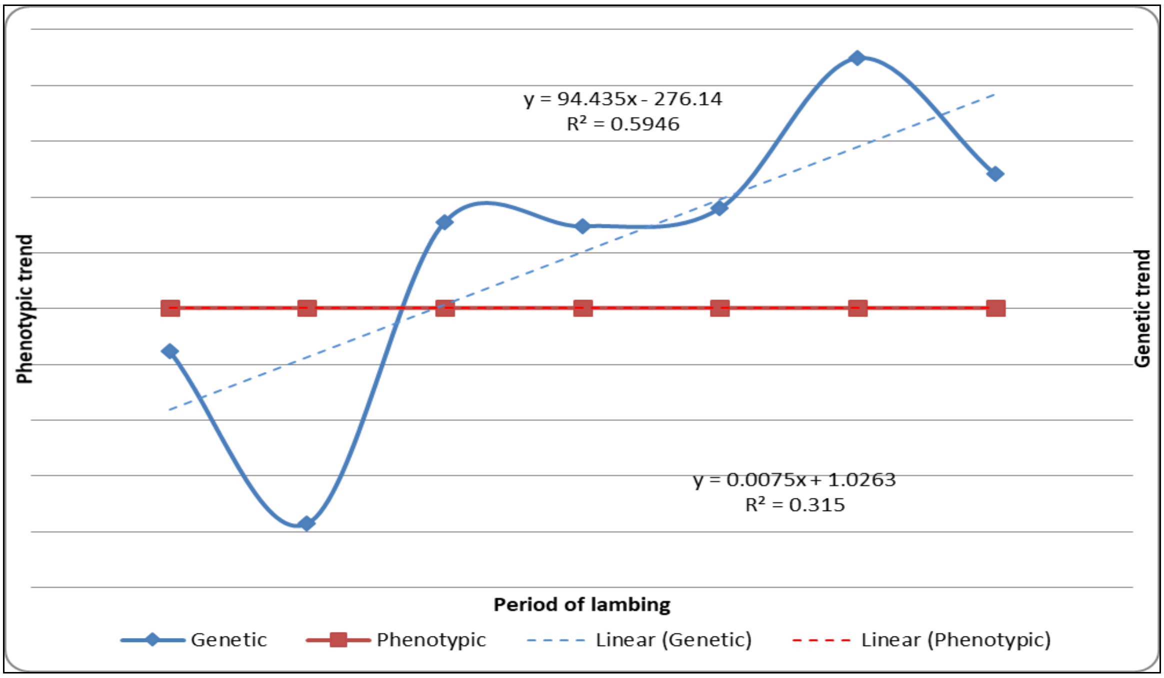

Fig 3: Period wise genetic and phenotypic trends of litter size, R^2 coefficient of determination; y dependent variable; x independent variable

Conclusion

Direct heritability estimates shows that when selection is carried out for those traits, response could be attained to some extent. Since maternal heritability estimates are moderate, excluding the in the model will lead to over estimation of direct heritability. High and positive genetic and phenotypic correlation among the studied traits indicates that selection based on any trait will lead to correlated response on the other. Overall somewhat favourable trends have been attained for all the traits, indicating that response is in positive direction, and if environmental interaction is taken care of, genetic improvement can be attained in a better way.

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Conflict of Interest

Not available

Financial Support

Not available

Reference

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