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Meta-analysis of genetic parameters for growth traits in meat, wool and dual-purpose sheep breeds in the world using a random-effects model

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Abstract

Background: There is large variation in genetic parameters in literature for growth traits in sheep. Reliable estimation of genetic parameters is required for developing breeding programmes.

Objectives: The aim of this study was to aggregate results of different studies by meta-analysis to improve reliability of estimated parameters.

Methods: In the current study, 221 papers that have been published between 1995 and 2021 were reviewed. Using a random-effects model in the Comprehensive Meta-Analysis software, direct and maternal heritabilities, as well as, genetic and phenotypic correlations between growth traits were estimated in meat (M), wool (W) and dual-purpose (D) sheep breeds. The growth traits in this study were birth weight, 3-month weight, 6-month weight, 9-month weight and yearling weight.

Results: The combined direct heritability was the lowest for birth weight (0.190 $\pm$ 0.004, 0.198 $\pm$ 0.003 and 0.196 $\pm$ 0.004 for M, W and D breeds, respectively) and the highest for yearling weight (0.264 $\pm$ 0.010, 0.304 $\pm$ 0.005 and 0.285 $\pm$ 0.020 for M, W and D breeds, respectively). The maternal heritability was the lowest for yearling weight (0.085 $\pm$ 0.003, 0.055 $\pm$ 0.002 and 0.052 $\pm$ 0.005 for M, W and D breeds, respectively) and the highest for 6-month weight (0.240 $\pm$ 0.088, 0.164 $\pm$ 0.001 and 0.162 $\pm$ 0.006 for M, W and D breeds, respectively). The phenotypic and genetic correlations were lower between the weights measured at more distant intervals. The lowest genetic correlation was observed between birth weight and yearling weight (0.290 $\pm$ 0.051 for W breeds).

Conclusions: The small standard errors could indicate that the aggregation of results from different studies improved the reliability of estimated parameters and reduced range of 95% confidence intervals. Hence, the results could be used with greater level of confidence in sheep breeding programmes.

1 | INTRODUCTION

Small ruminant production contributes significantly to the national economy and economic livelihood of rural communities in many countries. The rising price of red meat has increased the importance of sheep meat production in recent years. Consequently, sheep producers are keen to improve the quantity and quality of their sheep meat to increase profits. To achieve this aim, superior management practices and genetic improvement for meat traits are required (Fogarty, 1995; Mekuriaw & Haile, 2014). Moreover, farm animal species play crucial roles in satisfying demands for meat on a global scale, and they are genetically being developed to enhance the efficiency of meat production (Amiri Roudbar et al., 2017). In particular, one of the important breeders' aims is to increase skeletal muscle growth in farm animals (Arabpour et al., 2021; Zamani et al., 2015). The enhancement of muscle development and growth is crucial to meet consumers' demands regarding meat quality (Mohammadabadi et al., 2021).

Genetic parameters including heritability and genetic correlation between economically important traits are needed for planning breeding strategies in livestock (Oliveira et al., 2017). In sheep breeding for meat production, reliable genetic parameters for meat traits such as growth traits are essential to develop robust genetic evaluation and improvement programmes (Safari et al., 2005). However, especially for minor breeds, the genetic parameters estimated in small sample size studies are associated with large standard errors (SEs). In such cases, combining estimates from different studies is recommended to increase the reliability of the genetic parameters (Safari et al., 2005).

The genetic parameters in different studies are often estimated at different stages of growth, with different sample sizes and for different sheep breeds. This could lead to considerable variability among the estimated parameters in different studies (Akanno et al., 2013). A practical solution is to combine genetic estimates from different studies using a random-effects model which can handle variability of parameters properly (Ravi, 2000). Meta-analysis has been defined as 'the statistical analysis of a large collection of analysis results from individual studies for the purpose of integrating the findings' (Glass, 1976). Using a suitable meta-analysis model, the genetic parameters are expected to be estimated more accurately by combining the results from many studies (Koots & Gibson, 1996; Lobo et al., 2000).

There are two popular statistical models for meta-analysis, the fixed-effect model and the random-effects model. Under the fixed-effect model, there is one true effect size that underlies all the studies in the analysis and that all differences in observed effects are due to sampling error. By contrast, under the random-effects model, true effect could vary from study to study due to the differences (heterogeneity) among studies (Borenstein et al., 2010).

A meta-analysis has been performed to estimate accurate genetic parameters for growth traits in pigs (Akanno et al., 2013), goats (Campos et al., 2017) and beef cattle (Diaz et al., 2014; Giannotti et al., 2005). In sheep, there are a few published papers on meta-analysis of economically important traits (Fogarty, 1995; Medrado et al., 2021; Safari et al., 2005). However, these authors have combined the results from the studies which were conducted mainly on European sheep breeds. A meta-analysis with 191 articles was carried out to estimate genetic parameters for some economic traits in sheep. A total of 191 articles were evaluated using a random effect model. The meta-analysis estimated heritability ranging from 0.1213 to 0.3912 for growth traits, from 0.0398 to 0.3047 for reproductive traits, and from 0.2063 to 0.3299 for carcass traits (Medrado et al., 2021).

The main objective of this study was to calculate robust estimates and SEs for direct heritability (h_a^2) and maternal heritability (h_m^2) as well as the phenotypic (r_p) and genetic (r_g) correlations between growth traits at different ages in meat (M), wool (W) and dual-purpose (D) sheep breeds. We used a random-effects model to combine the results of the papers published between 1995 and 2021 sheep breeds.

2 | MATERIALS AND METHODS

2.1 | Scope and traits

This meta-analysis study was performed to estimate reliable genetic parameters of growth traits in M, W and D sheep breeds. The growth traits in our study were birth weight (BW), 3-month weight (3MW), 6-month weight (6MW), 9-month weight (9MW) and yearling weight (YW). Systematic search for papers was performed in Web of Science (https://www.webofknowledge.com), Scopus/Elsevier (https://www.elsevier.com/), ScienceDirect (https://www.sciencedirect.com), PubMed (https://pubmed.ncbi.nlm.nih.gov/), Google Scholar (https://scholar.google.com), IranDoc (https://ganj.irandoc.ac.ir/), Magiran (https://www.magiran.com) and Scientific Information Database (SID) (https://www.sid.ir/). To retrieve the papers that were reviewed in the current study, in each of these databases we searched for the keywords 'heritability', 'growth traits', 'body weight', 'genetic correlation', 'phenotypic correlation' and 'sheep'. At first, there was not any time limitation in the search process, and the results of search were transferred to the information management software EndNote X9 (Hupe, 2019). Then, the papers published between 1995 and July 2021 were selected. Duplicated papers retrieved from different databases were excluded. In the screening stage, the title and abstract of the papers were carefully checked and the irrelevant papers were excluded. The quality of the papers was evaluated using a checklist consisting of six general criteria including title, abstract, introduction,

material and methods, results, and discussion. For evaluating the qualification of papers, the full text of papers was re-evaluated after screening. In the final stage, the papers that reported the genetic parameters for growth traits especially in minor sheep breeds were selected for our meta-analysis study.

2.2 | Extracting data and quality control

The title of paper, name of the first author, year of publication, geographic location (i.e., country) of the study and breed and sample size in the study were stored for the selected papers. On the other hand, the reported h_a^2, h_m^2, r_p and r_g for growth traits and their associated confidence interval (CI) and SE were extracted from these papers. For the papers that only reported the CI or upper and lower limits, the SEs were calculated using Equation 1.

$$SE_i = \frac{CI_i}{k} = \frac{\text{Upper limit }_i - \text{Lower limit }_i}{2 \times k},$$ (1)

where SE_i is the estimated SE in ith study and $k = 1.645$, 1.960 and 2.575 for 90%, 95% and 99% CIs, respectively.

In the Comprehensive Meta-Analysis software (Borenstein et al., 2006), the correlation coefficients (r) could be automatically converted to the Fisher's Z scale (Z) to ensure normal distribution of the imported correlations. In the study Z, SE and the number of observations (n) were calculated using Equations 2–4. Hence, it could determine and exclude the outlier Zs which were more than 1.5 times of the interquartile range (i.e., quartile 3—quartile 1) below quartile 1 or above quartile 3 (Koots et al., 1994; Oliveira et al., 2017).

$$Z_i = 0.5 \ln\left(\frac{1+r_i}{1-r_i}\right),$$ (2)

$$SE_{Zi} = \sqrt{n_i - 3},$$ (3)

$$n_i = \frac{1-r_i}{SE_i^2} + 2.$$ (4)

The heritability estimates which had relative SE greater than 100% were excluded from the current study. For all growth traits, the SE of h_a^2 and h_m^2 was estimated using Equation 5 (Ravi, 2000).

$$SE_j = \sqrt{\frac{\sum_{i=1}^{k} SE_i^2 S_i^2}{\sum_{i=1}^{k} S_i}} / S_j,$$ (5)

where SE_j and S_j were approximated estimate of standard error and sample size in the jth study, respectively; k was the total number of studies in which SE was reported. SE_i and S_i are the reported standard error and sample size in the ith study, respectively.

The I^2 index in the Comprehensive Meta-Analysis software was used to evaluate the heterogeneity of the genetic parameters reported in the selected studies. In summary, heterogeneity test in meta-analysis studies examined the null hypothesis that the estimated parameter is

the same in all studies. Consequently, the estimated I^2 in Equation 6 can be divided into four categories: <25% (very low heterogeneity), 25%–50% (low heterogeneity), 50%–75% (moderate heterogeneity) and >75% (high heterogeneity) (Higgins et al., 2003; Oliveira et al., 2017).

$$I^2 = \frac{Q - df}{Q} \times 100,$$ (6)

where Q and df are the calculated Q statistics and degrees of freedom from Cochran's Q test, respectively (Cochran et al., 1954). For each of the genetic parameters, I^2 was calculated to determine whether the variation observed between studies was different from the expected sampling error variance.

2.3 | Meta-analysis

A meta-analysis with a random-effects model was performed for estimating the heritability and correlations between growth traits using the Comprehensive Meta-Analysis software (Equation 7) (Borenstein et al., 2006). The standard error and the range of the estimated parameters with CI of 95% were also reported in the software.

$$\hat{\theta}_i = \bar{\theta} + u_i + e_i,$$ (7)

where $\bar{\theta}$ is the estimated average for each of the parameters, $\hat{\theta}_i$, u_i and e_i are the published estimate, random effect of the study (i.e., deviation from the average) and residual effect in the ith paper. Hence, the effect of variation among studies as $u_i \sim N(0, \tau^2)$ and within study sampling error as $e_i \sim N(0, \sigma^2_e)$ are incorporated in the model, where τ^2 and σ^2_e are heterogeneity and residual variances, respectively. For the r_p and r_g between growth traits, the estimated average Z (i.e., $\bar{Z}$) in the random-effects model was re-transformed to correlation coefficient ($\bar{r}$) using Equation 8 in the Comprehensive Meta-Analysis software.

$$\bar{r} = \frac{e^{2\bar{Z}} - 1}{e^{2\bar{Z}} + 1}.$$ (8)

3 | RESULTS

Based on the initial search in the databases, 2001 papers were found: 994 in Web of Science, 330 in Scopus, 278 in Science Direct, 228 in PubMed, 72 in IranDoc, 45 in Magiran, 43 in Google Scholar and 11 in SID. Four hundred and thirteen duplicated papers and 894 papers were excluded after evaluating the titles, and 347 papers were also excluded after evaluating the abstracts, from the current study. Reviewing the full text of the papers, 120 additional papers were also excluded as they were citing the genetic parameters reported in other papers. Finally, 221 papers were selected for this meta-analysis study, of which 121, 61 and 39 were associated with M, W and D sheep breeds, respectively (Tables 1–3).

TABLE 1 Breeds, countries and references for meat breeds

Breed	Country	References
Afrino	South Africa	Snyman et al. (1997), Snyman et al. (1995)
Afshari	Iran	Ghafouri-Kesbi et al. (2018)
Arabi	India	Shokrollahi et al. (2012), Roshanfekr (2014)
Barki	Egypt	Sallam et al. (2019), Sallam et al. (2019), Shemeis (2008), El-Awady (2011), Gad and El-Vakil (2013)
Blackhead Tsigai	India	Pelmus et al. (2013), Singh et al. (2006)
Chios	Emirates	Al-Shorepy (2001)
D'man	Morocco	Boujenane et al. (2015), Aloulou et al. (2002)
Djallonkťe	Kenya	Bosso et al. (2007), Agbolosu et al. (2005)
Doyogena	Ethiopia	Habtegiorgis et al. (2020), Hassen et al. (2003)
Elsenburg Dormer	South Africa	Van-Wyk et al. (2003)
Finn	USA	Borg et al. (2009)
Garole	India	Prakash et al. (2020)
Ghezel	Iran	Jasouri et al. (2014)
Guilan	Iran	Zendedel-Dalir-Haghighat et al. (2015), Eteqadi et al. (2014)
Harnali	India	Bangar et al. (2020), Lalit et al. (2016), Kumar et al. (2017)
Horro	South Africa	Abegaz et al. (2002, 2010)
Katahdin	USA	Ngere et al. (2017)
Kourdi	Iran	Shahdadi and Saghi (2017), Firouzi et al. (2009), Saghi and Shahdadi (2015), Nassiri et al. (2004), Naghavian et al. (2016), Namvar et al. (2017), Shahdadi and Saghi (2016)
Latvian native	Latvia	Puste et al. (2013)
Lipska	Serbia	Petrović et al. (2012)
Lleyn	Turkey	Ceyhan et al. (2015)
Lori	Iran	Mohammadi et al. (2015), Beiranvand et al. (2016), Beiranvand et al. (2013)
Lori-Bakhtiari	Iran	Rashedi-Dehsahrae (2019), Farhadi and Roshanfekr (2016), Vatankhah et al. (2008)
Madras Red	India	Ganesan et al. (2013)
Malpura	India	Gowane et al. (2015), Gowane et al. (2010), Parkash et al. (2012)
Margra	India	Ivekanand et al. (2017)
Meatmaster	New Zealand	Brito et al. (2017)
Mecheri	India	Jeichitra et al. (2016)
Mehraban	Iran	Latifi et al. (2014), Aghali-Gamasaee et al. (2009), Yavarifard et al. (2015), Aghaali-Gamasae et al. (2010), Zamani et al. (2008), Ghafouri-Kesbi and Baneh (2012), Ghafouri Kesbi et al. (2008)
Mengali	India	Tariq et al. (2010)
Menz	Ethiopia	Gizaw et al. (2007)
Merinolandschaf	Serbia	Petrovic et al. (2012)
Mexican native	Mexico	De la Cruz et al. (2019)
Moghani	Iran	Najafi et al. (2011), Bayeriyar et al. (2011), Ghavi-Hossein-Zadeh and Ardalan (2010a), Ghavi-Hossen-Zade et al. (2010b), Behmaram and Rashedi-Dehsahraei (2019)
Morada nova	Brazil	Shiotsuki et al. (2014)
Morkaraman	Turkey	Kopuzlu et al. (2014)
Moroccan timahdit	Morocco	El-Fadili et al. (2000), Boujenane et al. (2002)
Munjal	India	Malik et al. (2018), Yadaz et al. (2018)
Muzaffarnagari	South Africa, India	Mandal et al. (2015), Mandal et al. (2009), Mandal et al. (2003), Gopal et al. (2014)
Nilagiri	India	Venkatarmanan et al. (2016a), Venkataramanan (2016b), Venkatarmanan et al. (2015)
Nordic	Denmark	Norberg et al. (2005)
Omani	Egypt	Al-Subeihi et al. (2020)
Romanov	Spain	Hanford et al. (2006), Maria et al. (1993), Faid-Allah et al. (2017), David et al. (2009)

(Continues)

TABLE 1 (Continued)

Breed	Country	References
Sanjabi	Iran	Ahmadi et al. (2004), Sadeghi et al. (2006), Mohammadi et al. (2010), Miraei-Ashtiani et al. (2007)
Sardi	Morocco	Jannounea et al. (2015), Boujenane and Diallo (2017)
Segurena	Morocco, Spain	Analla et al. (1997), Lupi et al. (2015)
Shal	Iran	Savar-Sofla et al. (2017), Mohammadi et al. (2012), Amou-Posht et al. (2018), Mohammadi et al. (2013), Patiabadi et al. (2018)
Sjenicka Pramenka	Serbia	Zeljić et al. (2019)
Sonadi	India	Sharma et al. (2019)
Sonmez	Turkey	Taskin et al. (2012)
Suffolk	Brazil	Notter (1998), Portes et al. (2018), Tamiosol et al. (2013)
Taleshi	Iran	Narimani et al. (2009), Banh et al. (2010)
Thai native	Thailand	Supakorn et al. (2013)
Zandi	Iran	Shayesteh et al. (2016), Senemari et al. (2008), Dadian et al. (2008), Mohammadi et al. (2010), Lavvaf et al. (2007), Senemari et al. (2011), Mohammadi et al. (2011), Mohammadi et al. (2014)
Zel	Iran	Yeganehpour et al. (2015)

TABLE 2 Breeds, countries and references for wool breeds

Breed	Countries	References
Alpine Fine-wool	China	Li and Purvis (2012)
Baluchi	Iran	Hassani et al. (2009), Akhtar et al. (2014), Abbasi et al. (2012), Gholizadeh and Ghafouri-Kesbi (2015), Saghi et al. (2012)
Bharat Merino	India	Tomar et al. (2000), Dixit et al. (2001), Singh and Kushwaha (1995)
Chiapas	Spain	Lopez-Ordaza et al. (2012)
Chokal	India	Kushwaha et al. (2009)
Karagouniko	Greece	Goliomytis et al. (2006)
Karakul	Iran	Talebi (2012), Mirhoseini et al. (2015)
Kermani	Iran	Kargar et al. (2007), Moradi-Shahrbabak et al. (2014), Barazandeh et al. (2008), Eftekhari-Shahroudi et al. (2002), Bahreini-Behzadi et al. (2007), Mokhtari et al. (2008)
Magra	India	Vivekanand et al. (2018)
Makoui	Iran	Naderi (2018), Yazdi et al. (1997), Mohammadi et al. (2013), Jafari et al. (2012)
Marwari	India	Singh et al. (2016), Nirban et al. (2015)
Merino	Australia, New Zealand, South Africa, Spain, India, Turkey, Hungary, Uruguay	Ozder et al. (2009), Gowane et al. (2010), Ozcan et al. (2005), Snyman et al. (1997), Safari et al. (2007), Komlosi (2008), Dixit et al. (2009), Wuliji et al. (2001), Swan et al. (2008), Jaleta (2001), Olivier et al. (2001), Cloete et al. (2004), Matebesi-Ranthimo et al. (2017), Massender et al. (2019), Jurado et al. (1994), Izquierdo et al. (2002), Ekiz et al. (2004), Ciappesoni et al. (2013), Komlosi (2008), Li and Brown (2015), Neser et al. (2000), Rather et al. (2020b),
Nellore	India	Kumar et al. (2017), Reddy et al. (2017)
Polish native	Poland	Wolc et al. (2011)
Rambouillet	USA, Canada	Vesely et al. (1970), Bromley et al. (2000)
Sabi	South Africa, Zimbabwe	Matika et al. (2003), Matika et al. (2001), Assan et al. (2002)
Sakiz	Turkey	Ceyhan et al. (2009)
Scottish Blackface	Scotland	Riggio et al. (2008)
Thalli	Pakistan	Hussain et al. (2013)
Tygerhoek Merino	South Africa	Duguma et al. (2002a, 2002b)

TABLE 3 Breeds, countries and references for dual-purpose breeds

Breed	Countries	References
Avikalin	India	Mahala et al. (2020), Prince et al. (2010), Mahala et al. (2020), Ahmad et al. (2005)
Awassi	Iraq, Turkey, Brazil, Jordan	Haile et al. (2019), Alkass et al. (1991), Galal et al. (2008), Juma and Alkass (2006), Al-Samarai et al. (2016), Jawasreh et al. (2018), Tatliyer and Bas (2020)
Bergamácia	Brazil	Mcmanus and Miranda (1998)
Columbia	Columbia	Hanford et al. (2002), Bromley et al. (2000)
Corriedale	India	Rather et al. (2020a), Khan et al. (2020)
Dorper	South Africa, Kenya	Kariuki et al. (2010), Neser et al. (2001), Kariuki et al. (2010), Kiya et al. (2019), Neser et al. (2001), Zishiri et al. (2013)
Iran-Black	Iran	Kamjoo et al. (2014), Amiri-Roudbar et al. (2017)
Junin	Peru, Portugal	Burfening et al. (1995)
Katahdin	Mexico	Manzanilla Pech et al. (2012)
Polypay	USA	Hanford et al. (2003), Bromley et al. (2000)
Rideau-Arcott	Canada, USA	Boareki et al. (2020)
Sandyno	India	Venkatarmanan et al. (2015), Venkatarmanan et al. (2016b)
Santa Ines	Brazil	de Sousa et al. (1999), Sarmento et al. (2006), Carvalho et al. (2014), Barbosa et al. (2015), Aguirre et al. (2016), El-Fadili and Leroy (2001)
Targhee	USA	Hanford et al. (2003), Bromley et al. (2000)

The heterogeneity I^2 index was high for all of the genetic parameters in this study (Tables 4–7). The estimated averages of h^2_a for growth traits were moderate in magnitude and ranged between 0.190 (95% CI: 0.188–0.219) for BW in M breeds and 0.304 (95% CI: 0.285–0.327) for YW in W breeds. The standard errors associated with the h^2_a were low and ranged between 0.004 and 0.033 (Table 4). The estimated averages for h^2_m were smaller than h^2_m and ranged between 0.052 (95% CI: 0.021–0.081) for YW in D breeds and 0.240 (95% CI: 0.181–0.263) for 6MW in M breeds. The standard errors of the estimated h^2_m were generally low and ranged between 0.001 and 0.088 (Table 5).

The estimated averages for r_g and r_p between growth traits are shown in Tables 6 and 7, respectively. The r_g were all positive and ranged from 0.29 (95% CI: 0.258–0.320) between BW and YW in W breeds, to 0.879 (95% CI: 0.780–0.935) between 9MW and YW in D breeds. Generally, r_g was the highest between 9MW and YW, and the lowest between BW and YW, in all three breed groups. For each of the growth traits, the estimated r_p was lower than the corresponding r_g. All of the estimated averages for r_p were also positive and ranged from 0.232 (95% CI: 0.176–0.286) between BW and YW in W breeds, to 0.820 (95% CI: 0.690–0.899) between 9MW and YW in D breeds.

4 | DISCUSSION

The genetic parameters for most of the economic traits have been often estimated using large sample sizes in major sheep breeds. Nevertheless, the results of such studies could be combined to improve the reliability of the estimates even further. For example, Fogarty (1995) and Safari et al. (2005) reviewed genetic parameters for production, growth and reproduction traits in sheep to have reliable estimates

for their national genetic evaluation programme in Australia. There are different methods to pool the published genetic parameters. For instance, Cammack et al. (2009) summarized the parameters in the form of ranges, Utrera and Van Vleck (2004) presented the estimates as unweighted means, Safari et al. (2005) reported the weighted means, and Koots and Gibson (1996) and Lobo et al. (2000) reported both unweighted and weighted means.

The genetic parameters estimated in multiple studies for a specific breed, production system and country can be pooled with a fixed-effects model to calculate the weighted means. In fixed-effects models, the variation in the reported genetic parameters in different studies were assumed to be resulted from the sampling error variance. However, especially for minor breeds that the number of studies for each breed and sample size are limited, the results of a wide range of studies should be combined to improve the reliability of genetic estimates as much as possible. Consequently, the variation in genetic estimates could be associated with the variability of the parameters across breeds. Thus, a random effects model is often recommended to combine the genetic estimates from different populations of sheep (Medrado et al., 2021; Safari et al., 2005). The large variability of parameters in the selected papers confirmed that a random effects model was suitable for our study. The high heterogeneity in the meta-analysis of the genetic parameters (i.e., $I^2 > 75\%$) could be due to differences in breed as well as differences in year, production system and region of the studies.

Growth traits in this meta-analysis had moderate h^2_a, which means selective breeding could be used as a suitable tool to improve these traits even in minor sheep breeds. The estimated averages of h^2_a for growth traits were in line with the previous reports. For example, Safari et al. (2005) reported the average of h^2_a for growth traits ranged

TABLE 4 The estimated direct heritability ± standard error (h^2_a ± SE), confidence interval (CI 95%) and heterogeneity index (I^2) in meta-analyses for meat, wool and dual-purpose sheep breeds

Trait	Number of papers	h^2_a ± SE	CI 95% [lower limit, upper limit]	h^2_a range in papers	I^2 (%)
Meat breeds					
BW	118	0.190 ± 0.004	[0.188, 0.219]	0.03–0.54	97.561
3MW	114	0.221 ± 0.025	[0.191, 0.251]	0.06–0.67	99.763
6MW	90	0.253 ± 0.012	[0.227, 0.278]	0.05–0.62	99.380
9MW	55	0.254 ± 0.013	[0.223, 0.285]	0.01–0.49	99.729
YW	70	0.264 ± 0.010	[0.235, 0.292]	0.02–0.97	99.730
Wool breeds					
BW	56	0.198 ± 0.033	[0.187, 0.208]	0.03–0.68	99.561
WW	66	0.234 ± 0.009	[0.183, 0.254]	0.03–0.65	98.481
6MW	19	0.266 ± 0.020	[0.221, 0.286]	0.01–0.83	97.944
9MW	16	0.278 ± 0.013	[0.239, 0.293]	0.06–0.78	93.979
YW	17	0.304 ± 0.005	[0.285, 0.327]	0.02–0.75	94.612
Dual-purpose breeds					
BW	46	0.196 ± 0.004	[0.161, 0.218]	0.03–0.44	96.789
WW	40	0.201 ± 0.005	[0.181, 0.220]	0.10–0.59	98.860
6MW	35	0.219 ± 0.010	[0.196, 0.240]	0.08–0.59	93.048
9MW	43	0.263 ± 0.007	[0.222, 0.303]	0.14–0.90	94.987
YW	45	0.285 ± 0.020	[0.251, 0.306]	0.01–0.51	98.501

Abbreviations: BW, birth weight; 3MW, 3-month weight; 6MW, 6-month weight; 9MW, 9-month weight; YW, yearling weight.

TABLE 5 The estimated maternal heritability ± standard error (h^2_a ± SE), confidence interval (CI 95%) and heterogeneity index (I^2) in meta-analyses for meat, wool and dual-purpose sheep breeds

Trait	Number of papers	h^2_m ± SE	CI 95% [lower limit, upper limit]	h^2_m range in papers	I^2 (%)
Meat breeds					
BW	81	0.122 ± 0.008	[0.114, 0.142]	0.01–0.97	99.617
3MW	62	0.145 ± 0.007	[0.115, 0.154]	0.01–0.89	99.977
6MW	41	0.240 ± 0.088	[0.181, 0.263]	0.02–0.89	99.999
9MW	30	0.129 ± 0.073	[0.081, 0.140]	0.02–0.62	99.999
YW	30	0.085 ± 0.003	[0.051, 0.092]	0.01–0.09	99.837
Wool breeds					
BW	35	0.105 ± 0.002	[0.093, 0.177]	0.03–0.14	94.058
WW	25	0.125 ± 0.001	[0.083, 0.157]	0.02–0.25	91.482
6MW	20	0.164 ± 0.001	[0.147, 0.182]	0.02–0.25	84.333
9MW	12	0.071 ± 0.001	[0.047, 0.096]	0.01–0.18	65.665
YW	18	0.055 ± 0.002	[0.045, 0.086]	0.01–0.17	92.216
Dual-purpose breeds					
BW	26	0.116 ± 0.04	[0.101, 0.155]	0.07–0.59	96.903
WW	19	0.122 ± 0.005	[0.113, 0.140]	0.01–0.28	97.390
6MW	11	0.162 ± 0.006	[0.137, 0.177]	0.03–0.24	96.473
9MW	9	0.120 ± 0.004	[0.102, 0.134]	0.05–0.21	94.557
YW	10	0.052 ± 0.005	[0.021, 0.081]	0.03–0.22	95.917

Abbreviations: BW, birth weight; 3MW, 3-month weight; 6MW, 6-month weight; 9MW, 9-month weight; YW, yearling weight.

TABLE 6 The estimated genetic correlation coefficient ± standard error (r_g ± SE), confidence interval (CI 95%) and heterogeneity index (I^2) in meta-analyses for growth traits in meat, wool and dual-purpose sheep breeds

Trait 1	Trait 2	Number of papers	r_g ± SE	CI 95% [lower limit, upper limit]	r_g range in papers	I^2 (%)
Meat breeds						
BW	3MW	68	0.408 ± 0.019	[0.368, 0.447]	0.36–0.89	98.893
	6MW	48	0.384 ± 0.032	[0.350, 0.423]	0.01–0.45	99.287
	9MW	32	0.366 ± 0.050	[0.350, 0.406]	0.14–0.90	99.565
	YW	41	0.320 ± 0.031	[0.296, 0.365]	0.01–0.89	99.415
3MW	6MW	50	0.824 ± 0.063	[0.783, 0.858]	0.68–0.96	97.105
	9MW	32	0.672 ± 0.108	[0.591, 0.703]	0.09–0.90	97.648
	YW	40	0.636 ± 0.037	[0.582, 0.684]	0.21–0.92	98.531
6MW	9MW	32	0.844 ± 0.073	[0.790, 0.886]	0.62–0.89	87.682
	YW	36	0.727 ± 0.023	[0.682, 0.767]	0.54–0.90	97.017
9MW	YW	33	0.847 ± 0.105	[0.775, 0.897]	0.22–0.88	94.36
Wool breeds						
BW	3MW	50	0.448 ± 0.022	[0.379, 0.513]	0.14–0.90	99.015
	6MW	38	0.357 ± 0.018	[0.283, 0.427]	0.02–0.91	99.161
	9MW	25	0.331 ± 0.089	[0.311, 0.413]	0.57–0.90	99.638
	YW	30	0.290 ± 0.051	[0.258, 0.320]	0.19–0.84	99.117
3MW	6MW	35	0.737 ± 0.078	[0.655, 0.802]	0.12–0.98	99.213
	9MW	20	0.716 ± 0.170	[0.589, 0.836]	0.45–0.89	97.25
	YW	30	0.660 ± 0.113	[0.590, 0.730]	s0.16–0.89	99.189
6MW	9MW	23	0.860 ± 0.131	[0.794, 0.915]	0.02–0.87	96.951
	YW	27	0.637 ± 0.147	[0.537, 0.775]	0.34–0.68	98.834
9MW	YW	22	0.755 ± 0.093	[0.649, 0.833]	0.03–0.84	96.612
Dual-purpose breeds						
BW	3MW	27	0.485 ± 0.031	[0.432, 0.548]	0.22–0.84	99.209
	6MW	18	0.403 ± 0.077	[0.226, 0.554]	0.11–0.87	99.361
	9MW	13	0.383 ± 0.035	[0.327, 0.434]	0.19–0.91	94.883
	YW	14	0.329 ± 0.014	[0.230, 0.421]	0.13–0.85	84.44
3MW	6MW	16	0.862 ± 0.085	[0.711, 0.937]	0.12–0.99	99.409
	9MW	9	0.763 ± 0.081	[0.616, 0.851]	0.54–0.95	95.689
	YW	13	0.588 ± 0.077	[0.425, 0.544]	035–0.94	99.09
6MW	9MW	9	0.864 ± 0.074	[0.776, 0.919]	0.79–0.99	79.494
	YW	14	0.799 ± 0.086	[0.684, 0.876]	0.45–0.97	96.882
9MW	YW	13	0.879 ± 0.093	[0.780, 0.935]	0.56–0.98	97.337

Abbreviations: BW, birth weight; 3MW, 3-month weight; 6MW, 6-month weight; 9MW, 9-month weight; YW, yearling weight.

between 0.15 (for BW) and 0.41 (for adult weight). We also found that the h^2_a was the lowest for BW and the highest for YW. Further, the highest h^2_a for growth traits was for YW in W breed. This could be due to the high heritability of fleece weight which largely contributed to the overall weight in W breeds. Generally, h^2_a for weight traits increased from birth to adulthood in M, W and D breeds. It was expected because the additive effects of the genes could be considered the best situation when the lambs become independent of their dams

and were closer to their adult weights (Fogarty, 1995; Medrado et al., 2021).

The estimated averages for h^2_m were low to moderate in the current study. The influence of the maternal effects on BW could be the consequence of differences in the uterine environment. Whereas the milk production and maternal ability of ewes could impact 3MW (~weaning weight) and 6MW of lambs (Kushwaha et al., 2009). As lambs grow towards maturity and were separated from their dams, the h^2_m was

TABLE 7 The estimated phenotypic correlation coefficient ± standard error (r_p ± SE), confidence interval (CI 95%) and heterogeneity index (I^2) in meta-analyses for growth traits in meat, wool and dual-purpose sheep breeds

Trait 1	Trait 2	Number of papers	r_p ± SE	CI 95% [lower limit, upper limit]	r_p range in papers	I^2 (%)
Meat breeds						
BW	3MW	69	0.316 ± 0.012	[0.263, 0.366]	0.06–0.79	99.536
	6MW	49	0.256 ± 0.012	[0.200, 0.311]	0.06–0.52	99.343
	9MW	30	0.238 ± 0.017	[0.153, 0.310]	0.01–0.51	99.480
	YW	40	0.225 ± 0.012	[0.193, 0.313]	0.57–0.79	99.371
3MW	6MW	50	0.678 ± 0.043	[0.619, 0.730]	0.20–0.93	99.34
	9MW	30	0.627 ± 0.019	[0.570, 0.678]	0.14–0.28	99.218
	YW	40	0.546 ± 0.018	[0.489, 0.599]	0.07–0.93	99.264
6MW	9MW	30	0.752 ± 0.172	[0.657, 0.824]	0.52–0.96	98.718
	YW	35	0.644 ± 0.043	[0.576, 0.703]	0.23–0.95	97.378
9MW	YW	30	0.809 ± 0.147	[0.729, 0.867]	0.40–0.97	99.596
Wool breeds						
BW	3MW	40	0.324 ± 0.007	[0.275, 0.371]	0.08–0.89	99.101
	6MW	35	0.293 ± 0.005	[0.248, 0.336]	0.16–0.71	98.633
	9MW	25	0.257 ± 0.005	[0.210, 0.304]	0.02–0.83	98.389
	YW	30	0.232 ± 0.008	[0.176, 0.286]	0.01–0.79	98.948
3MW	6MW	33	0.652 ± 0.066	[0.556, 0.731]	0.04–0.98	99.696
	9MW	25	0.580 ± 0.040	[0.474, 0.670]	0.11–0.76	99.558
	YW	30	0.480 ± 0.024	[0.398, 0.554]	0.30–0.97	99.378
6MW	9MW	25	0.668 ± 0.069	[0.550, 0.755]	0.17–0.9	99.599
	YW	27	0.612 ± 0.050	[0.514, 0.694]	0.01–0.99	99.531
9MW	YW	21	0.711 ± 0.093	[0.592, 0.800]	0.08–0.92	97.149
Dual-purpose breeds						
BW	3MW	21	0.408 ± 0.020	[0.318, 0.491]	0.07–0.75	99.39
	6MW	16	0.306 ± 0.017	[0.211, 0.396]	0.01–0.66	98.858
	9MW	11	0.280 ± 0.005	[0.215, 0.342]	0.19–0.55	93.990
	YW	15	0.240 ± 0.018	[0.238, 0.434]	0.17–0.60	99.017
3MW	6MW	16	0.643 ± 0.069	[0.509, 0.749]	0.03–0.99	99.505
	9MW	11	0.534 ± 0.027	[0.417, 0.633]	0.18–0.95	98.991
	YW	13	0.510 ± 0.013	[0.445, 0.569]	0.35–0.88	98.992
6MW	9MW	10	0.736 ± 0.047	[0.624, 0.818]	0.44–0.90	98.579
	YW	12	0.719 ± 0.049	[0.608, 0.802]	0.01–0.44	99.130
9MW	YW	11	0.820 ± 0.116	[0.690, 0.899]	0.55–0.92	99.307

Abbreviations: BW, birth weight; 3MW, 3-month weight; 6MW, 6-month weight; 9MW, 9-month weight; YW, yearling weight.

expected to decline (Abegaz et al., 2002). We also found that the lowest h^2_m was for YW in M, W and D breeds. The estimated average h^2_m for 3MW and 6MW was higher than BW. This could indicate that maternal variance due to variation in milk production and maternal ability of ewes had a large effect on the growth of lambs (Mekuriaw & Haile, 2014). The estimated h^2_m for M breeds were higher than W and D breeds at all ages. This was in line with the previous studies such as Safari et al. (2005) and could be associated with importance of mater-

nal effects as well as faster growth rate and higher weaning weights in M breeds.

There were some reports of negative correlations between growth traits in literature which could be due to small sample size or other issues in the studies. As expected, the estimated average r^2_g and r^2_p between all of the growth traits was positive in this random-effects models. The moderate to high r_g between BW, 3MW and 6MW could be associated with direct additive effects of the genes as well as the influ-

ence of maternal ability of ewes. The r_g between 9MW and YW was expected to be least affected by maternal effects. The r_g was high for growth traits measured at adjacent ages (i.e., short intervals) because body weight at any age was a function of initial weight and the amount of weight gain since the previous recording (Jembere et al., 2017). As the rate of weight gain decreases with increasing age, the r_g was generally the highest between 9MW and YW.

Although r_p between growth traits was lower than r_g, the r_p for the weights at close age classes was high and increased with age from birth to yearling. It could show the impact of environmental factors on growth of lambs in addition to maternal and additive genetic effects.

The estimated genetic parameters for growth traits in our meta-analyses had small SEs. This could have indicated that the aggregation of results from different studies improved the reliability of estimated parameters and reduced the range of 95% CIs. Hence, the results from our meta-analysis models could be used with greater level of confidence in sheep breeding programmes.

5 | CONCLUSION

A meta-analysis with 221 articles was carried out to estimate genetic parameters. It was managed to estimate reliable genetic parameters for growth traits in sheep breeds. Genetic parameters were estimated in meat, wool and dual-purpose sheep breeds. Random-effects meta-analysis model can handle variability of parameters quite well. The reduction in the standard error of parameters in the current study compared to each of the individual studies supported that reliable parameters for breeding programmes were achievable by combining results of different studies.

AUTHOR CONTRIBUTIONS

Investigation, project administration, supervision, validation, visualization, writing—original draft, and writing—review and editing: Sheida Varkoohi. Formal analysis, methodology, and writing—review and editing: Nader Salary. Formal analysis and resources and Writing—review and editing: Majid Khansefid.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

ETHICS STATEMNET
The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. No ethical approval was required, and this study did not include live animals.

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