SMARTER

SMAll RuminanTs breeding for Efficiency and Resilience

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Submitted scientific publication on the genetic parameters between efficiency, resilience and reproduction related traits in sheep and goats

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About the SMARTER research project

SMARTER will develop and deploy innovative strategies to improve Resilience and Efficiency (R&E) related traits in sheep and goats. SMARTER will find these strategies by: i) generating and validating novel R&E related traits at a phenotypic and genetic level ii) improving and developing new genome-based solutions and tools relevant for the data structure and size of small ruminant populations, iii) establishing new breeding and selection strategies for various breeds and environments that consider R&E traits.

SMARTER with help from stakeholders chose several key R&E traits including feed efficiency, health (resistance to disease, survival) and welfare. Experimental populations will be used to identify and dissect new predictors of these R&E traits and the trade-off between animal ability to overcome external challenges. SMARTER will estimate the underlying genetic and genomic variability governing these R&E related traits. This variability will be related to performance in different environments including genotype-by-environment interactions (conventional, agro-ecological and organic systems) in commercial populations. The outcome will be accurate genomic predictions for R&E traits in different environments across different breeds and populations. SMARTER will also create a new cooperative European and international initiative that will use genomic selection across countries. This initiative will make selection for R&E traits faster and more efficient. SMARTER will also characterize the phenotype and genome of traditional and underutilized breeds. Finally, SMARTER will propose new breeding strategies that utilise R&E traits and trade-offs and balance economic, social and environmental challenges.

The overall impact of the multi-actor SMARTER project will be ready-to-use effective and efficient tools to make small ruminant production resilient through improved profitability and efficiency.

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1 Summary

Genetic selection focused purely on production traits has proven very successful in improving the productive performance of livestock. However, heightened environmental and infectious disease challenges have raised the need to also improve the resilience of animals to such external stressors, as well as their efficiency in utilizing available resources. A better understanding of the relationship between efficiency and production and health traits is needed to properly account for it in breeding programs and to produce animals that can maintain high production performance in a range of environmental conditions with minimal environmental footprint. The aim of this study was to perform a meta-analysis of genetic parameters for production, efficiency and health traits in sheep and goats. The dataset comprised 963 estimates of heritability and 572 genetic correlations collated from 162 published studies. A three level meta-analysis model was fitted. Pooled heritability estimates for milk production traits ranged between 0.27±0.03 and 0.48±0.13 in dairy goats and between 0.21±0.06 and 0.33±0.07 in dairy sheep. In meat sheep, the heritability of efficiency traits ranged from 0.09±0.02 (prolificacy) up to 0.32±0.14 (residual feed intake). For health traits pooled heritability was 0.07±0.01 (faecal egg count - FEC) and 0.21±0.01 (somatic cell score - SCS) in dairy goats and 0.14±0.04 (FEC) and 0.13±0.02 (SCS) in dairy sheep. In meat sheep, the heritability of disease resistance and survival traits ranged between 0.07±0.02 (mastitis) and 0.50±0.10 (breech strike). Pooled estimates of genetic correlations between resilience and efficiency traits in dairy goats were not significantly different from zero with the exception of SCS and fat content (-0.19±0.01). In dairy sheep only the unfavourable genetic correlation between SCS and protein content (0.12±0.03) was statistically significant. In meat sheep only the correlations between growth and FEC (-0.28±0.11) as well as between growth and dagginess (-0.33±0.13) were statistically significant and favourable. Results of this meta-analysis provide evidence of genetic antagonism between production and health in dairy sheep and goats. This was not observed in meat sheep where most of the pooled estimates had

high standard errors and were nonsignificant. Based on the obtained results, it seems feasible to simultaneously improve efficiency and health in addition to production by including the different types of traits in the breeding goal. However, a better understanding of potential trade-offs between these traits would be beneficial. Particularly more studies focused on reproduction and resilience traits linked to the animal's multitrait response to challenges are required.

2 Introduction

Genetic selection focused purely on production traits has proven very successful in improving the productive performance of livestock. However, heightened environmental and infectious disease challenges have raised the need to also improve the resilience of animals to such external stressors, as well as their efficiency in utilizing available resources. A better understanding of the relationship between efficiency and production and health traits is needed to properly account for it in breeding programs and to produce animals that can maintain high production performance in a range of environmental conditions with minimal environmental footprint.

3 Main results and Conclusions

- Main results

This study found evidence of genetic antagonisms between resilience and efficiency for dairy goats and diary sheep, but not for meat sheep. Lack of significant results in meat sheep can be explained by a large variability of estimates reported in literature. Even though the pooled estimates were nonsignificant, antagonisms may exist but only in specific populations and environments. Overall, pooled genetic correlations among all of the analysed resilience and efficiency traits in dairy goats, dairy sheep and meat sheep ranged from -0.33 to 0.35. In many cases the genetic correlations were not significantly different from zero. This could indicate possibilities for simultaneous improvement of efficiency and resilience by including both types of traits in the breeding goal. However, the variability of estimates was often large with range of values containing negative as well as positive values, especially in meat sheep. The variability in correlations between FEC and growth might reflect the importance of the environmental conditions for the co expression of disease resistance and production potential or so to say genotype by environment interactions. Therefore, a better understanding of potential trade-offs between efficiency and resilience traits would be beneficial. For some of the analysed genetic correlations (particularly in dairy goats), it would be desirable to simply include more studies to obtain more robust pooled estimates. It is also worth noting that for many traits of interest we had too few estimates to include them in this meta-analysis. This relates particularly to reproduction traits.

This study, was submitted as a paper to the journal ANIMAL the 11th of august2021 (see Appendix)

- Genetic correlation with reproduction traits

In meat sheep, genetic parameters of reproduction traits have already been reviewed by Fogarty et al. (1995) and by Safari et al. (2005). In the database we constituted for the paper Mucha et al. (2022),we could estimate a pooled genetic correlation only between body weight and prolificacy, with a value of -0.02 ± 0.05. This value indicates genetic independency between both traits, similarly to what was reviewed in the above mentioned reviews.

In dairy sheep, there is only one publication to our knowledge about genetic correlation of reproduction traits and efficiency or resilience (David et al., 2008). Authors found that the genetic correlation between fertility in ewe lambs (PR1), and fertility in adult ewes (PRA) was 0.55, indicating that fertility is not the same trait in ewe lambs and adult ewes. The genetic correlation between milk yield and lamb fertility was not significantly different from zero. The genetic correlation between milk yield and fertility in adult ewe (−0.23) was in the range of antagonistic correlations reported in dairy cattle. Consequently, these results show that selection for milk yield can induce an indirect decrease in fertility.

Similarly, in goats there is only one publication to our knowledge about genetic correlation of one indicator or reproductive success with lifetime efficiency. Genetic correlation of age at first kidding and interval between the first and second kidding with productive life were estimated in US dairy goat (Castañeda-Bustos et al., 2014). Estimates were not significantly different from zero (-0.08 to 0.11).

This literature review highlights the need for further studies on the genetic link between reproductive traits and resilience and efficiency.

4 Deviations or delays

Delay: Submission of a full paper was delayed by nine months although the paper was presented at the EAAP conference in 2020. Following this, the authors were invited from the Editorial Board of Animal to submit the paper as an invited review. For this reason the paper was then reformatted and better-aligned to the requirement of the journal. Despite initial discussions, we did not include aspects related to reproduction largely due to there being a lack of published papers with estimates of genetic parameters for reproduction which was insufficient to include them in this meta-analysis.

5 Acknowledgements

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6 Appendix

1. Paper published in Animal: Mucha et al. Animal (2022), 16:3. https://doi.org/10.1016/j.animal.2022.100456
2. Supplementary Information of the paper

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Animal Board Invited Review: Meta-analysis of genetic parameters for resilience and efficiency traits in goats and sheep

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ABSTRACT

Genetic selection focused purely on production traits has proven very successful in improving the productive performance of livestock. However, heightened environmental and infectious disease challenges have raised the need to also improve the resilience of animals to such external stressors, as well as their efficiency in utilising available resources. A better understanding of the relationship between efficiency and production and health traits is needed to properly account for it in breeding programmes and to produce animals that can maintain high production performance in a range of environmental conditions with minimal environmental footprint. The aim of this study was to perform a meta-analysis of genetic parameters for production, efficiency and health traits in sheep and goats. The dataset comprised 963 estimates of heritability and 572 genetic correlations collated from 162 published studies. A threelevel meta-analysis model was fitted. Pooled heritability estimates for milk production traits ranged between 0.27 ± 0.03 and 0.48 ± 0.13 in dairy goats and between 0.21 ± 0.06 and 0.33 ± 0.07 in dairy sheep. In meat sheep, the heritability of efficiency traits ranged from 0.09 ± 0.02 (prolificacy) up to 0.32 ± 0.14 (residual feed intake). For health traits, pooled heritability was 0.07 ± 0.01 (faecal egg count) and 0.21 ± 0.01 (somatic cell score) in dairy goats and 0.14 ± 0.04 (faecal egg count) and 0.13 ± 0.02 (somatic cell score) in dairy sheep. In meat sheep, the heritability of disease resistance and survival traits ranged between 0.07 ± 0.02 (mastitis) and 0.50 ± 0.10 (breech strike). Pooled estimates of genetic correlations between resilience and efficiency traits in dairy goats were not significantly different from zero with the exception of somatic cell score and fat content (−0.19 ± 0.01). In dairy sheep, only the unfavourable genetic correlation between somatic cell score and protein content (0.12 ± 0.03) was statistically significant. In meat sheep only, the correlations between growth and faecal egg count (−0.28 ± 0.11) as well as between growth and dagginess (−0.33 ± 0.13) were statistically significant and favourable. Results of this meta-analysis provide evidence of genetic antagonism between production and health in dairy sheep and goats. This was not observed in meat sheep where most of the pooled estimates had high standard errors and were non-significant. Based on the obtained results, it seems feasible to simultaneously improve efficiency and health in addition to production by including the different types of traits in the breeding goal. However, a better understanding of potential trade-offs between these traits would be beneficial. Particularly, more studies focused on reproduction and resilience traits linked to the animal's multi-trait response to challenges are required.

Implications

The meta-analysis provided robust estimates of heritability and genetic correlations between production efficiency and health traits utilising information from a selection of published papers. The statistical results indicate that it is feasible to simultaneously select for high performance, efficiency, and health in multi-trait breeding programmes. We also found evidence of antagonism, as well as large variability of pooled correlations. Subsequent studies investigating potential trade-offs between resilience and efficiency are therefore warranted.

Introduction

Genetic selection has been successful in increasing the production performance of farm animals. For instance, in dairy sheep,

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genetic gain for milk yield has been reported to be between 0.81 and 6.0 L/yr depending on breed (Carta et al., 2009). In meat sheep, significant genetic gain has been achieved for traits such as litter size and BW (Hanford et al., 2005). The drastic increase in genetic gain in production performance through artificial selection has however raised the question whether the ability of farmed animals to cope with infections or other environmental stressors is being eroded by selection for high levels of production (Rauw et al., 1998). This hypothesis is supported by observed genetic antagonisms between traits such as growth and milk production with health traits, indicating that trade-offs exist that hinder simultaneous genetic improvement in production, fitness, and health traits.

In dairy cattle, for instance, the genetic antagonism between milk production and resistance to mastitis (Rupp and Foucras, 2010) has been well documented, suggesting that udder health has been deteriorating as a consequence of selection for production traits. To correctly estimate the effect of selection on longevity, and avoid bias due to voluntary culling, Essl (1998) reported in his review the results of several selection experiments in dairy cattle. The latter were based on either milk yield, BW or growth rate and almost exclusively resulted in negative responses for fitness or longevity traits. Similar results were obtained in poultry, where intensive selection for growth had a negative effect on resistance to infection (Van Der Most et al., 2011).

In small ruminants, the evolution towards more extensive production systems, and the anticipated long-term change in climate, will lead to increasingly variable and challenging environments that will also heighten disease threat (Tomley and Shirley, 2009). The challenge for breeding those livestock is therefore to improve animals' resilience simultaneous with improving feed efficiency and other traits important for a sustainable livestock sector such as growth, production, product quality and reproduction. Modern breeding programmes need to be environmentally friendly and require resilience not only to specific diseases but also to a wide range of pathogens and other environmental stressors (Berghof et al., 2019; Knap and Doeschl-Wilson, 2020). As joint breeding for multiple traits can fall foul of trade-offs between traits, a better understanding of the relationship between efficiency and resilience traits is needed to properly account for trade-offs in breeding programmes and to breed efficient high producing animals that can thrive across a wide range of environments.

Many studies have produced heritability and genetic correlation estimates for production, efficiency, health and fitness traits for meat and dairy sheep and dairy goats under different environmental conditions, including disease challenge. The aim of this study was to combine the results from these individual studies in a statistical meta-analysis in order to obtain a deeper insight into the genetic relationship between key efficiency (which encompass production traits and feed efficiency) and resilience traits. Resilience has been defined in various ways in the animal science literature and is often used interchangeably with robustness, or with disease resistance or tolerance within the context of infectious disease (see Box 1 in Berghof et al., 2019).

Resilience traits in the present study focus primarily on traits associated with disease resistance, and especially on mastitis, gastrointestinal parasitism and footrot as these are the main infectious diseases of sheep and goats with respect to industry and public concern, economic impact, zoonotic potential and animal welfare (Davies et al., 2009). In meat sheep, lamb survival and longevity were included as additional resilience traits. It is worth noting that the studies selected for meta-analysis were carried out under a wide range of environmental conditions. Hence, the meta-analysis gives insights not only in the average level of heritability and genetic correlations across environments but also about the variance in these parameters. This provides a better insight into the robustness of genetic parameter estimates across environments.

Material and methods

Dataset

The dataset comprised genetic parameters for efficiency and resilience traits collated from 13 partners of the EU H2020 SMARTER project (n°772787) coming from seven countries (France, Ireland, Italy, Spain, Switzerland, United Kingdom, and Uruguay). Additionally, it was supplemented with papers published by other research groups to get a more complete overview of parameters reported for the analysed traits. For the purpose of this project, efficiency comprised of production traits and feed efficiency, whereas resilience comprised of disease resistance and survival. As parameters for key production traits for meat sheep have previously been summarised (Fogarty, 1995; Safari et al., 2005), the search for papers was restricted to studies published after 1995. In case of dairy goats and dairy sheep, where the available data were more limited, no restriction on the publication date was imposed. Altogether 232 published papers together with some unpublished results were considered. This original dataset contained 2 151 estimates of heritability and genetic correlation for 81 sheep (including composite breeds) and 14 goat breeds. Subsequently, the dataset was filtered to select traits with a suitable number of heritability and genetic correlation estimates together with accompanying information about each study such as breed, age of animals and number of phenotypes (for details, see Supplementary Tables S1-S3). The age of animals was based on lactation number for dairy traits and age at measurement for meat traits. Each estimate of genetic parameters was required to have an accompanying standard error. Only traits with a minimum of three estimates (heritability or correlation) from two different studies were included in meta-analysis. Traits that did not meet this threshold were excluded from further analyses.

Accordingly, pooled values for heritability and genetic correlation were estimated in dairy goats and dairy sheep for five production traits, including milk yield, protein yield, fat yield, protein content, fat content, and two traits related to disease resistance i.e. somatic cell score as a proxy for resistance to mastitis and faecal egg count as a proxy for resistance to infestation with gastrointestinal parasites. In meat sheep, those genetic parameters were estimated for the following 10 efficiency traits: BW, body condition score, backfat thickness measured by ultrasound, residual feed intake, feed intake, feed conversion ratio, growth, muscle depth measured by ultrasound, prolificacy, methane emissions; and for the following 12 resilience traits: breech strike, dagginess (faecal soiling of the perineum region) and faecal consistency as proxies for resistance to flystrike, footrot, lamb survival, longevity, mastitis phenotypes (being either a binary trait (absence vs evidence of mastitis), or somatic cell score), and number of worms, parasitism antibodies, haematocrit, parasitism immunoglobulin and faecal egg count as alternative proxies for animals' resistance to the infestation with gastrointestinal parasites. The three proxies for resistance to flystrike are scaled scores with the higher value indicating less resistance (maximal faecal soiling, highly fluid faeces or high number of strikes). Footrot was also assessed through scaled scores with greater values indicating severe footrot. Lamb survival was considered from birth to 365 days, with different intervals (for example from birth to 30 days, from birth to weaning, from weaning to 365 days).

After initial data exploration, the following six datasets were created: (1) 81 estimates of heritability from 16 studies on dairy goats (Supplementary Table S1); (2) 119 estimates of heritability from 26 studies on dairy sheep (Supplementary Table S2); (3) 763 estimates of heritability from 118 studies on meat sheep (Supplementary Table S3); (4) 13 estimates of genetic correlations (between resilience and efficiency traits) from four studies on dairy goats (Supplementary Table S4); (5) 99 estimates of genetic correlations (44 between efficiency and resilience traits; 55 between efficiency traits) from 12 studies on dairy sheep (Supplementary Table S5); (6) 465 estimates of genetic correlations from 50 studies on meat sheep (Supplementary Table S6). In dairy goats, Saanen and Alpine breeds contributed the largest number of genetic parameters for meta-analysis with 29 and 22 estimates of heritability along with 4 and 3 estimates of genetic correlations, respectively (Supplementary Table S7). Other breeds contributed between 1 and 6 estimates of heritability and no estimates of genetic correlations except for Polish White Improved and Polish Fawn Improved. In dairy sheep, Lacaune and Churra breeds contributed the largest number of parameters with 37 and 30 heritability estimates, respectively (Supplementary Table S8). The largest number of genetic correlations was contributed by Lacaune, Red-Faced Manech and East-Friesian breeds with 33, 15, and 15 estimates, respectively (Supplementary Table S8). In meat sheep, Merino breed contributed the largest number of heritability estimates with a total of 153 values (Supplementary Table S9). Twelve breeds contributed between 10 and 50 estimates of heritability, 14 breeds contributed between 5 and 9 estimates and 20 breeds contributed less than 5 estimates. New Zealand composite breeds and Romney contributed the largest number of genetic correlations with 110 and 92 values, respectively. Merino contributed 54 estimates of genetic correlations. Six breeds contributed between 10 and 50 estimates of genetic correlations, eight breeds contributed between 5 and 9 estimates and six breeds contributed less than five estimates (Supplementary Table S9). Twenty-six breeds contributed heritability estimates but no genetic correlation estimates.

Cluster analysis

Heritabilities for each trait and genetic correlations between pairs of traits from different studies were grouped into clusters, to gather the estimates according to similar conditions in which they were obtained. Hierarchical Ward clustering was the method used to group the original estimates from the analysed studies (Sharma, 1996). Clustering took into account variables such as breed, age of animals (based on lactation number for dairy or age at measurement for meat traits), and sample size (number of phenotypes used in each study). Categorical variables (breed) were grouped into distinct classes. Quantitative variables (h^2, r_g, sample size) were standardised into z-scores (mean 0, SD 1).

The similarity measure between studies j and k used for the clustering was the Gower distance (Gower, 1971), defined as:

$$S_G = \frac{\sum_{i=1}^{n} w_{i,j,k} \cdot S_{i,j,k}}{\sum_{i=1}^{n} w_{i,j,k}}$$

which sums over all variables i of studies j and k; the weight $w_{i,j,k}$ is equal to 0 or 1, depending on whether the comparison for variable i is valid or not (which allows to account for missing data). For binary and categorical variables, $S_{i,j,k}$ takes a value of 1 (equal) or 0 (different). For continuous variables, it can be calculated as:

$$S_{i,j,k} = 1 - \frac{\left|x_{i,j} - x_{i,k}\right|}{R_i}$$

where: x_{ij} and x_{ik} refer to the standardized values of variable i for study j and k, respectively, and R_i is the range of values for variable i across all studies. Clustering was performed using the R-software package 'cluster' (R Development Core Team, 2011).

Meta-analysis

A threelevel meta-analysis model was fitted using the REML algorithm using the R package metafor (Viechtbauer, 2010):

$$\widehat{\theta}_{ij} = \beta_0 + \zeta_{ij} + \zeta_j + \varepsilon_{ij}$$

where: $\underset{ij}{\widehat{\theta}}$ is the estimate of the true effect size (h^2 or r_g) in study i belonging to cluster j, β_0 is the intercept (average population effect), ζ_{ij} refers to the effect of study i nested in cluster j assumed to be $\zeta_{ij} \sim N(0, \sigma_w^2)$, where σ_w^2 is the within-cluster variance (assumed to be equal for all clusters), ζ_j refers to the effect of cluster j assumed to be $\zeta_j \sim N(0, \sigma_b^2)$, where σ_b^2 is the between-cluster variance, and ε_{ij} is the sampling error of individual studies assumed to be $\varepsilon_{ij} \sim N(0, \sigma_e^2)$.

Additionally, for comparison of the results of this study with those of other studies, a simple random-effects meta-analysis model was fitted using the R package 'meta' (Schwarzer et al., 2015). Description of the model is presented in Supplementary Material S1.

Following the approach of Koots et al. (1994), correlation coefficients (r) were transformed into normally distributed values using Fisher's r to Z transformation as follows:

$$Z = 0.5\log\left(\frac{1+r}{1-r}\right)$$

Standard errors associated with the transformed correlations were calculated as

$$se_Z = \frac{1}{\sqrt{(n-3)}}$$

where n is the number of records used to estimate the correlation coefficient. Meta-analysis of genetic correlations was performed using the transformed values. Pooled estimates of genetic correlations (Z) were back-transformed to their original scales.

Pooled estimates of heritability and correlations were declared significant at $P \leq 0.05$.

The I^2 index was used to quantify the relative degree of heterogeneity between (I_b^2) and within (I_w^2) clusters following the generalisation of I^2 proposed by (Nakagawa and Santos, 2012) as:

$$I_b^2(\%) = \frac{\sigma_b^2}{\sigma_b^2+\sigma_w^2+\sigma_e^2} \times 100$$

$$I_w^2(\%) = \frac{\sigma_w^2}{\sigma_b^2+\sigma_w^2+\sigma_e^2} \times 100$$

Values of I^2 above 50% indicate substantial heterogeneity.

Results

Meta-analysis of heritability

Dairy sheep and goats

Pooled heritability estimates for milk production traits ranged between 0.27 ± 0.03 and 0.48 ± 0.13 in dairy goats (Table 1) and between 0.21 ± 0.06 and 0.33 ± 0.07 in dairy sheep (Table 2). In both species, fat and protein content had the highest estimates of pooled heritability and the lowest were attributed to yield traits. Pooled heritability for resilience traits was 0.07 ± 0.01 (faecal egg count) and 0.21 ± 0.01 (somatic cell score) in dairy goats and 0.14 ± 0.04 (faecal egg count) and 0.13 ± 0.02 (somatic cell score) in dairy sheep (Table 2). It is worth noting that in dairy goats, estimates for resilience traits were obtained based on a relatively small number of studies which ranged from two to three studies (Table 1). In dairy sheep, only faecal egg count had a small number of studies (three papers), whereas somatic cell score had 22 studies

Table 1
Pooled estimates of heritability from meta-analysis in dairy goats.

Trait[1]	Pooled h^2 (±SE)	Min[2] h^2	Max[3] h^2	N obs[4]	N studies	I^2 between[5]	I^2 within[6]
MY	0.27 ± 0.02	0.11	0.46	22	15	95.35	0.77
FY	0.31 ± 0.03	0.20	0.39	10	6	19.42	74.24
PY	0.30 ± 0.02	0.04	0.38	10	6	53.96	36.62
FC	0.48 ± 0.09	0.16	0.62	13	8	17.05	82.00
PC	0.48 ± 0.13	0.14	0.67	13	8	2.78	96.74
SCS	0.21 ± 0.01	0.19	0.24	5	3	56.09	0
FEC	0.07 ± 0.01	0.04	0.15	8	2	0	0

[1] Trait: MY – milk yield, FY – fat yield, PY – protein yield, FC – fat content, PC – protein content, SCS – somatic cell score, FEC – faecal egg count.
[2] Minimum h^2 from individual studies included in meta-analysis.
[3] Maximum h^2 from individual studies included in meta-analysis.
[4] Number of observations used in meta-analysis.
[5] Heterogeneity between clusters.
[6] Heterogeneity within clusters.

(Table 2). Heritability for resilience traits from individual studies on dairy goats had a narrow range of 0.19 ± 0.03 to 0.24 ± 0.01 for somatic cell score and 0.04 ± 0.03 to 0.15 ± 0.12 for faecal egg count. In case of dairy goats, production traits, fat and protein yield had most of the individual estimates within a close range, except of one study. On the other hand, milk yield, fat content and protein content had a much wider range of estimates from individual studies (Table 1). In dairy sheep, most of the analysed traits had a wide range of heritability estimates (Table 2). Similarly to dairy goats, fat yield and protein yield had the smallest range of estimates among all production traits.

Meat sheep results

Results regarding the meta-analysis of heritability in meat sheep are given in Table 3. Four traits (residual feed intake, feed conversion ratio, methane emissions and body condition score) out of the ten studied efficiency traits had estimates from fewer studies, i.e. maximum of five different studies. Pooled heritability estimates for efficiency traits ranged from 0.09 ± 0.02 (prolificacy) to 0.32 ± 0.15 (residual feed intake), (Table 3). Among the 12 studied resilience traits, only four of them (faecal egg count, dagginess, parasitism immunoglobulin and lamb survival) had estimates in more than five studies (Table 3). Pooled heritability estimates for resilience traits ranged from 0.07 ± 0.02 (mastitis) to 0.50 ± 0.10 (breech strike). The ranges of estimates were large for all traits. Despite these wide ranges of values, the variability of individual estimates differed between traits with for example prolificacy and mastitis having more consistent heritability estimates across studies than faecal egg count and dagginess (Fig. 1). This was independent from the number of studies available.

Meta-analysis of correlations

Dairy sheep and goats

Pooled estimates of genetic correlations between resilience and efficiency traits in dairy goats (Table 4) were negative for somatic cell score and fat content (−0.19 ± 0.01) as well as somatic cell score and protein content (−0.06 ± 0.05). On the other hand, milk yield had a positive genetic correlation with somatic cell score (0.35 ± 0.31) and faecal egg count (0.17 ± 0.35) suggesting that higher milk yield was unfavourably associated with higher milk somatic cell counts and high faecal egg counts. However, in case of these last three correlations, standard errors of the pooled estimates were large and the pooled estimates were not significantly different from zero (Table 4). Additionally, the range of correlations from individual studies was wide. In the case of somatic cell score and milk yield, it ranged from 0 ± 0.02 up to 0.59 ± 0.22, and for faecal egg count and milk yield, it ranged from −0.21 ± 0.26 to 0.63 ± 0.01. It is also worth noting that the number of studies available for inclusion in this meta-analysis was limited to only two papers. Estimation of pooled correlations between efficiency traits as well as between faecal egg count and somatic cell score was not possible due to insufficient number of estimates reported in the literature.

In dairy sheep, pooled estimates of genetic correlations between somatic cell score and efficiency traits were close to zero (with milk yield and fat content) or moderately positive, ranging from 0.11 ± 0.15 to 0.17 ± 0.10 for protein content, protein yield and fat yield (Table 5). Due to large standard errors, they were mostly not significantly different from zero, except between somatic cell score and protein content (0.12 ± 0.03) which was positive and unfavourable. Notably, the range of estimates reported for

Table 2
Pooled estimates of heritability from meta-analysis in dairy sheep.

Trait[1]	Pooled h^2 (±SE)	Min[2] h^2	Max[3] h^2	N obs[4]	N studies	I^2 between[5]	I^2 within[6]
MY	0.24 ± 0.02	0.06	0.46	29	19	83.98	15.03
FY	0.21 ± 0.06	0.14	0.28	7	5	0.26	96.7
PY	0.22 ± 0.04	0.12	0.30	7	5	0.64	95.77
FC	0.28 ± 0.11	0.04	0.68	16	12	54.79	45.13
PC	0.33 ± 0.07	0.10	0.77	25	17	62.58	37.2
SCS	0.13 ± 0.02	0.03	0.27	29	22	52.64	44.26
FEC	0.14 ± 0.04	0.09	0.35	6	3	0	57.97

SCS – somatic cell score, FEC – faecal egg count.
[1] Trait: MY – milk yield, FY – fat yield, PY – protein yield, FC – fat content, PC – protein content.
[2] Minimum h^2 from individual studies included in meta-analysis.
[3] Maximum h^2 from individual studies included in meta-analysis.
[4] Number of observations used in meta-analysis.
[5] Heterogeneity between clusters.
[6] Heterogeneity within clusters.

Table 3
Pooled estimates of heritability from meta-analysis in meat sheep.

Trait[1]	Pooled h^2 (±SE)	Min[2] h^2	Max[3] h^2	N obs[4]	N studies	I^2 between[5]	I^2 within[6]
Efficiency traits							
BW	0.32 ± 0.04	0.02	0.93	193	73	42.72	57.16
GR	0.20 ± 0.03	0.02	0.56	49	25	74.2	19.16
BCS	0.21 ± 0.11	0.06	0.37	9	3	6.50	89.50
BFT	0.28 ± 0.03	0.05	0.63	53	34	28.59	68.88
MD	0.29 ± 0.02	0.05	0.50	44	31	74.62	19.74
FI	0.26 ± 0.04	0.02	0.49	14	7	76.05	0.00
RFI	0.32 ± 0.15	0.07	0.46	7	5	11.14	78.97
FCR	0.12 ± 0.03	0.03	0.24	7	2	35.86	1.80
CH4	0.17 ± 0.04	0.00	0.29	20	4	5.33	79.95
PROL	0.09 ± 0.02	0.01	0.19	33	17	16.97	80.17
Resilience traits							
LSurv	0.13 ± 0.04	0.01	0.63	73	11	7.29	91.37
Long	0.08 ± 0.04	0.03	0.13	5	3	8.62	88.26
MAS	0.07 ± 0.02	0.04	0.11	9	4	0.96	32.00
FR	0.15 ± 0.03	0.06	0.26	28	4	23.66	60.45
BrStr	0.50 ± 0.10	0.32	0.61	7	3	34.58	49.62
DAG	0.30 ± 0.06	0.06	0.63	37	15	38.65	58.01
FCons	0.14 ± 0.02	0.03	0.27	13	5	44.20	6.19
NBW[7]	0.10 ± 0.02	0.00	0.54	11	3	-	-
Par-Ab	0.18 ± 0.07	0.05	0.29	6	3	0.00	61.27
Par-Ig	0.36 ± 0.06	0.13	0.67	24	8	25.40	47.03
FEC	0.29 ± 0.03	0.00	0.82	116	32	68.99	30.58
HC	0.32 ± 0.14	0.08	0.56	5	2	4.91	66.42

[1] Trait: GR – growth, BCS – body condition score, BFT – ultrasonic backfat thickness, MD – ultrasonic muscle depth, FI –feed intake, RFI – residual feed intake, FCR – feed conversion ratio, CH4 – methane emissions, PROL – prolificacy, LSurv – lamb survival, Long – longevity, MAS – mastitis, FR – footrot, BrStr – breech strike, DAG – dagginess, FCons – faecal consistency, NBW – number of worms, Par-Ab – parasitism antibodies, Par-Ig – parasitism immunoglobulin, FEC –faecal egg count, HC – Haematocrit.

[2] Minimum h^2 from individual studies included in meta-analysis.

[3] Maximum h^2 from individual studies included in meta-analysis.

[4] Number of observations used in meta-analysis.

[5] Heterogeneity between clusters.

[6] Heterogeneity within clusters.

[7] Pooled heritability obtained from a simple random-effects model as the three-level meta-analysis model did not converge.

the correlation between somatic cell score and milk yield is very wide and half of them is positive, whereas the other half is negative (Fig. 2).

Genetic correlations between protein yield and milk yield, fat yield and milk yield, as well as fat yield and protein yield were highly positive in all of the studies included in this meta-analysis which resulted in high pooled estimates of 0.89 ± 0.02, 0.82 ± 0.04, and 0.80 ± 0.10, respectively. Correlations between fat content and milk yield, as well as protein content and milk yield were negative with pooled estimates of −0.28 ± 0.16 and −0.41 ± 0.05, respectively. Correlations between protein content and protein yield as well as fat content and protein yield ranged from negative or close to zero up to positive values. A complete list of pooled estimates of genetic correlations between the analysed efficiency traits is listed in Supplementary Table S10.

Meat sheep results

Pooled correlation estimates between resilience and efficiency pairs of traits were all obtained from a wide range of values, usually encompassing zero (Fig. 3). Higher growth rates were significantly associated with lower faecal egg count (pooled estimate of −0.28 ± 0.11) as well as lower dagginess (−0.33 ± 0.13). The other resilience by efficiency pairs of traits had pooled estimates ranging from −0.12 ± 0.16 (BW and faecal consistency) to 0.25 ± 0.19 (BW and parasitism immunoglobulin) and were not significantly different from zero (Table 6).

Correlations between resilience traits had consistently high estimates for proxies of the same disease. Pooled estimate of genetic correlation between dagginess and faecal consistency was very high (0.94 ± 0.55) and based only on positive estimates from individual studies (Supplementary Table S9). On the other hand, the pooled estimate for faecal egg count and parasitism immunoglobulin (−0.40 ± 0.05) was based on only negative estimates from individual studies (Supplementary Table S11) indicating that higher faecal egg count is linked with lower Ig. The pooled estimates of genetic correlations between proxies for flystrike traits (dagginess and faecal consistency) and gastrointestinal parasitism traits (faecal egg count and parasitism immunoglobulin) were all positive, ranging from 0.11 ± 0.12 to 0.24 ± 0.03, but only two out of the four correlations were statistically significant (Supplementary Table S11). Genetic correlations between efficiency traits were all positive except for BW and prolificacy as well as BW and residual feed intake. However, these two pooled genetic correlations were not statistically significant (Supplementary Table S12). It is noteworthy that four out of the five pooled estimates higher than 0.6 (BW and feed intake, feed intake and growth, feed intake and residual feed intake, BW and methane emissions) were obtained from positive values only.

Discussion

Meta-analysis of genetic parameters

Parameter estimation is usually one of the first steps in setting up a breeding programme or for including new traits into an existing scheme. The initial focus is often on performance traits such as milk yield in dairy breeds and growth in meat breeds. These traits are easy to record and thus the amount of data available for genetic analyses is most often sufficient to achieve good accuracy. As breeding programmes develop, the focus shifts from pure performance to health and efficiency related traits, which affect functional longevity of the animals (Boichard and Brochard, 2012). Integration of new traits into the breeding goal can be challenging particularly when the amount of data is limited which impedes estimation of genetic parameters. In such cases, use of pooled estimates based on a meta-analysis of parameters reported in other

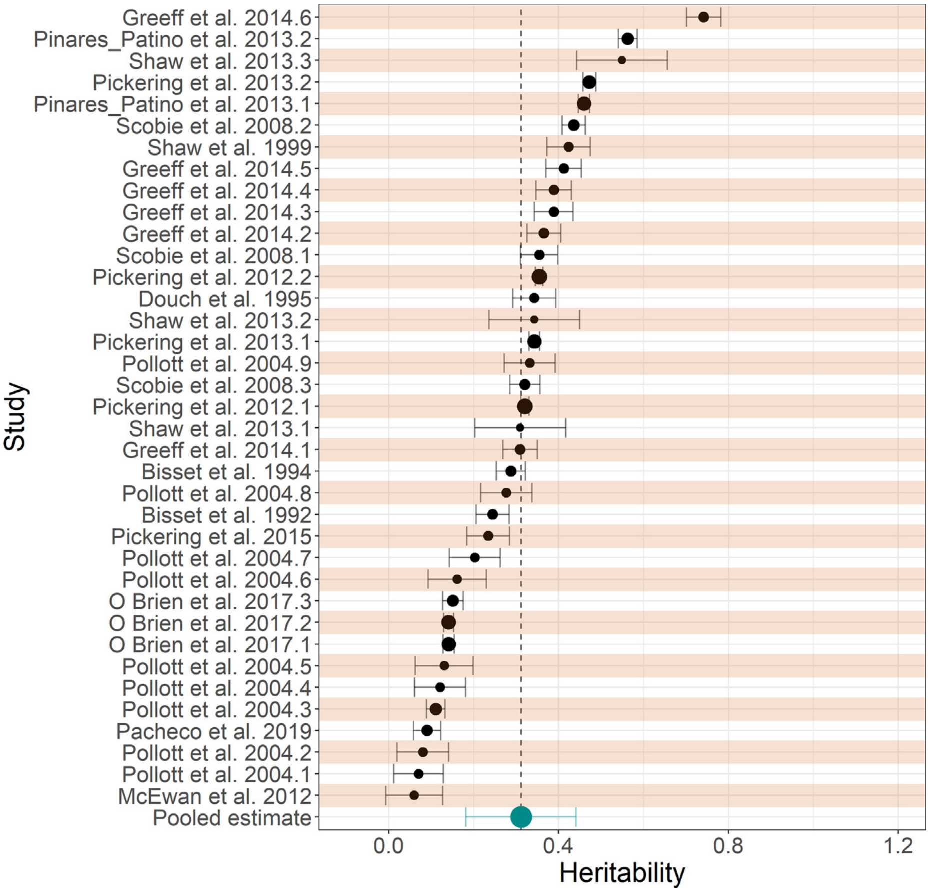

Fig. 1. Forest plot showing heritability estimates for dagginess in meat sheep.

Table 4
Pooled estimates of genetic correlations between resilience (SCS, FEC) and efficiency (MY, FC, PC) traits from meta-analysis in dairy goats.

Traits[1]	Pooled r_g (±SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	I^2 between[5]	I^2 within[6]
SCS & MY	0.35 ± 0.31^{ns}	0.00	0.59	3	2	3.75	93.46
SCS & FC[7]	−0.19 ± 0.01	−0.20	−0.18	3	2	0	
SCS & PC	−0.06 ± 0.05^{ns}	−0.13	0.00	3	2	41.32	42.89
FEC & MY	0.17 ± 0.35^{ns}	−0.21	0.63	4	2	27.94	71.95

[1] Traits: SCS – somatic cell score, FEC – faecal egg count, MY – milk yield, FC – fat content, PC – protein content.
[2] Minimum r_g from individual studies included in meta-analysis.
[3] Maximum r_g from individual studies included in meta-analysis.
[4] Number of observations used in meta-analysis
[5] Heterogeneity between clusters.
[6] Heterogeneity within clusters.
[7] Pooled correlation obtained from a simple random-effects model as the three-level meta-analysis model did not converge.
[ns] Pooled estimate did not differ significantly from zero.

Table 5
Pooled estimates of genetic correlations between resilience (SCS) and efficiency (MY, FY, PY, FC, PC) traits from meta-analysis in dairy sheep.

Traits[1]	Pooled r_g (±SE)	Min[2] r_g	Max[3] r_g*	N obs[4]	N studies	I^2 between[5]	I^2 within[6]
SCS & MY	−0.05 ± 0.10^{ns}	−0.30	0.23	16	11	22.77	74.98
SCS & FC	0.04 ± 0.05^{ns}	−0.16	0.16	8	8	62.09	34.15
SCS & PC	0.12 ± 0.03	0.02	0.24	12	9	70.99	20.91
SCS & FY	0.11 ± 0.15^{ns}	−0.04	0.31	4	4	6.02	92.35
SCS & PY	0.17 ± 0.10^{ns}	0.06	0.31	4	4	10.42	86.19

[1] Traits: SCS – somatic cell score, MY – milk yield, FY – fat yield, PY – protein yield, FC – fat content, PC – protein content.
[2] Minimum r_g from individual studies included in meta-analysis.
[3] Maximum r_g from individual studies included in meta-analysis.
[4] Number of observations used in meta-analysis.
[5] Heterogeneity between clusters.
[6] Heterogeneity within clusters.
[ns] Pooled estimate did not differ significantly from zero.

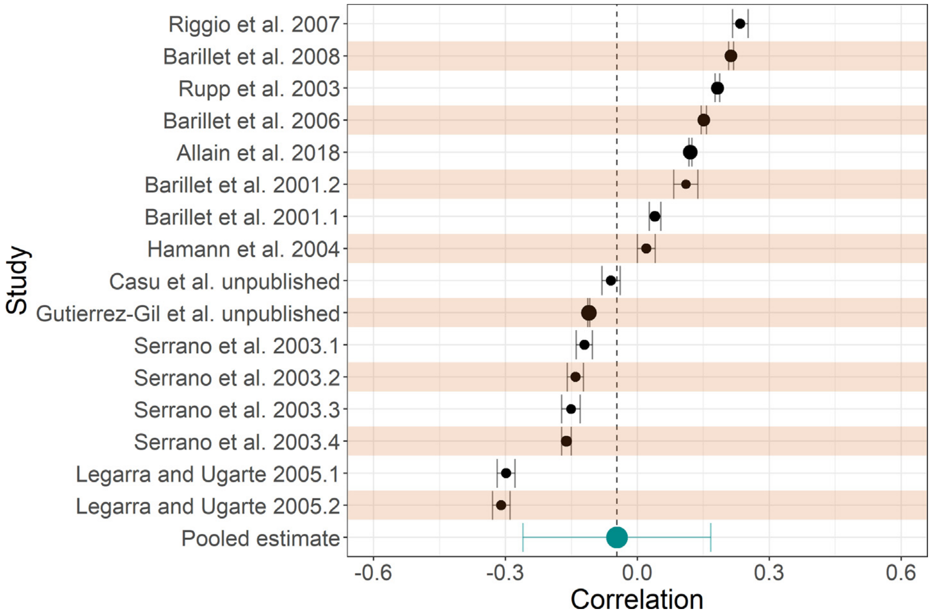

Fig. 2. Forest plot showing genetic correlation estimates between somatic cell score and milk yield in dairy sheep.

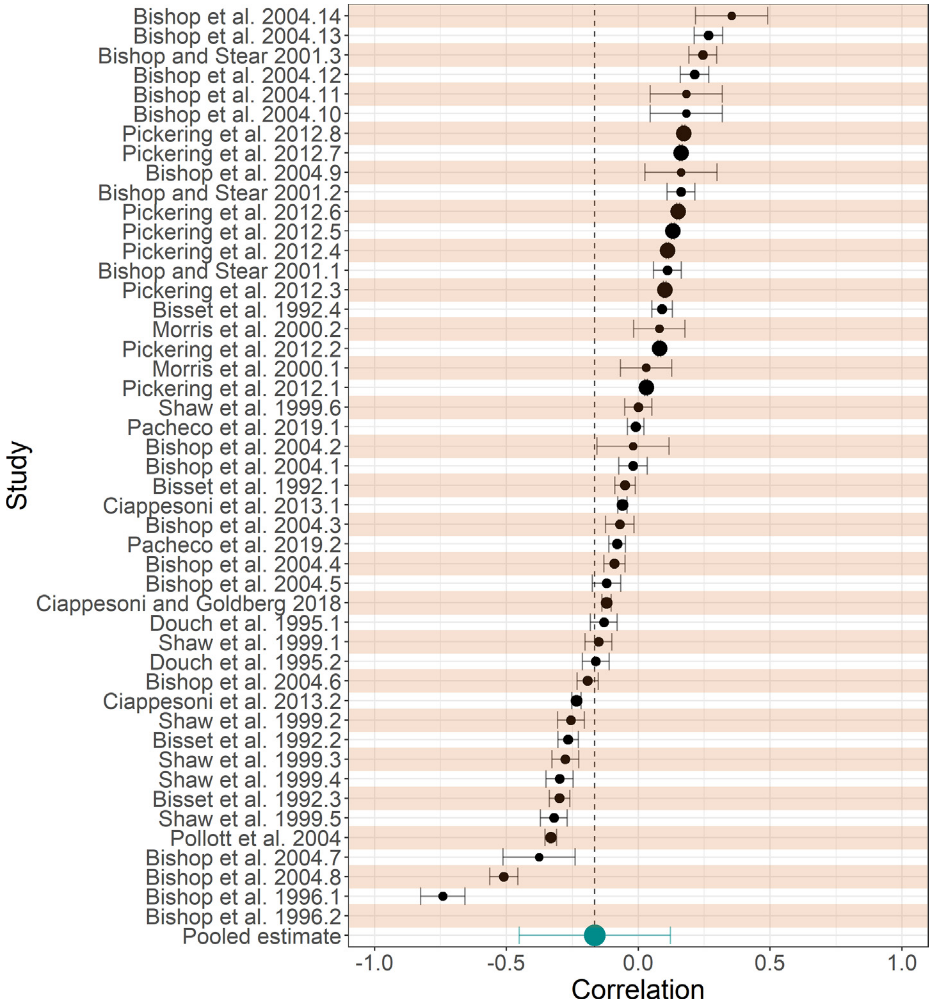

Fig. 3. Forest plot showing genetic correlation estimates between BW and faecal egg count in meat sheep.

Table 6

Pooled estimates of genetic correlations between resilience and efficiency traits from meta-analysis in meat sheep.

Traits[1]	Pooled r_g(±SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	I^2 between[5]	I^2 within[6]
BW & FEC	−0.16 ± 0.14[ns]	−0.90	0.34	47	12	12.26	86.38
BW & Par-Ig	0.25 ± 0.19[ns]	−0.48	0.87	49	4	6.95	69.52
BW & Fcons[7]	−0.12 ± 0.16[ns]	−0.43	0.43	5	3	-	-
BW & DAG	0.01 ± 0.07[ns]	−0.33	0.28	22	9	19.99	69.93
GR & FEC	−0.28 ± 0.11	−0.68	0.57	24	5	26.33	50.74
GR & DAG[7]	−0.33 ± 0.13	−0.54	−0.16	3	3	-	-

[1] Traits: GR – growth, DAG – dagginess, FCons – faecal consistency, Par-Ig – parasitism immunoglobulin, FEC –faecal egg count.

[2] Minimum r_g from individual studies included in meta-analysis.

[3] Maximum r_g from individual studies included in meta-analysis.

[4] Number of observations used in meta-analysis.

[5] Heterogeneity between clusters.

[6] Heterogeneity within clusters.

[7] Pooled correlation obtained from a simple random-effects model as the three-level meta-analysis model did not converge.

[ns] Pooled estimate did not differ significantly from zero.

populations might be a possible solution. Naturally, this is suboptimal and population specific parameters should be estimated when the availability of data improves. This allows us to account for environment which might differ between various populations. The environment might also change over time, and therefore, it is important to periodically reestimate genetic parameters.

The use of meta-analyses has had a very positive impact in many scientific fields particularly in resolving seemingly contradictory research outcomes (Gurevitch et al., 2018) however, its use in genetics and genomics has been limited so far. This study has gone some way towards filling the literature gap by pooling estimates to reach consensus for the relationships and trade-offs that have been reported for efficiency and resilience traits. Thorough literature review and integration of parameters published in multiple studies into a meta-analysis can provide more insight into the genetic relationship between traits of interest which we have shown here. This can be of particular value for traits which have a wide range of correlations reported in the literature. Accounting for factors that contribute to between-study heterogeneity might enable more meaningful pooled estimates.

Pooled heritabilities and correlations

In this study, we found significant pooled heritabilities for milk production traits both in dairy goats (0.27–0.48) and sheep (0.21–0.33) which are well within acceptable boundaries for inclusion into breed improvement programmes. Those for health traits and efficiency were generally more variable, being 0.07–0.49 and 0.09–0.3, respectively, which also indicate that it would be possible to make genetic improvement in these traits. It is important to understand the complexity of relationships among the new traits and the traits already present in the breeding goal. For this reason, the genetic correlations indicate the likely change in resilience traits that would occur if only production efficiency was included in breeding programmes. We found antagonistic relationships among yields of milk, fat and protein vs somatic cell score indicating that unless somatic cell score is included in the breeding goals together with productivity, then a downward (worse) trajectory for udder health would likely result. In case of the relationship between fat and protein content with somatic cell score, the results for sheep and goats were contradictory. Positive correlations were found in dairy sheep indicating that selection for high fat and protein content would result in higher somatic cell score. In dairy goats, the correlation was found to be negative. However, the estimate was based on two studies only. These antagonistic relationships are also reported for dairy cattle (Rupp and Foucras, 2010; Koeck et al., 2014), where the trade-offs between yields and milk solid content are accommodated within the selection index framework (and that is what we would recommend here). For meat sheep, the clear indication that faster-growing sheep have low faecal egg count and dagginess (r_g –0.28 ± 0.09) indicates that there is no evidence of trade-offs between these traits. It is possible that faster-growing sheep eat more and have higher throughput of forage compared to slower-growing animals which may act as a dilution for the faecal egg count in the faeces to explain the result. The r_g between faecal egg count and parasitism immunoglobulin (−0.40) is interesting because it indicates animals with lower immunoglobulin levels are more susceptible to intestinal parasitic infection. This is in agreement with the results of Barbosa Toscano et al. (2020) who also reported a negative correlation between both IgG and IgA with faecal egg count in Morada Nova lambs.

Number of studies considered

The number of studies used in this meta-analysis is relatively low compared to other analyses published for cattle, which used between 50 and 490 papers (Lobo et al., 2000; Utrera and Van Vleck, 2004; Diaz et al., 2014). It is however similar to previous meta-analyses in sheep which used between 165 and 178 published papers (Fogarty, 1995; Safari et al., 2005). The number of studies focused on estimation of heritability for efficiency traits both in dairy and meat sheep was relatively large although the number of heritability estimates for efficiency traits in dairy goats was smaller. A considerably smaller number of studies have focused on resilience traits such as somatic cell score in dairy goats and faecal egg count in both dairy goats and dairy sheep. The issue with low number of available estimates was particularly pertinent for the meta-analysis of genetic correlations between resilience and efficiency traits in dairy goats. In general, the number of studies that reported genetic correlations was much smaller compared to those that reported heritability estimates. This highlights the need for more research focusing on estimation of genetic correlations between traits as these are essential for proper inclusion of new traits in a balanced breeding programme which aims to improve both animal efficiency and resilience. This is particularly important for breeders if they want to maximise their profit by breeding high yielding animals and reduce losses related to veterinary costs due to diseases or poor animal welfare.

Previous meta-analyses of genetic parameters in goats were based on 84 papers focused on dairy and meat production and reproduction traits (Jembere et al., 2017). The current study used a comparable number of papers for calculation of pooled genetic parameters for milk production (6–15 studies) compared to the meta-analysis by Jembere et al. (2017) with 2–12 studies. It is worth mentioning that the two meta-analyses had only three papers in common for milk production traits (Valencia et al., 2007; Montaldo et al., 2010; Castañeda-Bustos et al., 2014). Jembere et al. (2017) included more papers focused on goats from Africa and Asia than the current meta-analysis. Our results for pooled heritability of milk yield are within the range of values reported by Jembere et al. (2017). However, they seem to be at the lower end of that interval which ranged from 0.23 ± 0.08 to 0.43 ± 0.05 depending on trait definition (daily or cumulative milk yield up to 90 or 150 DIM). Pooled estimates of heritability for fat yield and protein yield (0.36 ± 0.02 and 0.40 ± 0.02, respectively) obtained by Jembere et al. (2017) were higher than in the current study. Similarly, the estimates for fat content and protein content (0.52 ± 0.07 and 0.54 ± 0.07, respectively) obtained by Jembere et al. (2017) were higher compared to the current study. The differences could be partially explained by a different set of papers included in the two meta-analyses which represent a different breed composition and countries where the animals produced. Estimates from the current study often had much higher standard errors even though more observations were included in the analysis. This can be explained by the differences in methods used, where the current study applied a three-level meta-analysis model compared to a simpler weighted average approach used by Jembere et al. (2017). This is in line with results of the current study, where the three-level model also tended to provide larger confidence intervals (higher standard errors) compared to the simpler random-effects model.

Heterogeneity of analysed genetic parameters

Very high heterogeneity was observed for heritability and genetic correlation estimates. This reflects variation between the studies included in this meta-analysis. It also highlights the need to account for this heterogeneity by using an appropriate statistical approach such as the three-level random-effects meta-analysis model. This model allowed for partitioning of the observed heterogeneity into a between- and within-cluster component. Clusters reflect groups of observations obtained under similar conditions. This is particularly important for the present meta-analysis that comprised parameter estimates for production, efficiency and health traits obtained under a wide range of challenge conditions, which are not explicitly taken into account in this study as they were often unknown. Clustering however partly accounts for differences in the conditions under which the original estimates were obtained. Hence, the estimates obtained by our three-level meta-analysis model would be expected to be more robust across a range of conditions than simpler random-effects model that does not account for different underlying conditions.

Ideally, the heterogeneity within clusters should be relatively small, and most of the heterogeneity should be observed between the clusters. This was not always the case, particularly in dairy goats where the number of observations was limited. In this case, the small number of observations might have led to bias in estimation of heterogeneity (Higgins and Thompson, 2002). It has been reported that estimates of heterogeneity based on low number of observations (below eight) might be biased and it might be difficult to distinguish moderate heterogeneity from chance (Higgins and Thompson, 2002). A notable exception was milk yield, for which the number of observations was the highest, and the between-cluster heterogeneity was over 95% whereas the within-cluster heterogeneity was close to zero. Low within-cluster heterogeneity was also observed for faecal egg count and somatic cell score but this can be explained by the fact that the number of observations was so low that essentially the number of clusters was equal to the number of observations resulting in lack of heterogeneity within clusters. In dairy sheep for traits such as milk yield, protein content and somatic cell score which had the largest number of observations, heterogeneity within clusters was also relatively low compared to the remaining traits with a low number of records.

Multi-level meta-analysis model

Multi-level meta-analysis models enabled us to account for non-independence of observations from related sources (Hox et al., 2018). This is particularly important if we want to include multiple estimates from the same study or the same population. The simple meta-analysis models (fixed- or random-effects model) do not allow for this, and it is necessary to either choose just one estimate per study or to average these estimates. This leads to some degree of loss of information and decrease in statistical power (Nakagawa and Santos, 2012). Moreover, the application of multi-level meta-analysis models can be advantageous particularly when estimates (heritability or genetic correlations) are very different from study to study (Fernández-Castilla et al., 2020). They also allow to account for dependencies across studies when we have multiple studies performed by the same research group.

Generally, the results from the random-effects model (Supplementary Tables S13 to S21) were similar to those of the three-level meta-analysis. In dairy goats, dairy sheep and meat sheep estimates of heritability were very similar between the two models. However, the three-level model usually provided wider confidence intervals for the pooled estimates. It is worth noting that in some cases, the number of observations included in the meta-analysis based on the simple random-effects model was larger. The random-effects model did not require additional information from the original studies such as sample size or age of the animals. It was therefore possible to include papers that did not contain this information. In case of correlations, the three-level model also provided wider confidence intervals. Due to the small number of observations, estimates from both models were often not statistically significant. This was even more apparent in the case of the three-level model which produced larger standard errors. In cases where within-cluster heterogeneity was high, the three-level meta-analysis model is probably less suitable, and a simple random-effects model would suffice. This was particularly the case for correlations where the number of observations was low and thus clustering may not be reliable.

This study found evidence of genetic antagonisms between resilience and efficiency for dairy goats and dairy sheep, but not for meat sheep. Lack of significant results in meat sheep can be explained by a large variability of estimates reported in literature. Even though the pooled estimates were non-significant, antagonisms may exist but only in specific populations and environments. Overall, pooled genetic correlations among all of the analysed resilience and efficiency traits in dairy goats, dairy sheep and meat sheep ranged from −0.33 to 0.35. In many cases, the genetic correlations were not significantly different from zero. This could indicate possibilities for simultaneous improvement of efficiency and resilience by including both types of traits in the breeding goal. However, the variability of estimates was often large with range of values containing negative as well as positive values, especially in meat sheep. The variability in correlations between faecal egg count and growth might reflect the importance of the environmental conditions for the co-expression of disease resistance and production potential or so to say genotype by environment interactions. Environmental conditions can include the type and load of parasites or the feeding systems for instance. Cheynel et al. (2019) stated that growth and immunity are energetically costly functions that may compete when resources allocated are limited, which could highlight trade-offs and some negative correlation in challenging conditions. This was confirmed by previous simulation studies for sheep, which explicitly demonstrated that genetic correlations between resistance (e.g. faecal egg count) and growth can vary substantially from strongly favourable to moderately unfavourable depending on the infection stage of the animals at the time of recording, nutrient availability, as well as linkage or pleiotropic effects between underlying resistance traits affecting the parasite life-cycle within the host, as well as genotype by environment interactions (Vagenas et al., 2007; Doeschl-Wilson et al., 2008). Therefore, a better understanding of potential trade-offs between efficiency and resilience traits would be beneficial. For some of the analysed genetic correlations (particularly in dairy goats), it would be desirable to simply include more studies to obtain more robust pooled estimates. It is also worth noting that for many traits of interest, we had too few estimates to include them in this meta-analysis. This relates particularly to reproduction traits. Additionally, in this study, resilience was considered in a narrow sense encompassing essentially disease and survival. Further studies focused on a broader definition of resilience encompassing not only resistance to specific diseases but also to a wide range of pathogens and other environmental stressors are needed. In addition to empirical correlation estimates, mechanistic models of resource allocation into different biological functions may offer valuable insights into the environmental conditions and biological mechanisms underlying trade-offs, in particular if fitted to robust empirical data, such as those generated by meta-analyses (Doeschl-Wilson et al., 2008; Douhard et al., 2014).

Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.animal.2022.100456.

Ethics approval

This meta-analysis did not require any ethical approval.

Data and model availability statement

Data, models and R code used for the purpose of the present study are not deposited in an official repository. The data that support the study findings are available upon request.

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AW: Contributed to the formal analysis and writing of the original draft of the manuscript.

Declaration of interest

None.

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Meta-analysis of genetic parameters for resilience and efficiency traits in goats and sheep

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Supplementary material

Supplementary Table S1

Studies used for meta-analysis of heritability in dairy goats

Study	Traits[1]	Breed	Lactation	N phenotypes
Analla et al., 1996	MY, FC, PC	Murciano-Granadina	Multiple	10 289
Bagnicka et al., 2016	SCS	Polish White Improved & Polish Fawn Improved	Multiple	4 417
Boichard et al., 1989	MY, FC, PC, FY, PY	Alpine	1st	11 856
		Saanen	1st	5 744
Castañeda-Bustos et al., 2014	FC, PC, FY, PY	Multiple breeds: Alpine, La Mancha, Nubian, Saanen, Toggenburg	1st	23 770
Desire et al., 2018	MY	Alpine x Saanen x Toggenburg	1st	9 546
Heckendorn et al., 2017	MY, FEC	Alpine and Saanen	Multiple	2 445

Kala and Prakash, 1990	MY, FC, PC	Jamunapari	Multiple	338
		Barbari		264
Kominakis et al., 2000	MY	Skopelos	Multiple	1 251
McLaren et al., 2016	MY	Alpine x Saanen x Toggenburg	1st	4 170
Morris et al., 1997b	MY, FEC	Saanen	Multiple	4 738
Palhière et al., 2018	MY, FC, PC, FY, PY, SCS	Alpine	1st	206 785
		Saanen		135 197
Rabasco et al., 1993	MY, FC, PC, FY, PY	Verata	Multiple	440
Valencia et al., 2007	MY	Saanen	Multiple	1 413
Valencia-Posadas et al., 2017	MY	multiple breeds: Alpine, Saanen, Toggenburg, Nubian, LaMancha	1st	40 721
Rupp et al., 2011	MY, FC, PC, FY, PY, SCS	Alpine	1st	67 882
		Saanen		49 709
Biffani et al. 2020 unpublished results	MY, FC, PC, FY, PY	Alpine	Multiple	163 857
		Saanen		183 465

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[1] Traits: MY – milk yield, FC – fat content, PC – protein content, FY – fat yield, PY – protein yield, SCS – somatic cell score, FEC – faecal egg count

Supplementary Table S2

Studies used for meta-analysis of heritability in dairy sheep

Study	Traits[1]	Breed	Lactation	N phenotypes
Aguerre et al., 2018	FEC	Red-Faced Manech	multiple	1 307
Allain et al., 2018	MY, FC, PC, SCS	Lacaune	1st	377 945
Banos et al., 2017	SCS	Chios	multiple	2 436
Barillet and Boichard, 1987	MY, FC, PC, FY, PY	Lacaune	1st	1 487
Barillet et al., 2001	MY, FC, PC, SCS	Lacaune	1st	23 091
Barillet et al., 2006	MY, FC, PC, FY, PY, SCS	Lacaune	1st	121 283
Barillet et al., 2008	MY, FC, PC, FY, PY, SCS	Red-Faced Manech	1st	121 283
Baro et al., 1994	MY, PC, SCS	Churra	Multiple	10 171
Casu et al., 2010	SCS	Sarda x Lacaune backcross	1st	2 251
de la Fuente et al., 2011	MY, FC, PC, SCS	Churra	1st	1 891
			multiple	10 189
El-Saied et al., 1998	MY, PC, SCS	Churra	multiple	6 620
El-Saied et al., 1999	MY, PC, SCS	Churra	multiple	3 231
Gonzalo et al., 2003	SCS	Churra	multiple	4 692

Gutiérrez-Gil et al., 2010	FEC	Churra	Multiple	1 513
Gutierrez-Gil et al. 2020 unpublished results	MY, FC, PC, SCS	Churra	Multiple	664 355
Hamann et al., 2004	MY, FC, PC, FY, PY, SCS	East-Friesian	Multiple	9 729
Legarra and Ugarte, 2005	MY, SCS	Latxa	Multiple	9 805
Othmane et al., 2002	MY, FC, PC, SCS	Churra	Multiple	7 492
Riggio et al., 2007	MY, FC, PC, FY, PY, SCS	Valle del Belice	1st	13 066
Riggio et al., 2010	SCS	Valle del Belice	multiple	8 843
Rupp et al., 2003	MY, FC, PC, SCS	Lacaune	1st	139 973
Sechi et al., 2009	SCS, FEC	Sardinian x Lacaune backcross	Multiple	5 880
Serrano et al., 2001	MY, PC	Manchega	1st	22 804
	MY	Lataxa	1st	20 046
Serrano et al., 2003	MY, PC, SCS	Manchega	1st	12 025
			2nd	11 568
			3rd	9 251
			multiple	32 844
Tolone et al., 2013	MY, SCS	Valle del Belice	multiple	17 843
Casu et al. 2020 unpublished results	MY, FC, PC, SCS	Sarda x Lacaune backcross	multiple	9 352

[1] Traits: MY – milk yield, FC – fat content, PC – protein content, FY – fat yield, PY – protein yield, SCS – somatic cell score, FEC – faecal egg count

Supplementary Table S3

Studies used for meta-analysis of heritability in meat sheep

Study	Traits[1]	Breed	N phenotypes
Afolayan et al., 2008	PROL	Merino-based breed	7 899
Albers et al., 1987	GR, FEC	Merino	882
Allain et al., 2014	LSurv	Romane	7 880
Altarriba et al., 1998	PROL	Rasa Aragonesa	58 493
Amou Posht-e- Masari et al., 2013	PROL	Shall Sheep	1 316
Ap Dewit et al., 2002	BFT, MD, PROL, BW	Welsh Mountain Sheep	1 022 – 11 201
Assenza et al., 2014	GR, FEC	Romane x Martinic Black Belly back-cross	963 - 997
Berton et al., 2017	FEC, HC	Santa Ines	514 (HC) 517 (FEC)
Bishop et al., 1996	FEC, BW	Scottish Blackface	567
Bishop and Stear, 2001	FEC	Scottish Blackface	1 445
Bishop et al., 2004	BFT, MD, FEC, BW	Texel	212 – 2 677
Bisset et al., 1992	DAG, GR, FEC, BW	Romney	2 611
Bisset et al., 1994	DAG, FCons, GR, FEC, BW	Romney	3 395

Bouix et al., 1998	GR, FEC	Polish Long Wool Sheep	327 - 659
Boujenane et al., 2013	LSurv, BW	D’man	4 554
Brito et al., 2017b	BFT, MD, BW	Composite breed	8 604 – 14 564
Brito et al., 2017a	BFT, MD, BW	Composite breed	1 206 – 14 781
Cammack et al., 2005	RFI, FI, GR,	Composite breed	1 239
Cemal et al., 2017	BFT, MD, BW	Kivircik	2 627
Ciappesoni and Goldberg, 2018	FEC, BW	Corriedale	13 015 – 14 850
Ciappesoni et al., 2013	FEC, BW	Merino	15 004 – 29 730
Ciappesoni et al., 2014	BFT, BW	Texel	3 071 (BFT) 3 094 (BW)
Clarke et al., 2003	BFT, MD, BW	Merino	4 906 – 43 115
Cloete et al., 2001	BW	Merino	880
Cloete et al., 2009	LSurv, BW	Merino	5 390
Conington et al., 1995	BFT, MD, BW	Scottish Blackface	1 912 – 2 085
Crump et al., 2019	MAS	Texel	740
Davies et al., 2005	NBW, FEC, Par-Ig,	Scottish Blackface	489 - 962
De Vries et al., 1998	PROL	Zwartbles, Swifter	1 691 – 31 380

Dixit et al., 2001	GR, BW	Merino	1 560 – 2 425
Douch et al., 1995	DAG, FCons, GR, Par-Ab, FEC, Par-Ig, BW	Romney	1 547
Fitzmaurice et al., 2020	BFT, MD, BW	Texel, Sufflok, Mouton Charollais	5 556 – 12 074
Fitzmaurice et al., 2021	BFT, MD, BW	Texel, Sufflok, Mouton Charollais	6 504 – 13 219
Fogarty et al., 2003	BW	Merino	1 020 – 1 045
Fogarty et al., 2009	BFT, MD, PROL, BW	Merino	3 690 – 26 733
Fossceco and Notter, 1995	BW	Composite breed	753 - 942
Gauly et al., 2002	NBW, FEC, HC, Par-Ig	Rhon, Merinoland	122 - 257
Goldberg et al., 2012	FEC	Merino	2 110 – 9 458
Greeff et al., 2008	BFT, MD	Merino	4 706 – 4 748
Greeff et al., 2014	DAG, BrStr	Merino	1 909 – 2 581
Gruner et al., 2004	FEC	Romanov	138 – 1 404
Haile et al., 2020	PROL, BW	Bonga, Horro, Menz	1 615 – 8 389
Hanford et al., 2003	PROL, BW	Columbia	7 840 – 24 741
Huisman et al., 2008	BFT, MD, FEC, PROL, BW	Merino	1 500 – 18 946
Husain et al., 2007	BFT, MD, BW	Beulah Specklefaced	7 441 – 10 038
Ingham et al., 2003	BFT, MD, BW	Merino	1 657 – 1 761

Johnson, P. L. et al., 2018	BFT, RFI, FI, GR, BW	Composite breed	600
Jones et al., 2004	BFT, MD, BW	Texel, Sufflok, Mouton Charollais	18 747 – 50 673
Jonker et al., 2018	BW, CH4	Composite breed	1 251 – 8 655
Kaseja et al., 2018	FR, MAS	Texel	3 500 (MAS) 5 200 (FR)
Lambe et al., 2008	BFT, LSurv, Long, MD, BW	Scottish Blackface	3 645 – 15 515
Lambe et al., 2001	GR	Scottish Blackface	2 331
Larsgard and Olesen, 1998	BFT, GR, MD, BW	Composite breed	972
Lee et al., 1995	BFT, FI, BW, FCR	Merino	553 – 2 278
Lee et al., 2002	BFT, FI, BW, FCR	Merino	1 292 – 1 729
Lee et al., 2015	Long	Composite breeds	35 688 – 658 871
Lôbo et al., 2009	GR, BW	Composite breed	1 177 - 11 943
Lopez Villalobos et al., 1999	LSurv	Romney	25 874
Macé et al., 2018	BCS, BW	Romane	2 000
Macé et al., 2019	GR, LSurv, PROL, BW	Romane	2 628 - 2 632
Maniatis and Pollott, 2002a	BFT, MD, BW	Suffolk	829 - 892

Maniatis and Pollott, 2002b	BFT, MD, BW	Suffolk	28 673 - 55 683
Martin et al., 2015	PROL	Lacaune	5 775
Massender et al., 2019	BFT, GR, MD, BW	Canadian multi-breed	1 299 - 29 082
Massender et al., 2021	BFT, GR, MD, BW	Canadian multi-breed	3 875 - 40 680
Matika et al., 2016	BW	Scottish Blackface	751
Maxa et al., 2007	GR, PROL, BW	Suffolk, Oxford Down, Shropshire, Texel	7 970 - 51 699
Maxa et al., 2009	LSurv	Oxford Down, Shropshire, Texel	30 701 - 61 953
Mcewan et al., 1992	DAG, FCons, GR, FEC, BW	Romney	891
McHugh et al., 2017	GR, BW	Irish population	12 166 - 14 711
McHugh et al., 2018	BW	Irish population	4 817 - 4 838
McLaren et al., 2017	Long	Lleyn, Dorset	13 652 - 14 047
McLaren et al., 2018	MAS	Texel	2 337 - 3 539
McRae et al., 2005	BFT, MD, BW	Charollais	570
Morris et al., 1997a	FEC, BW	Romney	1 324 - 1 979
Morris et al., 1998	FEC	Romney	785
Morris et al., 2000b	FEC	Romney	5 883 - 20 745
Morris et al., 2000a	LSurv	Romney	9 914 - 26 147

Mortimer et al., 2010	BFT, MD, BW	Merino-based breeds	6 682 - 7 176
Mortimer et al., 2017	BFT, MD, BW	Merino	2 653 - 9 135
Nagy et al., 1999	PROL, BW	Merino	5 669 - 31 375
Nieuwhof et al., 2008	FR, BW	Merino	1 225
O'Brien et al., 2017	DAG, BFT, FR, MAS, MD, BCS, BW	Belclare, Charollais, Suffolk, Texel and Vendéen	3 378 - 31 410
Pacheco et al., 2019	DAG, FEC, BW	Scottish Blackface	3 951
Pacheco et al., 2020 unpublished results	Par-Ig	Scottish Blackface	1 040
Paganoni et al., 2017	RFI, FI, CH4	Merino	406 - 2 665
Pickering et al., 2012	DAG, FEC, PROL, BW	Multi-breed	45 309 - 1 747 837
Pickering et al., 2013	DAG, BW	Multi-breed	17 215 - 70 763
Pickering et al., 2015	DAG, BrStr	Romney	1 579
Pinares-Patiño et al., 2013	DAG, MD, BW, CH4	Multi-breed	4 869 - 48 591
Pollott and Greeff, 2004	BFT, MD, FEC, BW	Merino	8 355 - 53 031
Pollott et al., 2004	DAG, FCons, FEC, BW	Merino	834 - 8 454
Raadsma et al., 1994	FR	Merino	1 255 - 1 562
Reintke et al., 2020	BFT, BCS, BW, CH4	Rhon, Merinoland	696 - 1 493

Rius-Vilarrasa et al., 2009	BFT, GR, MD, BW	Multi-breed	6 417
Safari et al., 2008	MD, PROL	Merino	4 706 - 20 299
Scobie et al., 2008	DAG, BrStr	Composite breed	2 095 - 5 349
Shaw et al., 1999	DAG, FCons, GR, Par-Ab, FEC, Par-Ig, BW	Romney	1 547
Shaw et al., 2012	FEC, Par-Ig	Romney, Texel, Finnish Landrace	315
Shaw et al., 2013	DAG, FEC, Par-Ig, BW	Romney, Texel, Finnish Landrace	353
Simm et al., 2002	BFT, MD, BW	Suffolk	1 932
Snowder and Van Vleck, 2003	RFI, FI, GR, BW	Targhee	952
Snyman et al., 1996	BW	Merino	6 753 - 8 480
Southey et al., 2001	LSurv	Composite breed	7 020 - 8 642
Southey et al., 2003	LSurv	Composite breed	8 642
Southey et al., 2004	LSurv	Composite breed	8 301
Stear et al., 1997	NBW, FEC	Scottish Blackface	501
Strain et al., 2002	Par-Ig	Scottish Blackface	964
Stratz et al., 2018	GR	Composite breed	1 582
Thiruvenkadan et al., 2011	BW	Mecheri Sheep	1 185 - 2 365
Tortereau et al., 2020	BFT, RFI, FI, GR, MD, BW	Romane	951

Van Vleck et al., 2000	GR	Composite breed	1 101 - 3 513
Van Vleck et al., 2003	PROL, BW	Targhee	32 715 - 37 020
Van Vleck et al., 2005	BW, PROL	Polypay	7 831 - 11 896
Watson et al., 1995	Par-Ab, FEC	Perendale	137 - 2 748
Woolaston and Piper, 1996	FEC	Merino	3 337
Woolaston and Windon, 2001	FEC	Merino	919 - 1 314
Yazdi et al., 1997	GR, BW	Baluchi	4 134 - 10 326

[1] Traits: GR – growth, BCS – body condition score, BFT – ultrasonic backfat thickness, MD – ultrasonic muscle depth, FI –feed intake, RFI – residual feed intake, FCR – feed conversion ratio, CH4 – methane emissions, PROL – prolificacy, LSurv – lamb survival, Long – longevity, MAS – mastitis, FR – footrot, BrStr – breech strike, DAG – dagginess, FCons – faecal consistency, NBW – number of worms, Par-Ab – parasitism anitbodies, Par-Ig – parasitism immunoglobulin, FEC –faecal egg count, HC - Haematocrit

Supplementary Table S4

Studies used for meta-analysis of genetic correlations in dairy goats

Study	Traits[1]	Breed	Lactation
Bagnicka et al., 2016	SCS & FC, SCS & MY, SCS & PC	Polish White Improved & Polish Fawn Improved	multiple
Heckendorn et al., 2017	FEC & MY	Alpine and Saanen	multiple
Morris et al., 1997	FEC & MY	Saanen	multiple
Rupp et al., 2011	SCS & FC, SCS & MY, SCS & PC	Alpine Saanen	1st

[1] Traits: MY – milk yield, FC – fat content, PC – protein content, SCS – somatic cell score, FEC – faecal egg count

Supplementary Table S5

Studies used for meta-analysis of genetic correlations in dairy sheep

Study	Traits[1]	Breed	Lactation
Allain et al., 2018	FC & MY, FC & PC, PC & MY, SCS & FC, SCS & MY, SCS & PC	Lacaune	1st
Barillet et al., 2001	FC & MY, PC & MY, SCS & MY	Lacaune	1st
Barillet et al., 2006	FC & FY, FC & MY, FC & PC, FC & PY, FY & MY, FY & PY, PC & FY, PC & MY, PC & PY, PY & MY, SCS & FC, SCS & FY, SCS & MY, SCS & PC, SCS & PY	Lacaune	1st
Barillet et al., 2008	FC & FY, FC & MY, FC & PC, FC & PY, FY & MY, FY & PY, PC & FY,PC & MY, PC & PY, PY & MY, SCS & FC, SCS & FY, SCS & MY, SCS & PC, SCS & PY	Red-Faced Manech	1st
Casu et al. 2020 unpublished results	SCS & MY, SCS & FC, SCS & PC	Sarda x Lacaune backcross	multiple
Gutierrez-Gil et al. 2020 unpublished results	FC & MY, FC & PC, PC & MY, SCS & MY, SCS & FC, SCS & PC	Churra	multiple
Hamann et al., 2004	FC & FY, FC & MY, FC & PC, FC & PY, FY & MY, FY & PY, PC & FY, PC & MY, PC & PY, PY & MY, SCS & FC, SCS & FY, SCS & MY, SCS & PC, SCS & PY	East Friesian	multiple
Legarra and Ugarte, 2005	SCS & MY	Latxa	multiple
Othmane et al., 2002	FC & MY, FC & PC, PC & MY, SCS & FC, SCS & MY, SCS & PC	Churra	multiple
Riggio et al., 2007	FC & FY, FC & MY, FC & PC, FC & PY, FY & PY, PC & FY, PC & MY, PC & PY, SCS & FC, SCS & FY, SCS & MY, SCS & PC, SCS & PY	Valle del Belice	1st
Rupp et al., 2003	FC & MY, FC & PC, PC & MY, SCS & FC, SCS & MY, SCS & PC	Lacaune	1st
Serrano et al., 2003	PC & MY, SCS & MY, SCS & PC	Manchega	1st, 2nd, 3rd, multiple

[1] Traits: MY – milk yield, FC – fat content, PC – protein content, FY – fat yield, PY – protein yield, SCS – somatic cell score

Supplementary Table S6

Studies used for meta-analysis of genetic correlations in meat sheep

Study	Traits[1]	Breed
Albers et al., 1987	GR & FEC	Merino
Ap Dewit et al., 2002	BW & MD, BW & BFT, BFT & MD	Welsh Mountain Sheep
Assenza et al., 2014	GR & FEC	Romane x Martinic Black Belly back-cross
Bishop et al., 1996	FEC & BW	Scottish Blackface
Bishop and Stear, 2001	FEC & BW	Scottish Blackface
Bishop et al., 2004	FEC & BW	Texel
Bisset et al., 1992	BW & GR, BW & FEC, DAG & FEC, BW & DAG, GR & FEC, GR & DAG	Romney
Bisset et al., 1994	DAG & FEC, BW & DAG, GR & DAG	Romney
Bouix et al., 1998	GR & FEC	Polish Long Wool Sheep
Brito et al., 2017b	BW & MD, BW & BFT, BFT & MD	Composite breed
Cammack et al., 2005	GR & FI, GR & RFI, FI & RFI	Composite breed
Ciappesoni and Goldberg, 2018	FEC & BW	Corriedale
Ciappesoni et al., 2013	FEC & BW	Merino
Ciappesoni et al., 2014	BFT & BW	Texel

Clarke et al., 2003	BW & MD, BW & BFT, BFT & MD	Merino
Conington et al., 1995	BW & MD, BW & BFT, BFT & MD	Scottish Blackface
Davies et al., 2005	FEC & Par-Ig,	Scottish Blackface
Dixit et al., 2001	GR & BW	Merino
Douch et al., 1995	BW & GR, BW & FEC, FEC & Par-Ig, FEC & FCons, DAG & FEC, FCons & Par-Ig, DAG & Par-Ig, DAG & FCons, BW & Par-Ig, BW & FCons, BW & DAG	Romney
Fitzmaurice et al., 2020	BW & MD, BW & BFT, BFT & MD	Texel, Sufflok, Mouton Charollais
Fitzmaurice et al., 2021	BW & MD, BW & BFT, BFT & MD	Texel, Sufflok, Mouton Charollais
Husain et al., 2007	BW & MD, BW & BFT, BFT & MD	Beulah Specklefaced
Ingham et al., 2003	BW & MD, BW & BFT, BFT & MD	Merino
Jones et al., 2004	BW & MD, BW & BFT, BFT & MD	Texel, Sufflok, Mouton Charollais
Jonker et al., 2018	BW & CH4	Composite breed
Lee et al., 1995	BW x BFT, BW & FI, BFT & FI	Merino
Lee et al., 2002	BW x BFT, BW & FI, BFT & FI	Merino
Macé et al., 2019	PROL & BW	Romane
Massender et al., 2019	BW & GR,	Canadian multi-breed
Massender et al., 2021	BW & GR, BW & MD, BW & BFT, BFT & MD	Canadian multi-breed

Maxa et al., 2007	BW & GR, BW & PROL	Suffolk, Oxford Down, Shropshire, Texel
Morris et al., 2000b	BW & FEC	Romney
Mortimer et al., 2010	BW & MD, BW & BFT, BFT & MD	Merino-based breed
Mortimer et al., 2017	BW & MD, BW & BFT	Merino
O’Brien et al., 2017	BW & MD, BW & BFT, BFT & MD, BW & DAG	Belclare, Charollais, Suffolk, Texel, Vendéen
Pacheco et al., 2019	BW & FEC, DAG & FEC, BW & DAG	Scottish Blackface
Pacheco et al., 2020 unpublished results	FEC & Par-Ig, DAG & Par-Ig, BW & Par-Ig	Scottish Blackface
Paganoni et al., 2017	RFI & FI	Merino
Pickering et al., 2012	BW & FEC, DAG & FEC, BW & DAG, BW & PROL	Multi-breed
Pickering et al., 2013	DAG & BW	Multi-breed
Pinares-Patiño et al., 2013	BW & CH4	Multi-breed
Pollott et al., 2004	BW & FEC, FEC & FCons, DAG & FEC, DAG & FCons, BW & FCons, BW & DAG	Merino
Reintke et al., 2020	BFT & BW	Rhon, Merinoland
Rius-Vilarrasa et al., 2009	BW & GR, BW & MD, BW & BFT, BFT & MD	Multi-breed
Shaw et al., 1999	BW & GR, BW & FEC, FEC & Par-Ig, FEC & FCons, DAG & FEC, FCons & Par-Ig, DAG & Par-Ig, DAG & FCons, BW & Par-Ig, BW & FCons, BW & DAG,GR & FEC, GR & DAG	Romney

Shaw et al., 2012	FEC & Par-Ig	Romney, Texel, Finnish Landrace
Shaw et al., 2013	FEC & Par-Ig, DAG & Par-Ig, BW & Par-Ig	Romney, Texel, Finnish Landrace
Simm et al., 2002	BW & MD, BW & BFT, BFT & MD	Suffolk
Snowder and Van Vleck, 2003	BW & GR, GR & FI, GR & RFI, BW & FI, BW & RFI, FI & RFI	Targhee
Tortereau et al., 2020	GR & FI, GR & RFI, BW & FI, BFT & FI, BW & RFI, FI & RFI	Romane

[1] Traits: GR – growth, BFT – ultrasonic backfat thickness, MD – ultrasonic muscle depth, FI –feed intake, RFI – residual feed intake, CH4 – methane emissions, PROL – prolificacy, DAG – dagginess, FCons – faecal consistency, Par-Ig – parasitism immunoglobulin, FEC –faecal egg count

Supplementary Table S7

Number of estimates (N estimates) and number of papers (N papers) per breed used to estimate pooled heritability (h^2) and genetic correlations (r_g) in dairy goats

Breed	N estimates h^2	N papers h^2	N estimates r_g	N papers r_g
Saanen	29	6	4	2
Alpine	22	4	3	1
Alpine and Saanen	5	1	3	1
Multiple breeds	6	2		-
Verata	5	1		-
Alpine x Saanen x Toggenburg	3	2	-	-
Jamunapari	3	1	-	-
Barbari	3	1	-	-
Murciano-Granadina	3	1	-	-
Polish White Improved and Polish Fawn Improved	1	1	3	1
Skopelos	1	1	-	-

Supplementary Table S8

Number of estimates (N estimates) and number of papers (N papers) per breed used to estimate pooled heritability (h^2) and genetic correlations (r_g) in dairy sheep

Breed	N estimates h^2	N papers h^2	N estimates r_g	N papers r_g
Lacaune	37	5	33	4
Churra	30	8	6	2
Manchega	16	2	12	1
Red-Faced Manech	9	2	15	1
Valle del Belice	9	3	13	1
East-Friesian	6	1	15	1
Sarda x Lacaune backcross	5	2	3	1
Latxa	4	2	2	1
Sardinian x Lacaune backcross	2	1	-	-
Chios	1	1	-	-

Supplementary Table S9

Number of estimates (N estimates) and number of papers (N papers) per breed used to estimate pooled heritability (h^2) and genetic correlations (r_g) in meat sheep

Breed	N estimates h^2	N papers h^2	N estimates r_g	N papers r_g
Merino	205	28	68	11
Composite breeds	149	20	117	9
Romney	81	11	92	5
Scottish Blackface	49	11	38	6
Texel	46	10	32	6
Suffolk	27	7	24	5
Romane	26	4	15	2
Irish population	20	3	8	1
Canadian multibreed	15	2	14	2
Mouton Charollais	13	4	15	3
Baluchi	12	1		
Targhee	9	2	9	1
Polish long wool sheep	9	1	7	1
BC MBlackBelly x Romane	8	1	8	1
Rhon	7	1		
Welsh mountain sheep	6	1	7	1
Merinoland	6	1		
Romanov	6	1		
Romney + Perendale + composite	6	1		
D'man	5	1		
Mecheri sheep	5	1		

Swifter	5	1		
Beulah Specklefaced	4	1	5	1
Oxford Down	4	2	2	1
Shropshire	4	2	2	1
Merinoland + Rhon	4	1	1	1
Bonga	3	1		
Columbia	3	1		
Horro	3	1		
Kivircik	3	1		
Perendale	3	1		
Polypay	3	1		
Zwartbles	3	1		
Corriedale	2	1	1	1
Menz	2	1		
Santa Ines	2	1		
Dorset	1	1		
Lacaune	1	1		
Lleyn	1	1		
Rasa Aragonesa	1	1		
Shall sheep	1	1		

Supplementary Table S10

Pooled estimates of genetic correlations between efficiency traits from meta-analysis in dairy sheep

Traits[1]	Pooled r_g (± SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	I^2 between[5]	I^2 within[6]
PY & MY	0.88±0.15	0.83	0.92	3	3	45.97	52.97
FY & MY	0.83±0.09	0.77	0.87	3	3	97.91	0
PC & MY	-0.39±0.07	-0.58	-0.04	13	9	85.11	13.49
FC & MY	-0.26±0.21^{ns}	-0.53	0.19	9	8	32.62	67.08
PY & FY	0.84±0.33	0.68	0.95	4	4	42.76	57.07
PC & FY	-0.05±0.09^{ns}	-0.16	0.14	4	4	41.2	55.43
FC & FY	0.36±0.20^{ns}	0.10	0.58	4	4	16.12	82.99
PC & PY	0.14±0.17^{ns}	-0.06	0.40	4	4	20.87	77.97
FC & PY	0.03±0.20^{ns}	-0.18	0.33	4	4	15.52	83.59
FC & PC	0.59±0.10	0.22	0.74	7	7	91.96	7.72

[1] Traits: MY – milk yield, PY – protein yield, FY – fat yield, PC – protein content, FC – fat content

[2] minimum r_g from individual studies included in meta-analysis

[3] maximum r_g from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between clusters

[6] heterogeneity within clusters

^{ns} – pooled estimate did not differ significantly from zero

Supplementary Table S11

Pooled estimates of genetic correlations between resilience traits from meta-analysis in meat sheep

Traits[1]	Pooled r_g (± SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	I^2 between[5]	I^2 within[6]
FEC & Par-Ig	-0.40±0.05	-0.78	0.29	231	6	67.96	0.00
FEC & Fcons[7]	0.11±0.04	-0.01	0.21	5	3	95.80*	
FEC & DAG	0.11±0.12^{ns}	-0.23	0.45	18	7	11.92	80.36
Fcons & Par-Ig	0.15±0.08^{ns}	-0.05	0.29	6	2	24.37	14.55
DAG & Par-Ig	0.24±0.03	-0.02	0.54	25	4	22.71	0.00
DAG & Fcons[7]	0.94±0.55	0.63	0.99	3	3	100.00*	

[1] Traits: DAG – dagginess, FCons – faecal consistency Par-Ig – parasitism immunoglobulin, FEC – faecal egg count,

[2] minimum r_g from individual studies included in meta-analysis

[3] maximum r_g from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between clusters

[6] heterogeneity within clusters

[7] pooled correlation obtained from a simple random effects model as the three level meta-analysis model did not converge

^{ns} – pooled estimate did not differ significantly from zero

* heterogeneity from random effects meta-analysis model

Supplementary Table S12

Pooled estimates of genetic correlations between efficiency traits from meta-analysis in meat sheep

Traits[1]	Pooled r_g (± SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	I^2 between[5]	I^2 within[6]
BW & GR	0.61±0.22	-0.42	0.97	30	9	46.83	52.96
BW & PROL	-0.02±0.05^{ns}	-0.23	0.14	13	3	35.84	56.90
BW & MD	0.40±0.13	-0.41	0.77	48	15	33.46	64.26
BW & BFT	0.27±0.09	-0.33	0.82	65	19	28.99	65.81
BW & FI	0.61±0.10	0.34	0.73	6	4	64.92	0.00
BW & RFI[7]	-0.05±0.04^{ns}	-0.13	0.00	3	2	77.50*	
FI & GR[7]	0.82±0.18	0.59	0.92	4	3	99.30*	
RFI & GR	0.14±0.18^{ns}	-0.03	0.33	4	3	0.00	77.43
BFT & MD	0.26±0.10	-0.39	0.68	25	14	27.20	68.30
BFT & FI[7]	0.21±0.11	-0.11	0.33	4	3	98.30*	
FI & RFI	0.76±0.022	0.33	0.99	12	4	78.27	18.73
BW & CH4	0. 71±0.18	0.52	0.83	8	2	21.91	75.21

[1] Traits: GR – growth, BFT – ultrasonic backfat thickness, MD – ultrasonic muscle depth, FI –feed intake, RFI – residual feed intake, CH4 – methane emissions, PROL – prolificacy,

[2] minimum r_g from individual studies included in meta-analysis

[3] maximum r_g from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between clusters

[6] heterogeneity within clusters

[7] pooled correlation obtained from a simple random effects model as the three level meta-analysis model did not converge

^{ns} – pooled estimate did not differ significantly from zero

* heterogeneity from random effects meta-analysis model

Supplementary Material S1

Random effects model

$$\hat{\theta}_i = \mu + \varepsilon_i + e_i$$

Where $\hat{\theta}_i$ is the published parameter estimate (h^2 or r_g) from the *i*-th study, μ is the population mean, ε_i is the between study heterogeneity assumed to be $\varepsilon_i \sim N\left(0,\tau^2\right)$ with τ^2 being between study variance, and e_i is the within study heterogeneity due to sampling error in the parameter estimate from the *i*-th study assumed to be $e_i \sim \left(0,\sigma_e^2\right)$ where $\hat{\sigma}_e^2$ is the within study variance. The I^2 index was used to quantify the degree of heterogeneity between the studies (Higgins and Thompson, 2002).

$$I^2\left(\%\right) = \frac{\hat{\tau}^2}{\hat{\tau}^2 + \hat{\sigma}_e^2} \times 100$$

Supplementary Table S13

Pooled estimates of heritability in dairy goats based on random effects model

Trait[1]	Pooled h^2 (± SE)	Min[2] h^2	Max[3] h^2	N obs[4]	N studies	HET[5]
MY	0.26±0.02	0.11	0.46	25	16	99.20
FY	0.32±0.02	0.20	0.39	10	6	90.50
PY	0.31± 0.01	0.04	0.38	10	6	88.50
FC	0.45± 0.04	0.16	0.62	13	8	99.10
PC	0.45±0.06	0.14	0.67	13	8	99.60
SCS	0.21± 0.01	0.19	0.24	5	3	57.20
FEC	0.07±0.01	0.04	0.15	8	2	0.00

[1] Trait: MY – milk yield, FY – fat yield, PY – protein yield, FC – fat content, PC – protein content, SCS – somatic cell score, FEC – faecal egg count

[2] minimum h^2 from individual studies included in meta-analysis

[3] maximum h^2 from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between studies (I^2)

Supplementary Table S14

Pooled estimates of heritability in dairy sheep based on random effects model

Trait[1]	Pooled h^2 (± SE)	Min[2] h^2	Max[3] h^2	N obs[4]	N studies	HET[5]
MY	0.25±0.02	0.06	0.54	41	28	99.0
FY	0.23± 0.02	0.14	0.28	8	6	94.9
PY	0.23±0.03	0.12	0.30	8	6	96.4
FC	0.31± 0.05	0.04	0.68	18	14	99.9
PC	0.35±0.04	0.10	0.77	27	19	99.7
SCS	0.12±0.01	0.03	0.27	31	24	97.1
FEC	0.15± 0.02	0.09	0.35	6	3	55.9

[1] Trait: MY – milk yield, FY – fat yield, PY – protein yield, FC – fat content, PC – protein content, SCS – somatic cell score, FEC – faecal egg count

[2] minimum h^2 from individual studies included in meta-analysis

[3] maximum h^2 from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between studies (I^2)

Supplementary Table S15

Pooled estimates of heritability in meat sheep based on random effects model

Trait[1]	Pooled h^2 (± SE)	Min[2] h^2	Max[3] h^2	N obs[4]	N studies	HET[5]
Efficiency traits						
BW	0.30 ± 0.02	0.02	0.93	193	73	99.7
GR	0.20 ± 0.02	0.02	0.56	49	25	96.8
BCS	0.25 ± 0.04	0.06	0.37	9	3	98.1
BFT	0.27 ± 0.02	0.05	0.63	53	34	98.4
MD	0.28 ± 0.01	0.05	0.50	44	31	98.4
FI	0.26 ± 0.04	0.02	0.49	14	7	95.6
RFI	0.26 ± 0.06	0.07	0.46	7	5	95.7
FCR	0.12 ± 0.03	0.03	0.24	7	2	84.3
CH4	0.19 ± 0.01	0.00	0.29	20	4	91.7
PROL	0.08 ± 0.007	0.01	0.19	33	17	94.6
Resilience traits						
LSurv	0.10 ± 0.01	0.01	0.63	73	11	98.3
Long	0.09 ± 0.02	0.03	0.13	5	3	95.7
MAS	0.08 ± 0.008	0.04	0.11	9	4	37.4
FR	0.15 ± 0.01	0.06	0.26	28	4	89.7
BrStr	0.50 ± 0.06	0.32	0.61	7	3	98.1
DAG	0.29 ± 0.03	0.06	0.63	37	15	99.2
FCons	0.13 ± 0.02	0.03	0.27	13	5	77.6
NBW	0.10 ± 0.02	0.00	0.54	11	3	32.2
Par-Ab	0.18 ± 0.05	0.05	0.29	6	3	94.1
Par-Ig	0.38 ± 0.03	0.13	0.67	24	8	95.2

FEC	0.30 ± 0.01	0.00	0.82	116	32	97.3
HC	0.34 ± 0.11	0.08	0.56	5	2	92.1

[1] Trait: GR – growth, BCS - body condition score, BFT - ultrasonic backfat thickness, MD – ultrasonic muscle depth, FI – feed intake, RFI – residual feed intake, FCR – feed conversion ratio, CH4 – methane emissions, PROL – prolificacy, LSurv – lamb survival, Long – longevity, MAS – mastitis, FR – footrot, BrStr – breech strike, DAG – dagginess, FCons – faecal consistency, NBW – number of worms, Par-Ab – parasitism anitbodies, Par-Ig – parasitism immunoglobulin, FEC – faecal egg count, HC – Haematocrit

[2] minimum h^2 from individual studies included in meta-analysis

[3] maximum h^2 from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between studies (I^2)

Supplementary Table S16

Pooled estimates of genetic correlations between resilience (SCS, FEC) and efficiency (MY, FC, PC) traits in dairy goats based on random effects model

Trait[1]	Pooled r_g (± SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	HET[5]
SCS & MY	0.26± 0.21^{ns}	0.00	0.59	3	2	99.9
SCS & FC	-0.19± 0.01	-0.20	-0.18	3	2	83.8
SCS & PC	-0.06± 0.04^{ns}	-0.13	0.00	3	2	98.9
FEC & MY	0.30± 0.21^{ns}	-0.21	0.63	4	2	99.7

[1] Trait: SCS – somatic cell score, FEC – faecal egg count, MY – milk yield, FC – fat content, PC – protein content

[2] minimum r_g from individual studies included in meta-analysis

[3] maximum r_g from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between studies (I^2)

^{ns} – pooled estimate did not differ significantly from zero

Supplementary Table S17

Pooled estimates of genetic correlations between resilience (SCS) and efficiency (MY, FY, PY, FC, PC) traits in dairy sheep based on random effects model

Trait[1]	Pooled r_g (± SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	HET[5]
SCS & MY	-0.02±0.04^{ns}	-0.30	0.23	16	11	100.0
SCS & FC	0.05± 0.03^{ns}	-0.16	0.16	8	8	99.5
SCS & PC	0.12±0.02	0.02	0.24	12	9	99.7
SCS & FY	0.19±0.08	-0.04	0.31	4	4	99.7
SCS & PY	0.21±0.06	0.06	0.31	4	4	99.3

[1] Trait: SCS – somatic cell score, MY – milk yield, FY – fat yield, PY – protein yield, FC – fat content, PC – protein content

[2] minimum r_g from individual studies included in meta-analysis

[3] maximum r_g from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between studies (I^2)

^{ns} – pooled estimate did not differ significantly from zero

Supplementary Table S18

Pooled estimates of genetic correlations between efficiency traits in dairy sheep based on random effects model

Trait[1]	Pooled r_g (± SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	HET[5]
PY & MY	0.88±0.12	0.83	0.92	3	3	99.9
FY & MY	0.83±0.09	0.77	0.87	3	3	100.0
FY & PY	0.87±0.22	0.68	0.95	4	4	100.0
PC & MY	-0.41± 0.05	-0.58	-0.04	13	9	99.9
FC & MY	-0.32± 0.09	-0.53	0.19	9	8	99.9
PC & FY	-0.05±0.07[ns]	-0.16	0.14	4	4	99.7
FC & FY	0.36± 0.12	0.10	0.58	4	4	99.9
PC & PY	0.14±0.11[ns]	-0.06	0.40	4	4	99.9
FC & PY	0.03± 0.12[ns]	-0.18	0.33	4	4	99.9
FC & PC	0.60±0.09	0.22	0.74	7	7	99.9

[1] Trait: MY – milk yield, PY – protein yield, FY – fat yield, PC – protein content, FC – fat content

[2] minimum r_g from individual studies included in meta-analysis

[3] maximum r_g from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between studies (I^2)

[ns] – pooled estimate did not differ significantly from zero

Supplementary Table S19

Pooled estimates of genetic correlations between resilience and efficiency traits in meat sheep based on random effects model

Traits[1]	Pooled r_g (± SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	HET[5]
BW & FEC	-0.08±0.04^{ns}	-0.90	0.34	47	12	99.6
BW & Par-Ig	0.36 ± 0.06	-0.48	0.87	49	4	99.3
BW & Fcons	-0.12 ± 0.16^{ns}	-0.43	0.43	5	3	99.8
BW & DAG	-0.03 ±0.03^{ns}	-0.33	0.28	22	9	99.3
GR & FEC	0.26 ± 0.07	-0.68	0.57	24	5	99.1
GR & DAG	-0.33 ± 0.13	-0.54	-0.16	3	3	99.3

[1] Traits: FEC –faecal egg count, Par-Ig – parasitism immunoglobulin, FCons – faecal consistency, DAG – dagginess, GR – growth

[2] minimum r_g from individual studies included in meta-analysis

[3] maximum r_g from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between studies (I^2)

^{ns} – pooled estimate did not differ significantly from zero

Supplementary Table S20

Pooled estimates of genetic correlations between efficiency traits in meat sheep based on random effects model

Traits[1]	Pooled r_g (± SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	HET[5]
BW & GR	0.59 ±0.12	-0.42	0.97	30	9	100
BW & PROL	-0.04 ± 0.03^{ns}	-0.23	0.14	13	3	99.3
BW & MD	0.42 ± 0.05	-0.41	0.77	48	15	99.9
BW & BFT	0.25 ± 0.04	-0.33	0.82	65	19	99.7
BW & FI	0.61 ± 0.10	0.34	0.73	6	4	98.4
BW & RFI	-0.05 ± 0.04^{ns}	-0.13	0.00	3	2	77.5
GR & FI	0.82 ± 0.19	0.59	0.92	4	3	99.3
GR & RFI	0.14 ± 0.10^{ns}	-0.03	0.33	4	3	97.6
BFT & MD	0.24 ± 0.07	-0.39	0.68	25	14	99.8
BFT & FI	0.21 ±0.11	-0.11	0.33	4	3	98.3
FI & RFI	0.78 ± 0.17	0.33	0.99	12	4	99.7
BW & CH4 (g/j)	0.69 ± 0.08	0.52	0.83	8	2	89.9
BW & CH4 (g/kg DMI)	0.06 ± 0.02	0.02	0.15	5	2	81.5

[1] Traits: GR – growth, PROL – prolificacy, MD – ultrasonic muscle depth, BFT – ultrasonic backfat thickness, FI –feed intake, RFI – residual feed intake, CH4 – methane emissions

[2] minimum r_g from individual studies included in meta-analysis

[3] maximum r_g from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between studies (I^2)

^{ns} – pooled estimate did not differ significantly from zero

Supplementary Table S21

Pooled estimates of genetic correlations between resilience traits in meat sheep based on random effects model

Traits[1]	Pooled r_g (± SE)	Min[2] r_g	Max[3] r_g	N obs[4]	N studies	HET[5]
FEC & Par-Ig	-0.40 ± 0.05	-0.78	0.29	31	6	98.3
FEC & FCons	0.11 ± 0.04	-0.01	0.21	5	3	95.8
FEC & DAG	0.03 ± 0.04^{ns}	-0.23	0.45	18	7	99.6
Fcons & Par-Ig	0.15 ± 0.06	-0.05	0.29	6	2	97.2
DAG & Par-Ig	0.24 ± 0.03	-0.02	0.54	25	4	93.9
DAG & FCons	0.94 ± 0.55	0.63	0.99	3	3	100

[1] Traits: FEC – faecal egg count, Par-Ig – parasitism immunoglobulin, FCons – faecal consistency, DAG – dagginess,

[2] minimum r_g from individual studies included in meta-analysis

[3] maximum r_g from individual studies included in meta-analysis

[4] number of observations used in meta-analysis

[5] heterogeneity between studies (I^2)

^{ns} – pooled estimate did not differ significantly from zero

Supplementary Material S2.

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