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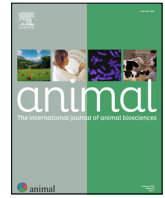
Animal Board Invited Review: Meta-analysis of genetic parameters for resilience and efficiency traits in goats and sheep

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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 multitrait response to challenges are required.

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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,

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:

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

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: $\widehat{\theta}_{ij}$ 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 h² (±SE)	Min[2] h²	Max[3] h²	N obs[4]	N studies	I² between[5]	I² 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 h² from individual studies included in meta-analysis.
[3] Maximum h² 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 h² (±SE)	Min[2] h²	Max[3] h²	N obs[4]	N studies	I² between[5]	I² 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 h² from individual studies included in meta-analysis.
[3] Maximum h² 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 h² (±SE)	Min[2] h²	Max[3] h²	N obs[4]	N studies	I² between[5]	I² 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 h² from individual studies included in meta-analysis.
[3] Maximum h² 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 esti-

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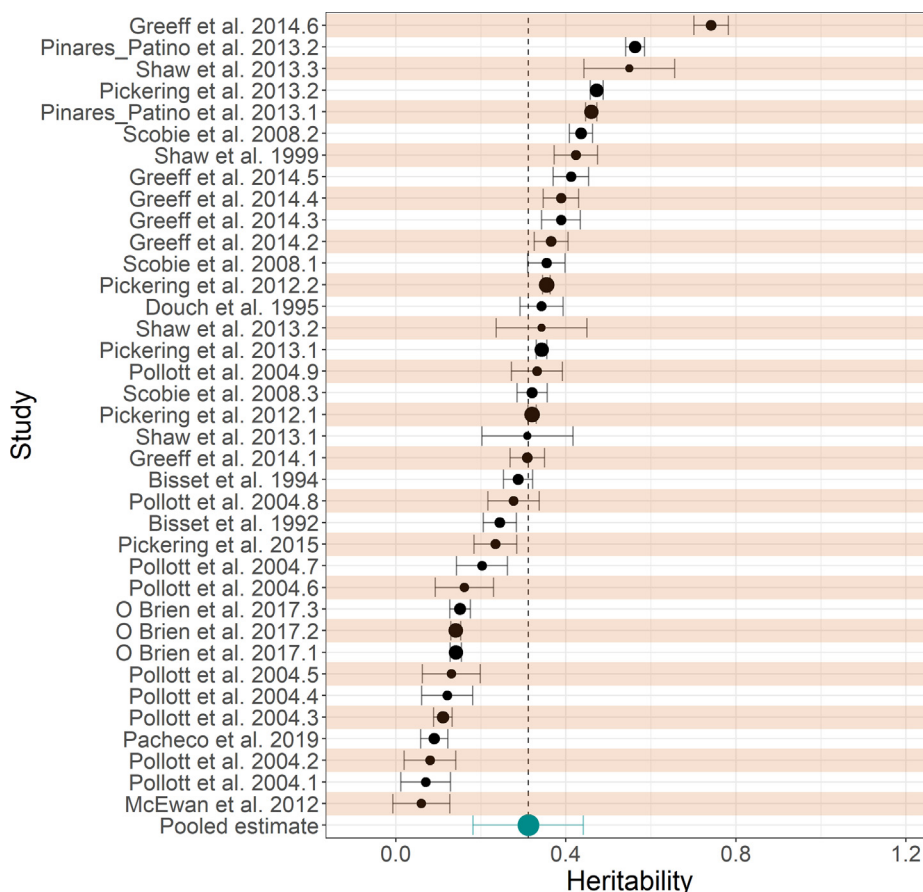
Fig. 1. Forest plot showing heritability estimates for dagginess in meat sheep.

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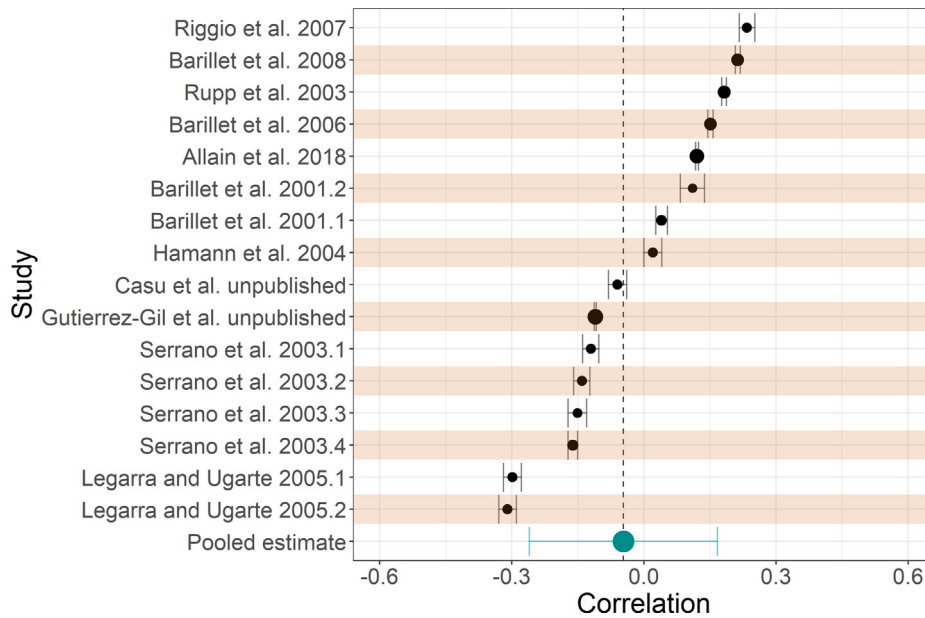[ns] Pooled estimate did not differ significantly from zero.

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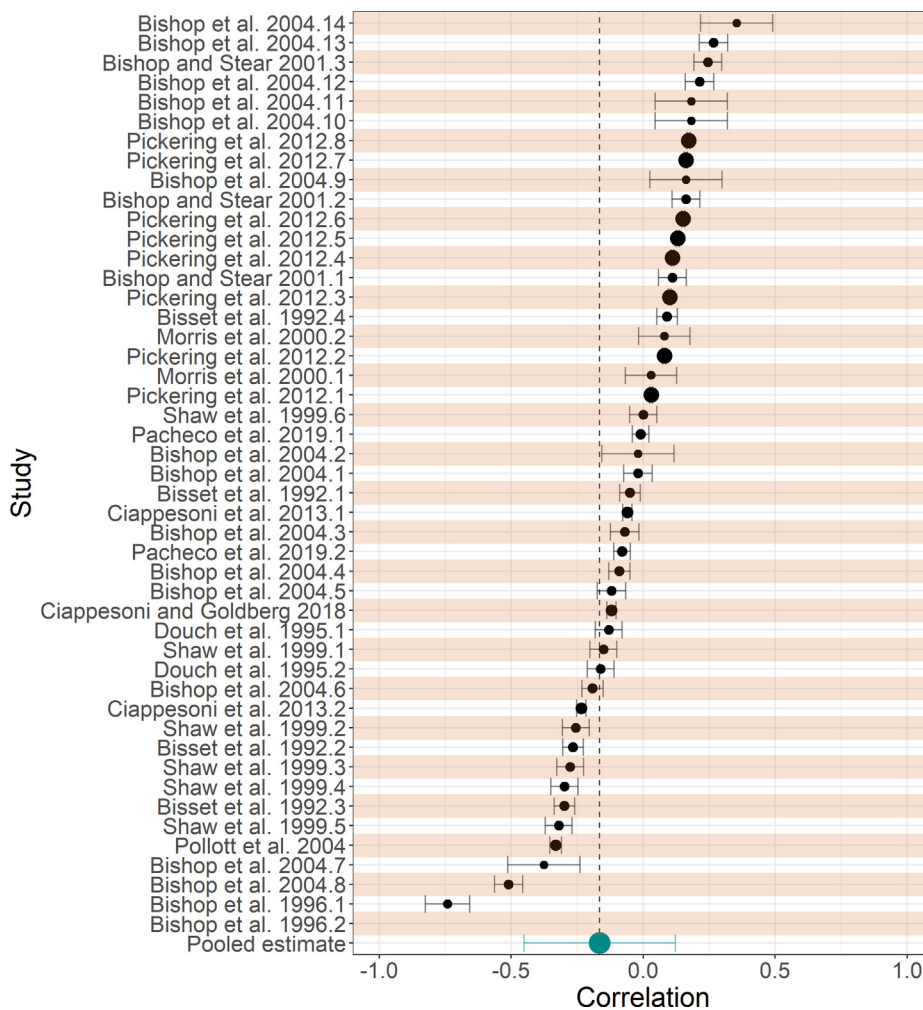

Fig. 3. Forest plot showing genetic correlation estimates between BW and faecal egg count in meat sheep.

Table 6
Pooled estimates of genetic correlations between resilience and efficiency traits from meta-analysis in meat sheep.

Traits[1]	Pooled $r_g(\pm SE)$	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 frame-

work (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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Declaration of interest

None.

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