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Genetic Feed Efficiency Traits in Dairy Cattle: A Systematic Meta-Analysis

Meta Analysis

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ABSTRACT

Efficient feed utilization is crucial for sustainable dairy cattle production. This systematic review and meta-analysis pooled heritability estimates for feed intake (FI), feed saved (FS), dry matter intake (DMI), feed conversion ratio (FCR), and residual feed intake (RFI) in dairy cattle and determined the genetic correlations between these traits and other production efficiency traits. Data from 68 studies published between 2000 and 2022 were analyzed using random effects meta-analysis and restricted maximum likelihood estimation. The pooled heritability estimates were as follows: 0.32 (95% CI: 0.29-0.36, I^2=98%, P<0.0001) for DMI, 0.29 (95% CI: 0.10-0.46, I^2=99%, P<0.0001) for FS, 0.17 (95% CI: 0.15-0.19, I^2=89.3%, P<0.0001) for RFI, and 0.11 (95% CI: 0.08-0.13, I^2=0%, P<0.0001) for FCR. Strong positive genetic correlations were observed between DMI and net energy of lactation intake (NELI) (0.90), RFI and average daily feed intake (ADFI) (0.80), and FCR and RFI (0.68). Conversely, negative genetic correlations were found between FCR and average feeding rate (AFR) (-0.38), FCR and average daily gain (ADG) (-0.34), FCR and longissimus muscle area (LMA) (-0.28), and FCR and hip height (HIPHT) (-0.14). These findings suggest potential indicators for selection indices and genetic improvement strategies, offering valuable insights for enhancing breeding programs and optimizing feed utilization in dairy cattle. Ultimately, this contributes to more sustainable livestock production and improved food security.

KEY WORDS dairy cattle, feed efficiency, heritability, meta-analysis.

INTRODUCTION

Because feed is the most expensive part of cattle breeding, even a slight improvement in the efficiency of feed consumption, which is regarded as a quantitative polygenic trait in dairy cows, could have major economic and environmental impacts, such as reducing greenhouse gas production (Van Middelaar *et al.* 2014; Connor, 2015). Reducing feed costs will positively affect the profitability of cattle breeders and the final price of meat and dairy products (Veerkamp, 1998; Alqaisi *et al.* 2019). Therefore, an animal with better feed efficiency is defined as consuming less feed without reducing performance or producing more by consuming a certain amount of feed (VandeHaar *et al.* 2016). Feed efficiency is a quantitative trait because feed energy consumption and utilization are related to many biological and physiological mechanisms in dairy cattle. Therefore, the change in the efficiency of feed consumption can occur under the influence of the change in the amount of feed consumption, feed digestion, energy allocation, metabolism, physiological stage, health status, rumen microbial composition, activity level, and body temperature regulation (Herd *et al.* 2003; Herd and Arthur, 2009; Patience *et al.* 2015; Hardie *et al.* 2017; Golshani Jourshari *et al.* 2023). Traits related to feed efficiency are heritable traits and can be improved through genetic and genomic selection (Hardie *et al.* 2017; Zhang *et al.* 2020). Genetic improvement in feed efficiency can be achieved by selecting cows with the highest feed efficiency as parents of future generations. The development of appropriate breeding programs, first of all, requires high-accuracy estimation and evaluation of genetic parameters (Mulder *et al.* 2006; Harder *et al.* 2020; Omer *et al.* 2022). Genetic parameters provide a clear insight into the amount of genetic progress in single-trait or multi-trait selection programs over years or generations, so it will help in conducting a better genetic evaluation (Ayalew *et al.* 2017; Tesema *et al.* 2020; Oliveira Junior *et al.* 2021). Usually, for the traits that are difficult to measure or when the heritability of the desired trait is low, selecting individuals based on traits that are strongly correlated with the desired trait is undertaken (Axelsson *et al.* 2013; Connor *et al.* 2013; Bastin *et al.* 2014; Connor, 2015; de Ondarza and Tricarico, 2017; Zavadilová *et al.* 2021).

To date, several meta-analyses have been conducted to estimate the genetic parameters in different species and traits: self-control behavioral trait (Willems *et al.* 2019), idiopathic scoliosis in humans (Cheng *et al.* 2022) economic traits in native chickens (Davoodi and Ehsani, 2018), feed consumption in fattening calves (Diaz *et al.* 2014), milk amino acids in dairy cows (Ghavi Hossein-Zadeh, 2021), productivity and flexibility traits in sheep and goats (Mucha *et al.* 2022), methane gas production indicator traits in cows and sheep (Brito *et al.* 2018). Since the efficiency of feed consumption in dairy cattle is a polygenic trait of high economic importance, different research about the traits related to the efficiency of feed consumption in dairy cows has been implemented (Vallimont *et al.* 2011; Spurlock *et al.* 2012; Hardie *et al.* 2017; Ferreira Júnior *et al.* 2018; Islam *et al.* 2020; Khanal *et al.* 2022). Therefore, this random meta-analysis study was conducted to develop pooled genetic parameters of DMI, FS, RFI, and FCR in dairy cows.

Despite extensive research on the heritability of feed efficiency traits, existing studies report varying heritability estimates and genetic correlations with other traits, highlighting the need for a comprehensive synthesis of this data. This meta-analysis aims to pool heritability estimates and examine genetic correlations across multiple studies to provide reliable estimates that can inform genetic selection and breeding strategies. The growing need to enhance feed efficiency in dairy cattle breeding programs calls for a comprehensive approach, as feed costs constitute a major part of production expenses. Improving traits such as dry matter intake (DMI), feed saved (FS), residual feed intake (RFI), and feed conversion ratio (FCR) is essential for sustainable dairy farming and increased economic efficiency. While previous studies have estimated heritability and genetic correlations for individual traits, there is a lack of thorough analyses that integrate multiple feed efficiency traits and examine their correlations with production outcomes. This research aims to address this gap by conducting a meta-analysis of existing studies, providing robust, pooled estimates of heritability and genetic correlations for these traits in dairy cattle.

MATERIALS AND METHODS

Search strategies

A search was conducted on 13 September 2023 using the keywords 'dairy cow', 'feed efficiency', 'FS', 'DMI', 'RFI', and 'FCR' in PubMed and CorrDB (https://www.animalgenome.org/CorrDB). To ensure comprehensive coverage, the search was limited to articles published between 2000 and 2022, covering 22 years.

Screening and selection of the studies

After searching, all retrieved studies were saved in an Excel file, and one reviewer performed the screening in two phases: title/abstract and full text. In the first phase, the reviewer checked the titles and abstracts of all retrieved studies against the eligibility criteria. A second reviewer checked the screened articles to ensure accuracy.

In the second phase, the first reviewer subjected articles that met the inclusion criteria to full-text screening. A second reviewer again checked these articles. In both screening phases, if the reviewer was uncertain whether to include or exclude an article, the second reviewer was consulted to discuss and make a final decision. At least one heritability parameter regarding the desired traits and non-repetitiveness of information was determined as a condition for deciding to include articles.

Data extraction

One reviewer extracted information from the final eligible studies, and a second reviewer checked the cases. An Excel sheet was designed for data extraction, capturing the following details: article title, year of publication, journal name, first author's name, country where the study was conducted, breed of dairy cow, number of cows studied, number of records, descriptive statistics (mean, standard deviation, minimum, and maximum), heritability, and the standard deviation of heritability traits.

Synthesizing evidence

In this study, to estimate pooled heritability in DMI, RFI, FCR, and FS traits, the metafor (Viechtbauer, 2010) and robumeta, R add-on packages (Fisher and Tipton 2015), were used. Data sets, including heritabilities, sample sizes, continuous variables (such as mean DMI, RFI, FCR, and FS), and categorical variables (breed and country) were used in the study. To accommodate normality for heritability values, their values were converted to Fisher's z values according to the following equation (1):

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

The variance of Z_i values have the following distribution (equation (2)):

$$S_Z^2 = \frac{1}{n-3} \tag{2}$$

The confidence interval was calculated as follows (equation (3)):

$$Z_i \pm \frac{Z^*}{\sqrt{n-1}} \tag{3}$$

Where:
Z^* is a critical value from the normal distribution, and the area between Z^*+ and $-Z^*$ equals the confidence interval. Moreover, r represents the heritability value, while n denotes the sample size.

Finally, the conversion of Z to Fisher's r was used again, which is expected to be reported for the heritability of the desired traits (equation (4)):

$$r = \frac{e^{2\,Zr}-1}{e^{2\,Zr}+1} \tag{4}$$

In examining the heterogeneity in this study, the Q-statistics (Chandler *et al.* 2019), which is the weighted sum of squared differences between individual study effects and the pooled effect across studies, with the weights being those used in the pooling method; I^2 statistic (Higgins *et al.* 2003), which measures the percentage of total variation across studies that is due to heterogeneity rather than chance, H^2 statistic (Higgins and Thompson, 2002), which is a measure of heterogeneity that assesses the degree of homogeneity among the studies included in a meta-analysis, and tau2 statistics (Viechtbauer, 2010) which is an estimate of the variance of the true effect sizes in the underlying distribution, were calculated. To detect the effectiveness of studies and to determine outliers, several statistics of standardized residuals (ei) (rstudent), difference in fit values (DFFITS), Cook's distances (Di) (cook. d), covariance ratios (cov. r), τ2 (tau2.del) and residual heterogeneity (QE.del) estimates were calculated for the studies included (Viechtbauer, 2010).

Since the studies were not from a statistical population and the extracted estimates of heritability in all studied traits had significant heterogeneity, the random effects model was used to obtain the pooled heritability values (Ghavi Hossein-Zadeh, 2021). Since most researchers aim to generalize results across multiple situations and the included studies are unlikely to be functionally equivalent, the random-effects model is usually a better choice. Finally, the state of heritability estimation of the traits in the studies and the final index indicating the combined heritability predicted and the confidence interval of the estimates were displayed in the forest diagram (Quintana, 2015). To determine if any single study significantly affected the heterogeneity of the meta-analysis, we first conducted a sensitivity analysis. Additionally, meta-regressions were performed for the country and publication year. Egger's test was used to assess publication bias.

Because some studies included two or more trials or comparisons, the number of trials in the meta-analysis exceeded the number of studies for each trait. Therefore, 157 parameters, which included 77 averages and 80 estimates of heritability in 4 traits—DMI, RFI, FCR, and FS—and 7 groups of dairy cows were selected for meta-analysis.

To obtain genetic correlations between DMI, RFI, FCR, and FI traits with other traits related to feed efficiency, growth traits, milk production, and traits related to body structure in dairy cows were extracted from the CorrDB database and their average (if there are several reports) was calculated (Hu *et al.* 2022).

The traits included: feed intake (FI), average feeding rate (AFR), dry matter intake (DMI), energy balance (ENBAL), feed conversion ratio (FCR), feed efficiency (FEEDEFF), net energy of lactation intake (NELI), residual feed intake (RFI), average daily gain (ADG), body weight (BW), fat thickness at the 12th rib (FATTH), intramuscular fat (IMF), longissimus muscle area (LMA), metabolic body weight (MBW), residual body weight gain (RGAIN), subcutaneous rump fat thickness (SCFR), body weight weaning (WWT), days to calving (DCALV), milk energy yield (EY), milk fat yield (FY), milk urea nitrogen content (MUNC), milk yield (MY), milk protein yield (PY), somatic cell score (SCS), scrotal circumference (SCRCIR), angularity (ANG), body condition score (BCS), body depth (BD), chest width (CHWDT), dairy form (DYF), hip height (HIPHT), rump angle (RANG), rump width (RUMWD), stature (STA), strength (STR), average daily feed intake (ADFI). Also, the Venn Diagram package in R software was used to determine the common correlated traits between the 4 studied traits in dairy cows and to draw a Venn diagram (Cheng *et al.* 2022).

Positive and negative correlation diagrams of traits were drawn using KuTools (https://www.extendoffice.com/product/kutools-for-excel.html), an attachment in Excel software.

RESULTS AND DISCUSSION

The search identified 68 documents in PubMed and CorrDB. After removing three duplicates, 65 papers entered the screening process. Following the title/abstract screening, 8 review articles were excluded, leaving 57 papers for full-text screening. In this phase, 21 articles were deemed inappropriate—17 due to a lack of required information and data, and 4 were simulation studies. Ultimately, 36 studies met the inclusion criteria and were included in the data analysis for this review. Figure 1 visualizes the screening and selection process.

Most of the articles were published in 2017 (n=5, 14%), 2020 (n=5, 14%), and 2021 (n=5, 14%). Four articles (11%) were published in 2018. Three articles were published in 2012 (8%) and 2014 (8%). The majority of the articles (n=25, 69%) were published in the Journal of Dairy Science, followed by the Journal of Animal Science (n=3, 8%) and Animal (n=3, 8%). The Journal of Animal Science also published two more articles (6%). The remaining three articles were published in three different journals: the Journal of Animal Breeding and Genetics, Animals, and the Turkish Journal of Veterinary and Animal Science. Regarding the country of the study, the highest share of research on animals came from the United States (n=7, 19%), followed by Canada (n=5, 14%) and Denmark (n=5, 14%). The characteristics of the included studies are shown in Table 1.

The meta-analysis of 45 heritability estimates from 24 studies for DMI yielded a pooled heritability of 0.32 (95% CI: 0.29-0.36, I^2=98%, P<0.0001), with one study removed due to significant heterogeneity, as illustrated in the forest plot (Figure 2).

Sensitivity analysis showed no significant change in heterogeneity upon removing individual studies, and meta-regression indicated that the country of study explained approximately 27% of the heterogeneity (P<0.0001), while the publication year had no significant effect. For RFI, 29 heritability estimates from 20 studies resulted in a pooled heritability of 0.17 (95% CI: 0.15-0.19, I^2=89.3%, P<0.0001), with one study excluded due to significant heterogeneity, as shown in Figure 3.

Sensitivity analysis revealed no single study significantly affected overall heterogeneity, and meta-regression showed no impact of the country or publication year on effect sizes.

The analysis of 3 heritability estimates from 2 studies for FCR yielded a pooled heritability of 0.11 (95% CI: 0.08-0.13, I^2=0%, P<0.0001), presented in Figure 4, with no meta-regression conducted due to the lack of heterogeneity.

For FS, the meta-analysis of 3 heritability estimates from 2 studies resulted in a pooled heritability of 0.29 (95% CI: 0.10-0.46, I^2=99%, P<0.0001), with high heterogeneity observed, and the publication year explaining 93% of this heterogeneity.

Significant genetic correlations were observed between the feed efficiency traits and other production traits. For example, DMI had a high positive genetic correlation with NELI (0.99), BW (0.68), RFI (0.65), EY (0.63), and MY (0.61). Negative correlations were found between DMI and AFR (-0.03), FEEDEFF (-0.12), and SCS (-0.15). RFI demonstrated a significant positive genetic correlation with ADFI (0.81), DMI (0.67), and FCR (0.65). FCR exhibited the greatest positive genetic correlation with RFI (0.67) and ADFI (0.39). The extracted genetic correlation values showed a positive and perfect correlation (0.99) between DMI and NELI. Since the net energy received from breastfeeding in terms of megacalories is a trait with low heritability (0.18), in the selection to improve NELI, DMI can be used as an indicator that has a higher heritability equal to 0.32. Also, DMI with BW, RFI, EY, and MY traits had high positive genetic correlation, equivalent to 0.68, 0.65, 0.63, and 0.61, respectively. DMI had a negative genetic correlation with the traits AFR (-0.03), FEEDEFF (-0.12), and SCS (-0.15). According to the supplementary file, FRI demonstrated a significant positive genetic correlation with ADFI, DMI, and FCR at values of 0.81, 0.67, and 0.65, respectively. The high genetic correlation between RFI and ADFI highlights the potential for using this heritable trait as an indicator in selection processes to enhance feed efficiency and improve RFI performance. Moreover, it has been found that RFI exhibits a moderate negative genetic correlation with DCALV, AFR traits, and WWT. The values of these correlations are -0.49, -0.49, and -0.23, respectively.

According to the supplementary file, FCR exhibited the greatest positive genetic correlation with RFI and ADFI at 0.67 and 0.39, respectively. Additionally, AFR, ADG, LMA, and HIPHT traits with FCR displayed the most significant negative genetic correlations ranging from -0.14 to -0.38.

The FI traits had the highest positive genetic correlation with the two traits, RFI (0.81) and ADG (0.50). For the IF trait, a negative correlation has been reported only with the trait IMF (-0.11). Common traits were obtained between a set of 4 traits (DMI, RFI, FCR, and FI) and other traits.

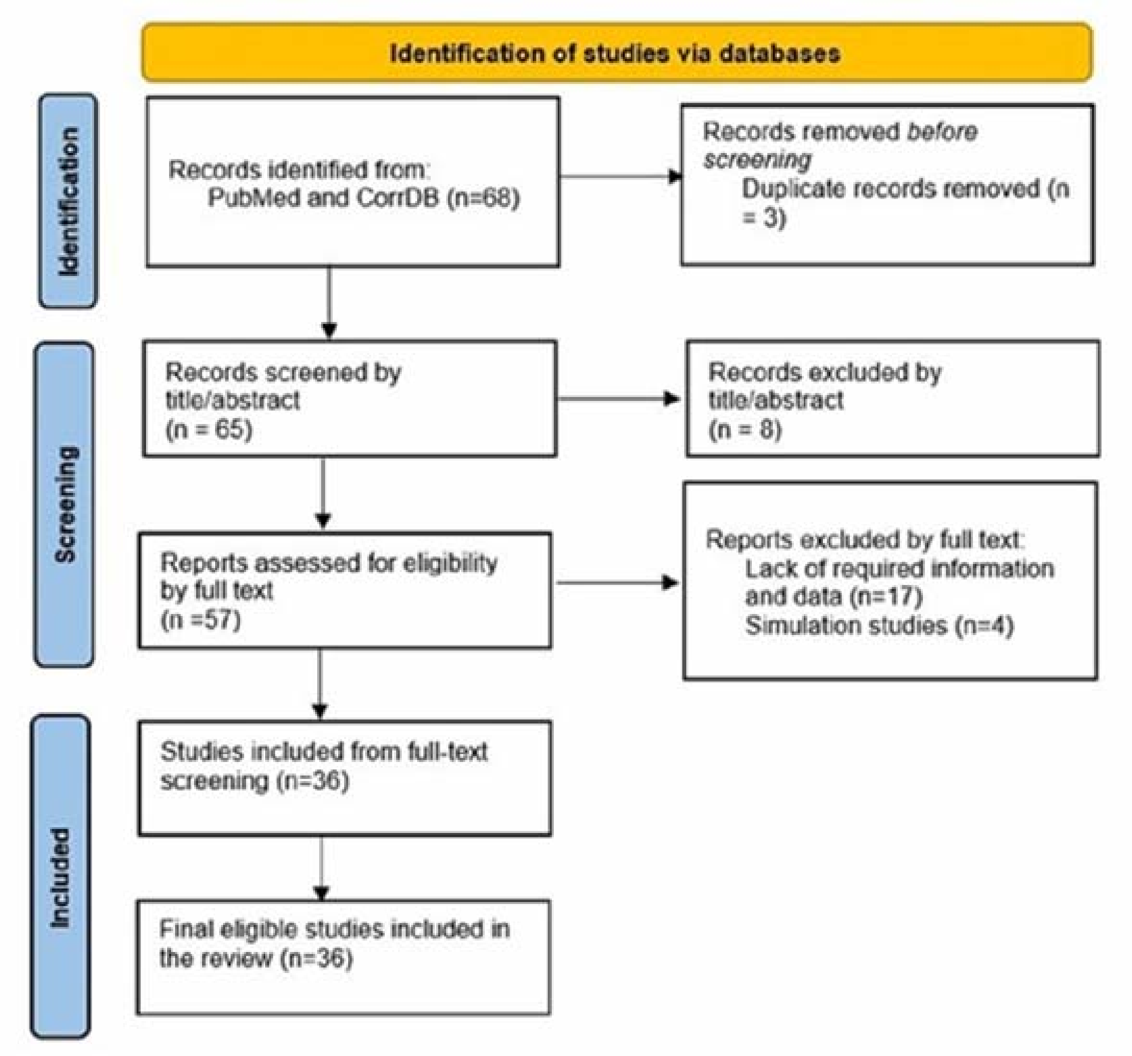

Figure 1 PRISMA diagram for screening and selecting studies

Figures 5 and 6 present diagrams illustrating the number of common and specific correlated traits across DMI, RFI, FCR, and FI. Each diagram highlights the unique and shared genetic correlations associated of these traits with other traits too, providing a visual representation of their interrelationships and potential for indirect selection in dairy cattle breeding programs.

The heritability estimates indicate that DMI and FS are highly heritable traits, whereas RFI and FCR are considered lowly inheritable traits (<0.2). This suggests that selecting for DMI or FS could lead to more significant genetic improvements in feed efficiency in dairy cattle. The high heritability of DMI implies that selecting for this trait could enhance feed efficiency, making it a valuable target for breeding programs.

Our findings align with previous research indicating that feed efficiency traits are heritable and can be improved through genetic selection.

The observed variability in heritability estimates across studies may be attributed to differences in breeds, environments, and methodologies. For instance, (Tarekegn *et al.* 2021) reported varying heritability values for DMI in different cattle breeds, while (Freetly *et al.* 2020) found differences in heritability for DMI based on the number of births in hybrid cows.

The strong genetic correlations between DMI, RFI, FCR, and other production traits suggest that these traits can be used as indicators in selection programs. For instance, selecting for DMI could indirectly improve NELI due to their high genetic correlation. The high genetic correlation between RFI and ADFI highlights the potential for using this heritable trait as an indicator in selection processes to enhance feed efficiency and improve RFI performance.

These results provide valuable insights for enhancing breeding programs aimed at improving feed efficiency in dairy cattle.

Table 1 Characteristics of the included studies

Reference	Journal	Country	Mean value	Heritability
Schweer *et al.* (2018)	*J. Anim. Sci.*	USA	DMI	DMI (5)
Ferreira Júnior *et al.* (2018)	*J. Anim. Sci.*	Brazil	DMI, RFI	RFI
Davis *et al.* (2014)	*J. Dairy Sci.*	New Zealand	DMI (2), RFI (2)	
Tarekegn *et al.* (2021)	*J. Dairy Sci.*	Sweden	DMI (2)	DMI (2)
Khanal *et al.* (2022)	*J. Dairy Sci.*	USA	DMI (2)	DMI (2), RFI (2), FS (2)
Richardson *et al.* (2021)	*J. Dairy Sci.*	Australia	FS	
Spurlock *et al.* (2012)	*J. Dairy Sci.*	Poland	DMI (2)	DMI (2)
Pryce *et al.* (2015)	*J. Dairy Sci.*	Australia	RFI, FS	RFI
Heida *et al.* (2021)	*J. Dairy Sci.*	Netherlands	DMI, RFI, FS	DMI, RFI, FS
Berry *et al.* (2014)	*J. Dairy Sci.*	Canada	DMI (9)	DMI (9)
Williams *et al.* (2011)	*J. Dairy Sci.*	Australia	DMI, RFI, FCR	
Schultz and Weigel (2019)	*J. Dairy Sci.*	USA		DMI
Shetty *et al.* (2017)	*J. Dairy Sci.*	Denmark	DM I(2)	
Waghorn *et al.* (2012)	*J. Dairy Sci.*	New Zealand	DMI	
Li *et al.* (2018)	*J. Dairy Sci.*	Sweden	DMI (3)	DMI (3)
Martin *et al.* (2021)	*Animal*	Denmark	DMI, RFI	
Li *et al.* (2020)	*J. Dairy Sci.*	USA		RFI
Li *et al.* (2017)	*J. Dairy Sci.*	Denmark	DMI	
Veerkamp *et al.* (2012)	*Animal*	Netherlands	DMI	DMI
Vallimont *et al.* (2010)	*J. Dairy Sci.*	Switzerland	DMI	DMI
Byskov *et al.* (2017)	*J. Dairy Sci.*	Denmark	DMI, RFI	DMI, RFI
Hardie *et al.* (2017)	*J. Dairy Sci.*	Canada	DMI (2), RFI (2)	DMI (2), RFI (2)
Connor *et al.* (2013)	*J. Dairy Sci.*	USA	DMI (2)	RFI
Tempelman *et al.* (2015)	*J. Dairy Sci.*	USA	DMI (3)	RFI (3)
Freetly *et al.* (2020)	*J. Anim. Sci.*	USA	DMI (2)	DMI (2), RFI (2)
Benfica *et al.* (2020)	*J. Anim. Sci.*	Brazil	DMI, RFI, FCR	DMI (2), RFI (2), FCR (2)
Coleman *et al.* (2010)	*J. Dairy Sci.*	Ireland	DMI (3), RFI (3)	
Lu *et al.* (2018)	*J. Dairy Sci.*	Canada		DMI, RFI
Brunes *et al.* (2020)	*J. Anim. Breed. Genet.*	Brazil	DMI, RFI, FCR	DMI, RFI, FCR
Vallimont *et al.* (2011)	*J. Dairy Sci.*	Switzerland		DMI, RFI
Manzanilla Pech *et al.* (2014)	*J. Dairy Sci.*	Netherlands		DMI
Islam *et al.* (2020)	*J. Dairy Sci.*	Denmark	DMI	RFI
Houlahan *et al.* (2021)	*Animals*	Canada		DMI, RFI
Manafiazar *et al.* (2016)	*Animal*	Canada	DMI, RFI	DMI, RFI
Yao *et al.* (2017)	*J. Dairy Sci.*	Netherlands		DMI (3), RFI (3)
Zamani *et al.* (2008)	*Turkish J. Vet. Anim. Sci.*	Iran		DMI (2), RFI (2)

FS: feed saved; DMI: dry matter intake; FCR: feed conversion ratio and RFI: residual feed intake.

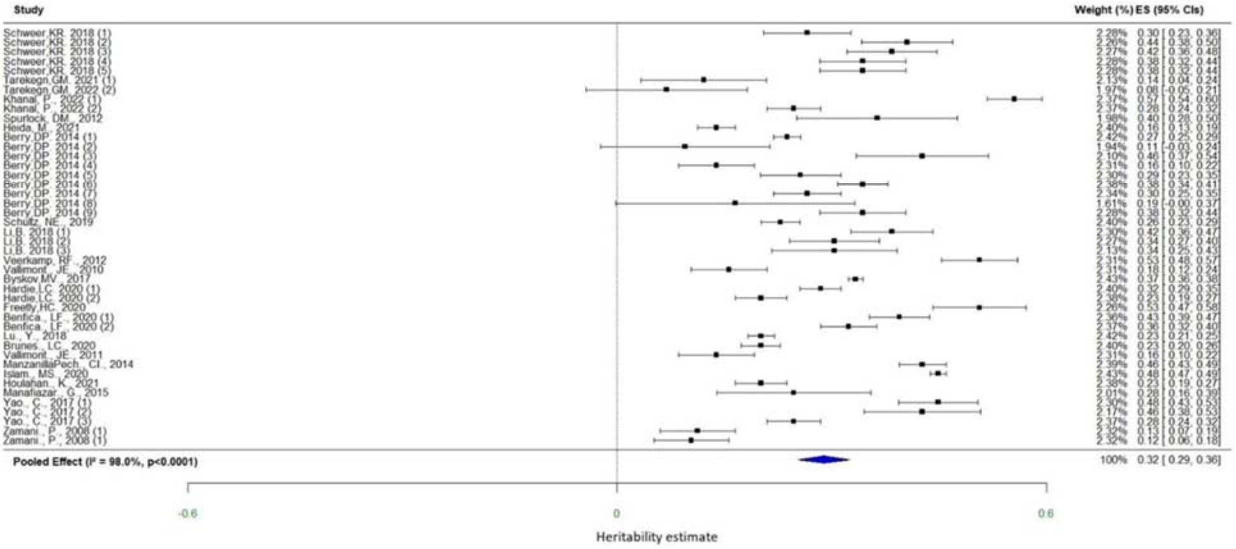

Figure 2 Forest plot showing heritability estimate for DMI

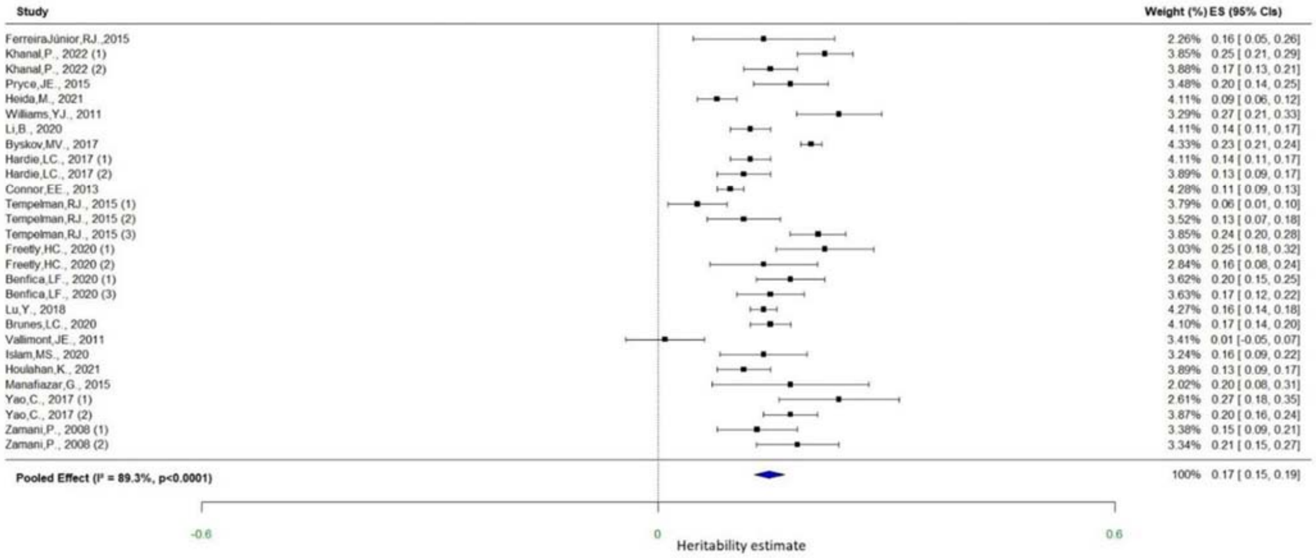

Figure 3 Forest plot showing heritability estimate for RFI

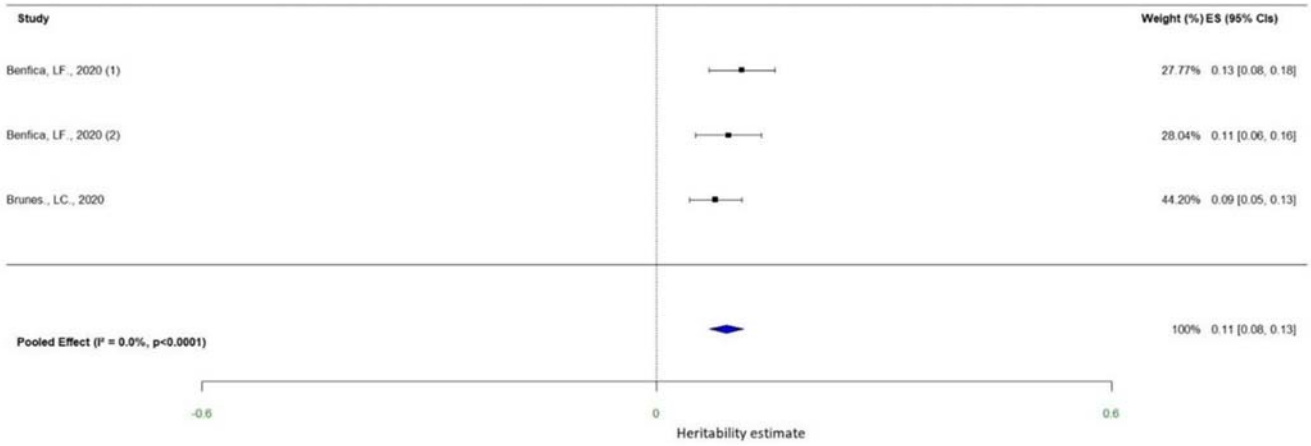

Figure 4 Forest plot showing heritability estimate for FCR

By focusing on traits with higher heritability, such as DMI and FS, breeders can achieve more significant genetic gains.

The findings suggest potential indicators for selection indices and genetic improvement strategies, offering valuable insights for enhancing breeding programs and optimizing feed utilization in dairy cattle.

The study's limitations include the high heterogeneity among studies and potential publication bias. Future research should aim to standardize methodologies and include more diverse datasets to provide more robust estimates. Researchers conducting meta-analyses on heritability in cows must consider various factors, such as research design and method discrepancies.

Standardization issues relating to trait measurement standards used between research work not only impact intra-study reproducibility but also inter-study comparatively, thereby causing inaccuracies within meta-analysis reports. In recent years, several meta-analyses and reviews on the genetics of feed efficiency traits in dairy cows have been published. In comparison to existing studies, this research presents novel contributions through its broader scope, advanced methodologies, and practical implications for dairy cattle breeding. While previous studies have primarily focused on specific traits or narrower genetic parameters (Berry *et al.* 2014; Oliveira *et al.* 2019; Brito *et al.* 2020; Jiang *et al.* 2024) this study provides a holistic approach by analyzing a broader range of traits simultaneously.

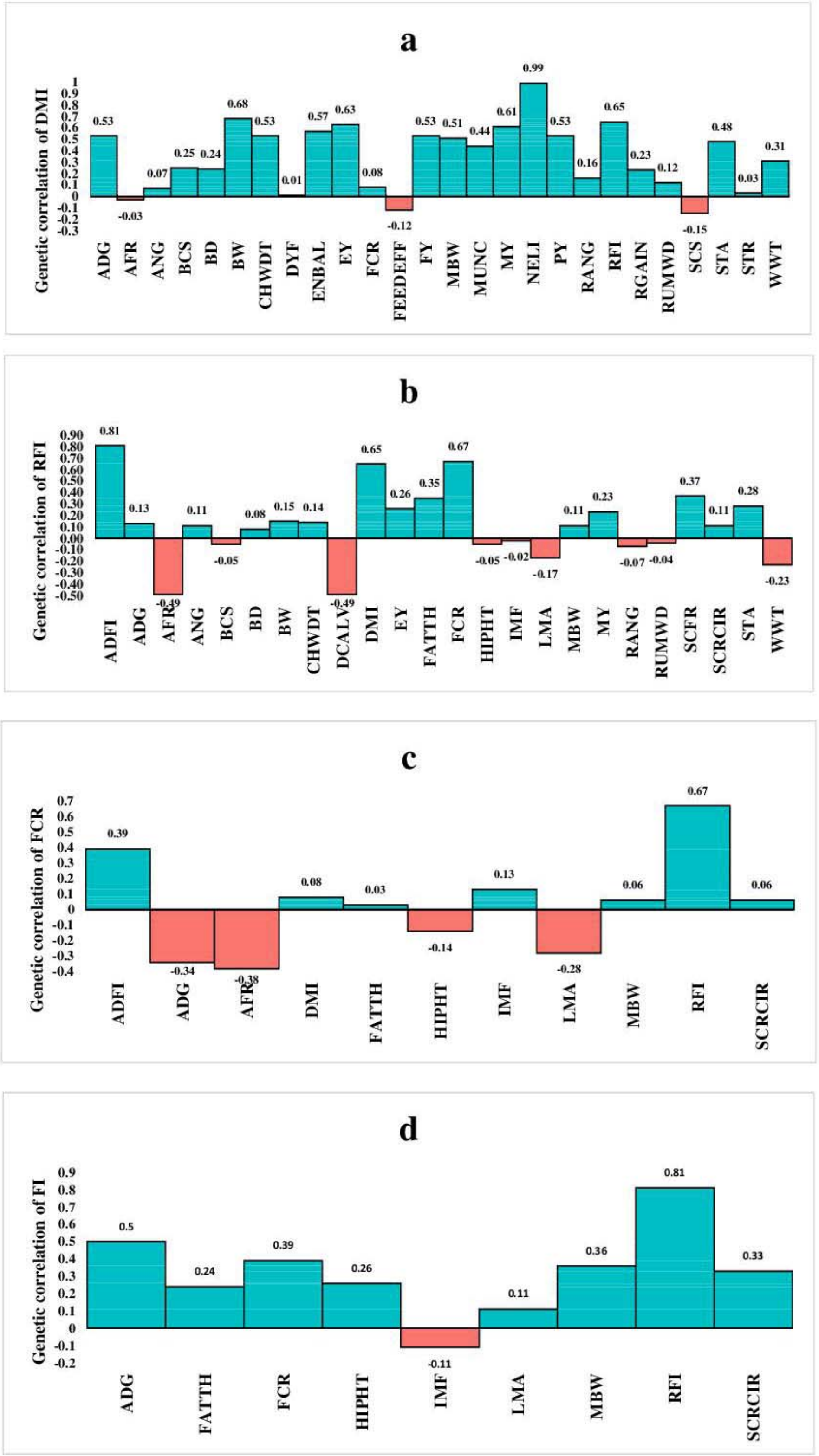

Figure 5 Genetic correlation of a) DMI, b) RFI, c) FCR, d) FI

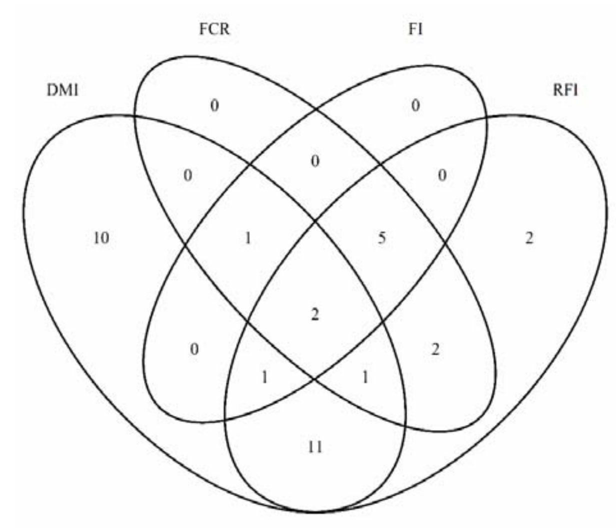

Figure 6 Common correlated traits among all DMI, RFI, FCR, and FI

The use of advanced meta-analytical techniques, including robust variance estimation (RVE), publication bias, and meta-regression, enhances the robustness and reliability of the pooled heritability estimates.

The current study presents a comprehensive meta-analysis of genetic feed efficiency traits in dairy cattle, synthesizing data from 68 studies published between 2000 and 2022. Utilizing random effects meta-analysis and restricted maximum likelihood estimation, the research aims to provide robust estimates of genetic parameters, thereby informing breeding strategies and genetic selection processes. The analysis reveals significant heterogeneity across various traits, underscoring the variability in estimates attributable to differences in study designs, breeds, and environmental factors. The meta-analysis adopts a holistic approach by examining a broad spectrum of traits simultaneously, thereby offering a more integrated understanding of genetic feed efficiency. The application of advanced meta-analytical techniques, including robust variance estimation and meta-regression, significantly enhances the reliability of the pooled heritability estimates. This methodological rigor is crucial for deriving insights that can be generalized across diverse dairy cattle populations.

The study reports pooled heritability estimates of 0.32 for DMI, 0.29 for FS, 0.17 for RFI, and 0.11 for FCR, all statistically significant at $P < 0.0001$. These findings suggest that DMI and FS exhibit higher heritability compared to RFI and FCR, indicating a greater potential for genetic improvement through selective breeding. Residual Feed Intake (RFI) and Feed Conversion Ratio (FCR) are economically critical traits in dairy cattle, yet their low heritability (0.17 and 0.11, respectively) poses a challenge for conventional genetic improvement. Given their polygenic nature and susceptibility to environmental fluctuations, breeding strategies beyond traditional selection are required to achieve meaningful genetic gains. One of the most promising approaches is genomic selection (GS), which captures the cumulative effects of numerous small-effect loci across the genome, enabling accurate prediction of breeding values even for low-heritability traits. When implemented using multi-trait genomic models, GS can leverage genetically correlated traits with higher heritability, such as dry matter intake (DMI), to improve prediction accuracy for RFI and FCR. Additionally, selecting for indicator traits—such as average daily gain (ADG) or longissimus muscle area (LMA)—that exhibit moderate to high genetic correlations with RFI and FCR can enhance selection efficiency. Furthermore, integrating multi-omics data (e.g., transcriptomic, metabolomic, and microbiome profiles) can uncover biological mechanisms underpinning feed efficiency, thus enriching prediction models. Incorporating genotype-by-environment (G×E) interactions, particularly through reaction norm or random regression models, allows the identification of robust genotypes across diverse management systems. Advancements in precision phenotyping, including automated intake monitoring and real-time sensor technologies, provide high-resolution data that can significantly enhance the accuracy of trait estimation. Moreover, the use of early-life indicators and longitudinal models facilitates earlier and more cost-effective selection decisions. Finally, the development of multi-trait selection indices that integrate both RFI and FCR with productivity traits and economic weights ensures a balanced approach to improving feed efficiency without compromising performance. Together, these strategies offer a comprehensive roadmap for addressing the genetic complexity of RFI and FCR while supporting more sustainable and cost-effective dairy production systems. Already some studies underscore our claims (Coleman *et al.* 2010; Williams *et al.* 2011; Berry *et al* 2014; Cheng *et al.* 2022; Omer *et al.* 2022).

Moreover, the analysis identifies strong positive genetic correlations between DMI and NELI (0.90), RFI and ADFI (0.80), and FCR and RFI (0.68). Conversely, negative genetic correlations are observed between FCR and AFR (-0.38), ADG (-0.34), LMA (-0.28), and HIPHT (-0.14). These correlations highlight the interconnected nature of feed efficiency traits and their potential as indirect selection criteria in breeding programs. The findings of this study carry substantial implications for the development of selection indices and genetic improvement strategies in dairy cattle breeding programs. Selecting for DMI, for instance, could enhance feed efficiency and indirectly improve NELI due to their high genetic correlation. Similarly, the strong genetic correlation between RFI and ADFI suggests the potential utility of RFI as an indicator trait in selection processes aimed at enhancing feed efficiency. By focusing on traits with higher heritability, such as DMI and FS, breeders can achieve more significant genetic gains, thereby optimizing feed utilization and promoting sustainable livestock production. Improved feed efficiency not only reduces feed costs—a major component of production expenses—but also contributes to lower greenhouse gas emissions, aligning with sustainable dairy farming practices. Improving feed efficiency in dairy cattle has direct implications for environmental sustainability, particularly in reducing greenhouse gas (GHG) emissions. Among the evaluated traits, Feed Saved (FS) demonstrates a higher heritability (0.29) than Residual Feed Intake (RFI; 0.17), suggesting that selection for FS can lead to more rapid and effective genetic progress. As FS accounts for the difference between predicted and actual feed intake—adjusted for maintenance and production requirements—it functions as a biologically meaningful composite trait that integrates RFI with energy-corrected milk yield and metabolic body weight. This trait not only aligns with economic goals by reducing feed costs, but also offers a practical pathway for reducing enteric methane emissions, which are directly associated with feed intake levels. Incorporating FS into national or international selection indices, particularly alongside production and emission metrics, could therefore accelerate the development of climate-smart dairy genetics. Furthermore, integrating FS with genomic selection, methane emission indicators, and genotype-by-environment interaction models would enhance the ability to select animals that are both efficient and environmentally resilient. As such, FS represents a valuable bridge trait linking animal productivity, farm profitability, and broader sustainability objectives.

While the study provides valuable insights into the genetic architecture of feed efficiency traits, it is essential to acknowledge the inherent variability and heterogeneity in the estimates. The significant heterogeneity observed (I^2 values ranging from 0% to 99%) underscores the need for cautious interpretation and context-specific application of the findings. The high levels of heterogeneity observed in our meta-analyses of Dry Matter Intake (DMI) and Feed Saved (FS)—with I^2 values of 98% and 99%, respectively—highlight substantial variability in heritability estimates across studies. While our meta-regression identified country-level differences as a partial contributor, additional factors likely account for much of the residual heterogeneity. These include differences in breed composition, as genetic architectures vary substantially between breeds such as Holstein, Jersey, and Swedish Red, each exhibiting distinct physiological efficiencies and nutrient partitioning mechanisms. Measurement protocols also differ considerably among studies, ranging from automated systems to manual or pen-based recordings, particularly for complex derived traits like FS, which may be estimated using varied equations or assumptions. Environmental and management conditions—such as feeding regime (pasture *vs.* TMR), housing, climate, and nutritional strategy—introduce genotype-by-environment interactions that affect phenotypic expression and contribute to between-study variance. Furthermore, disparities in accounting for lactation stage, parity, and the application of different statistical models (e.g., animal models, Bayesian approaches, or random regression) affect both the estimation and interpretation of heritability (Behdani *et al.* 2019). To reduce such variability and enhance future synthesis efforts, we advocate for greater methodological harmonization. This includes breed-specific reporting, standardized definitions of derived traits, transparency in metadata (e.g., management systems, parity structure), and increased data sharing for re-analysis using common statistical frameworks. Incorporating genotype-by-environment interaction models and aligning estimation procedures under established guidelines (e.g., ICAR, Interbull) would also support more robust cross-study comparisons. Addressing these sources of heterogeneity is critical to improving the accuracy and applicability of genetic parameter estimates in dairy cattle breeding programs.

Furthermore, the reliance on meta-analytical techniques necessitates consideration of potential biases, such as publication bias, which could influence the pooled estimates. The study's emphasis on genetic correlations offers a nuanced perspective on indirect selection strategies, particularly when direct measurement of desired traits is challenging. However, the practical implementation of these strategies requires careful consideration of the genetic and environmental interactions that may influence trait expression.

CONCLUSION

The study analyzed 44 heritability estimates for DMI, 28 observations for RFI, and three observations for FCR and FS. The results were meta-analyzed to determine the summary heritabilities, which were found to be 0.32 for DMI and 0.17 for RFI, as well as 0.11 and 0.29, respectively, for FCR and FS. Additionally, the genetic correlation between four feed efficiency traits (DMI, RFI, FCR, and FI) and other traits such as growth rate, milk production, and body composition were determined to obtain a comprehensive viewpoint towards devising an efficient strategy. The results of these Meta-analyses can assist in developing better selection strategies and genomic tools for feed efficiency by offering finer estimates of genetic parameters, detecting areas linked to it using genomics, and gaining insight into its physiological foundation.

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