Volume 10, Issue 8, August – 2025 International Journal of Innovative Science and Research Technology
ISSN No:-2456-2165 https://doi.org/10.38124/ijisrt/25aug022

Direct–Maternal Genetic Covariance in Ruminants: Magnitude, Direction, and Implications for Growth Trait Improvement

Never Assan[1]

[1]Zimbabwe Open University, Faculty of Agriculture, Department of Agriculture Management
Bulawayo Regional Campus, Bulawayo, Zimbabwe

Publication Date: 2025/08/18

Abstract: This systematic review examines the correlation between direct and maternal genetic effects on growth traits in sheep, goats, and cattle, with a focus on tropical production systems. Reported estimates of this correlation exhibit significant variability, ranging from strongly negative to moderately positive, reflecting considerable uncertainty and biological complexity. The sign and magnitude of this relationship are crucial in genetic evaluation, as they influence the estimation of breeding values and ultimately impact selection decisions. Recent literature emphasizes that omitting or inaccurately estimating the covariance between direct and maternal genetic effects can result in biased rankings of selection candidates and diminished genetic gains, particularly for pre-weaning traits where maternal influence is most significant. The variability in estimates is affected by several factors, including breed differences in maternal ability, environmental and management conditions, model specification (e.g., fixed assumptions of zero covariance), and the structure and quality of pedigree and performance data. In tropical systems, where environmental stressors and incomplete records are prevalent, these issues are especially pronounced. This review highlights the necessity for appropriate statistical modeling that accounts for direct maternal covariance to enhance the accuracy of genetic parameter estimation. For animal breeding programs in tropical regions, such considerations are essential for improving the efficiency and sustainability of genetic improvement strategies.

How to Cite: Never Assan (2025), Direct–Maternal Genetic Covariance in Ruminants: Magnitude, Direction, and Implications for Growth Trait Improvement. *International Journal of Innovative Science and Research Technology*, 10(8), 494-505. https://doi.org/10.38124/ijisrt/25aug022

I. INTRODUCTION

Genetic improvement of growth traits in ruminants is a foundational goal in livestock breeding programs, particularly given its direct impact on productivity, feed efficiency, and economic viability. Traits such as birth weight, weaning weight, and post-weaning average daily gain are integral to selection indices due to their moderate heritability and strong association with market value and production efficiency (Emamgholi Begli et al., 2020; Yusuf et al., 2023). However, these traits are influenced not only by the animal's genotype (direct genetic effects), but also by maternal effects, which encompass both the genetic merit and environmental contribution of the dam to the offspring's phenotype (Notter, 2021; Safari et al., 2023).

Direct genetic effects capture the influence of an individual's alleles on its phenotypic expression, and are often the primary target of selection strategies aimed at enhancing growth performance. Conversely, maternal effects—mediated through factors such as uterine environment, milk production, and maternal behavior—are especially critical during pre-weaning stages and must be carefully modeled to avoid bias in estimated breeding values (Emamgholi Begli et al., 2020; Yusuf et al., 2023). Neglecting maternal contributions can confound genetic evaluations and result in suboptimal selection decisions, particularly in tropical and low-input systems where environmental heterogeneity amplifies such effects (Bakhshalizadeh et al., 2022; Getachew et al., 2021).

A pivotal component in the genetic evaluation of early-life traits is the covariance between direct and maternal genetic effects, often represented by the correlation coefficient ramr_{am}ram. This parameter quantifies the degree to which genes influencing an animal's growth also affect its maternal performance, or vice versa. Negative values of ramr_{am}ram suggest antagonism between direct and maternal contributions—i.e., selection for rapid individual growth may compromise maternal ability, and vice versa—thereby complicating breeding strategies aimed at improving both dimensions (Togtokhbayar et al., 2020; Mandal et al., 2021). This antagonism has been particularly noted in traits like birth and weaning weight, where the maternal genetic effect has a strong, time-sensitive influence.

Extensive literature documents the challenges of estimating direct–maternal genetic correlations, including difficulties related to data structure, pedigree completeness, model specification, and environmental confounding (Boujenane & El-Hazzab, 2024; Safari et al., 2023). Studies in various ruminant breeds—such as Merino sheep, Boer × Central Highland goats, and dual-purpose Arbas-type goats—have revealed that omission or misestimation of maternal covariance leads to biased heritability estimates, inaccurate EBV rankings, and diminished selection response (Notter, 2021; Yusuf et al., 2023). In particular, studies employing random regression and maternal covariance models have demonstrated significant improvements in model fit and predictive accuracy when both genetic components are explicitly modeled (Bakhshalizadeh et al., 2022).

In tropical and resource-limited production systems, maternal effects may be exaggerated due to environmental stressors such as heat, seasonal forage fluctuations, or variable management regimes. These factors further complicate estimation of ramr_{am}ram and necessitate robust modeling approaches that can accommodate diverse non-genetic influences. Moreover, substantial variation in reported estimates across studies suggests that direct–maternal covariances are highly population-specific, rendering generalization across breeds or environments inappropriate (Safari et al., 2023; Boujenane & El-Hazzab, 2024).

Despite decades of research on the genetic architecture of growth traits, the magnitude and interpretation of direct–maternal genetic correlations remain inconsistently reported. These discrepancies are often attributed to differing statistical methodologies, underlying assumptions, and data constraints (Togtokhbayar et al., 2020; Emamgholi Begli et al., 2020). Importantly, failure to properly account for ramr_{am}ram in genetic evaluations may result in suboptimal selection, distorted animal rankings, and slowed genetic progress (Mandal et al., 2021; Yusuf et al., 2023).

This study aims to quantify the magnitude and direction of direct–maternal genetic correlations for growth traits in ruminants and to critically assess their implications for genetic evaluation and selection programs. A deeper understanding of these relationships is essential for developing biologically realistic and statistically robust animal models that ensure long-term genetic improvement while preserving maternal functionality in ruminant livestock systems.

II. MATERIALS AND METHODS

This study adopted a quantitative genetics framework to investigate the magnitude and implications of direct–maternal genetic correlations about growth traits among ruminant livestock. The research methodology entailed a systematic review of published estimates of genetic parameters for growth traits in cattle, sheep, and goats. A comprehensive and structured literature search was undertaken across multiple scientific databases, including Web of Science, Scopus, CAB Abstracts, and PubMed, encompassing peer-reviewed publications released between 2015 and 2025. The search strategy incorporated a combination of targeted keywords such as "direct genetic effect," "maternal genetic effect," "genetic correlation," "birth weight," "weaning weight," "growth traits," "ruminants," "animal model," and "heritability."

To ensure the scientific rigor and relevance of the selected studies, inclusion criteria were strictly defined. Eligible studies were required to: (i) employ mixed models or animal models for the estimation of genetic parameters, (ii) explicitly report both direct and maternal additive genetic variances along with their covariance, and (iii) identify the breed studied and specify the production system under which the animals were raised (e.g., tropical, extensive, or intensive systems).

From each qualifying publication, the following key parameters were systematically extracted for analysis: direct and maternal heritability estimates; the genetic correlation between direct and maternal effects; associated standard errors or confidence intervals; the specific trait analyzed (e.g., birth weight, weaning weight); the ruminant species and breed; and the environmental context of the production system, classified as tropical or temperate. This comprehensive synthesis provided a robust foundation for evaluating patterns and biological implications of direct–maternal genetic interactions in the genetic improvement of ruminant livestock.

III. RESULTS AND DISCUSSION

➢ *Conceptual Framework for Understanding Direct–Maternal Genetic Covariance in Ruminants: Magnitude, Direction, and Implications for Growth Trait Enhancement*

This conceptual framework delineates the interaction between direct and maternal genetic effects on growth traits in ruminant livestock, emphasizing the magnitude and direction of their covariance and the implications for genetic improvement programs. Direct genetic effects refer to the influence of an individual's genotype on its phenotypic expression, particularly for traits such as birth weight, weaning weight, post-weaning growth, and mature body size. These effects constitute a fundamental component of the total additive genetic variance and are pivotal targets in selection programs aimed at enhancing productivity in ruminant livestock systems (Yusuf et al., 2023; Emamgholi Begli et al., 2020).

In the context of genetic evaluation, accurate estimation of direct genetic effects enables the identification of superior breeding stock based on their inherent potential for growth and performance. Linear mixed models and animal models are widely employed to estimate breeding values for growth traits, wherein direct additive genetic variance is separated from other sources of variation such as maternal, environmental, and residual effects (Boujenane & El-Hazzab, 2024; Safari et al., 2023).

Recent advancements in genomic technologies and pedigree-based models have allowed for more precise quantification of direct effects, thereby increasing the accuracy of selection and the rate of genetic gain (Togtokhbayar et al., 2020; Notter, 2021). Moreover, direct effects are often modulated by genotype-by-environment interactions, which can either mask or enhance the expression of genetic potential under varying management or climatic conditions (Mandal et al., 2021).

Despite their central role in genetic improvement, direct effects must be interpreted within the broader genetic architecture of traits, particularly when antagonistic relationships exist with maternal effects. Ignoring the covariance between direct and maternal genetic effects may lead to overestimation or underestimation of genetic parameters and distort breeding value predictions (Bakhshalizadeh et al., 2022). Consequently, contemporary genetic evaluation models increasingly emphasize the joint estimation of direct and maternal effects to provide a holistic framework for decision-making in ruminant breeding programs (Yusuf et al., 2023).

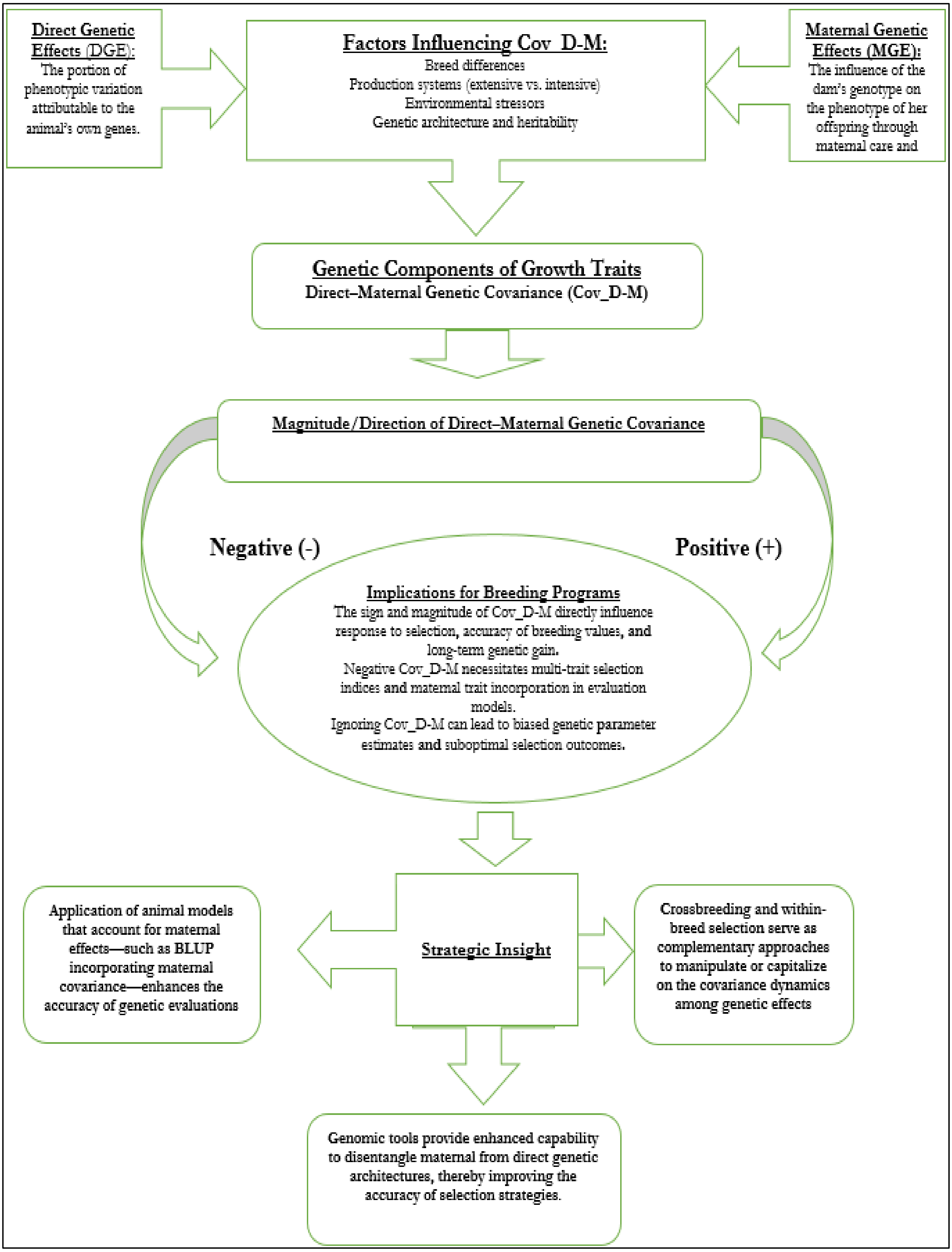
Maternal effects in animal genetics encompass the influence exerted by the dam's genotype and her environment on the phenotype of her progeny, independent of the direct transmission of genes. This phenomenon is pivotal in the context of genetic evaluation models targeting growth performance in ruminant livestock production. Failure to properly account for maternal effects can lead to biased estimates of breeding values and reduced accuracy in selection programs (Bakhshalizadeh et al., 2022; Mandal et al., 2021).

Both linear models and animal models used in the genetic evaluation of body weight and growth-related traits in ruminants must incorporate maternal effects to accurately partition phenotypic variance into its constituent components. In particular, the partitioning of direct additive genetic effects and maternal additive genetic effects—along with their potential covariance—is essential for effective genetic parameter estimation and selection (Yusuf et al., 2023; Emamgholi Begli et al., 2020).

Over time, significant progress has been made in methodologies for estimating maternal effects, underpinned by evolving biometric frameworks. The antagonistic relationship often observed between direct and maternal genetic effects further complicates genetic evaluation, necessitating robust statistical approaches to disentangle their contributions. This antagonism may arise from underlying biological mechanisms such as resource allocation trade-offs and maternal-offspring conflict, which introduce additional complexity in estimating genetic parameters (Togtokhbayar et al., 2020; Notter, 2021).

Moreover, inaccuracies in modeling the covariance between direct and maternal effects—stemming from data structure limitations, environmental heterogeneity, or incorrect model assumptions—can undermine selection response. Thus, recent research has emphasized the refinement of statistical tools and model selection criteria for more reliable estimates of maternal contributions in growth trait evaluations (Boujenane & El-Hazzab, 2024; Safari et al., 2023).

ISSN No:-2456-2165
https://doi.org/10.38124/ijisrt/25aug022



Direct Genetic Effects (DGE): The portion of phenotypic variation attributable to the animal's own genes.

Factors Influencing Cov_D-M:
Breed differences
Production systems (extensive vs. intensive)
Environmental stressors
Genetic architecture and heritability

Maternal Genetic Effects (MGE): The influence of the dam's genotype on the phenotype of her offspring through maternal care and

Implications for Breeding Programs
The sign and magnitude of Cov_D-M directly influence response to selection, accuracy of breeding values, and long-term genetic gain.
Negative Cov_D-M necessitates multi-trait selection indices and maternal trait incorporation in evaluation models.
Ignoring Cov_D-M can lead to biased genetic parameter estimates and suboptimal selection outcomes.

Application of animal models that account for maternal effects—such as BLUP incorporating maternal covariance—enhances the accuracy of genetic evaluations

Crossbreeding and within-breed selection serve as complementary approaches to manipulate or capitalize on the covariance dynamics among genetic effects

Genomic tools provide enhanced capability to disentangle maternal from direct genetic architectures, thereby improving the accuracy of selection strategies.

Fig 1 Conceptual Framework for Understanding Direct–Maternal Genetic Covariance in Ruminants: Magnitude, Direction, and Implications for Growth Trait Enhancement

➢ *Determinants of Covariance Between Direct and Maternal Genetic Effects in Livestock Growth Traits*

The covariance between direct and maternal genetic effects (DMG covariance) on livestock growth traits is modulated by both heritable and non-heritable influences. Non-genetic factors—including nutritional regime, health status, housing environment, and herd-level management practices—can modulate the phenotypic expression of maternal genetic merit, thereby influencing the magnitude and sign of the DMG covariance. Empirical evidence increasingly reports negative estimates of this covariance; however, the extent to which non-genetic confounders contribute to these patterns remains insufficiently elucidated. Discrepancies in genetic parameter estimates across studies are often attributable to heterogeneity in the treatment of environmental covariates within analytical models. When models are parameterized with congruent environmental fixed effects and appropriate random structures, they tend to yield more robust and biologically consistent estimates (Meyer et al., 2022; Yu & Boerner, 2021). Conversely, omission of key environmental sources of variation may result in biased partitioning of phenotypic variance, leading to spurious or inflated estimates of DMG covariance (Meyer, 1997). Attempts to disentangle environmental from genetic components—such as by regressing animal models on maternal phenotype proxies (e.g., weaning weight)—can mitigate some confounding; nonetheless, quantitative genetic evidence indicates that a substantive proportion of the DMG covariance retains a genetic basis (Lopez et al., 2020).

➢ *Climatic Stressors and Covariance Between Direct and Maternal Genetic Effects*

Climatic stressors—particularly thermal stress, seasonal nutrient deficits, and prolonged drought—compromise the phenotypic expression of maternal genetic merit for traits such as lactational performance, maternal care, and metabolic support to offspring. Under such stressors, genotype expression becomes environmentally constrained, resulting in attenuated maternal effects and a diminished magnitude of direct maternal genetic covariance. Empirical evaluations of heat-adapted genotypes, including Boran and N'Dama cattle as well as indigenous goat ecotypes, consistently demonstrate a reduction in maternal genetic expression and DMG covariance during periods of high environmental stress, particularly in hot, arid seasons (Mwai et al., 2021; Yakubu et al., 2024). These findings underscore the necessity of incorporating climate resilience parameters—such as heat tolerance indices and seasonal environmental covariates—into genetic evaluation models, particularly in low-input, agro-pastoral systems prevalent in Sub-Saharan Africa. Nutritional insufficiency during critical periods of gestation and lactation further constrains the expression of genetically superior maternal phenotypes, introducing genotype-by-environment interactions (G×E) that obscure true breeding values. Consequently, the exclusion of maternal nutritional context from genetic models may lead to systematic underestimation or misallocation of maternal additive genetic variance (Meyer, 2021; Marai et al., 2022).

• *Production System Architecture and Covariance Between Direct and Maternal Genetic Effects*

Production system architecture—particularly the dichotomy between extensive and intensive management regimes—profoundly influences dam–offspring interaction dynamics and the resulting genetic parameter estimates. In extensive production systems, which predominate across Sub-Saharan Africa, maternal performance is heavily contingent upon the dam's capacity for self-sustained foraging, predator vigilance, and environmental buffering. These conditions amplify environmental variance during early ontogeny, often manifesting as negative direct–maternal genetic covariances due to the disproportionate influence of maternal environment on early growth trajectories (Tibbo et al., 2023; Oguno et al., 2022). Failure to appropriately model these system-specific interactions introduces structural bias into variance component estimation, potentially leading to erroneous inferences regarding genetic merit and misdirected selection responses.

Furthermore, management interventions such as early culling, preferential retention based on pre-weaning growth, or truncation selection based solely on early performance traits exacerbate the entanglement between direct and maternal genetic components. Such practices introduce preselection bias and alter the distribution of genetic variance across cohorts. Selection for early growth—a trait with a strong direct genetic basis—without concurrent weighting of maternal attributes may induce an unfavorable correlated response, whereby cumulative maternal genetic merit declines over successive generations (Kahi et al., 2020). To mitigate these antagonistic genetic trajectories, the deployment of multi-trait selection indices that explicitly incorporate maternal breeding values is essential for balanced genetic progress and long-term population sustainability.

• *Genotype-by-Environment (G×E) Interactions and Covariance Between Direct and Maternal Genetic Effects*

Genotype-by-environment (G×E) interactions introduce a critical dimension of complexity in the estimation and interpretation of maternal genetic effects and their covariance with direct genetic effects. These interactions arise when the relative performance of genotypes changes across varying environmental conditions, leading to non-uniform expression of genetic potential. In the context of maternal traits, a dam exhibiting high maternal ability under optimal, resource-rich conditions may experience phenotypic suppression of the same traits under environmental stressors such as thermal load, nutritional scarcity, or pathogen pressure. This environmental sensitivity alters the covariance structure between direct and maternal genetic effects, often attenuating or reversing the positive associations observed under favorable conditions (Van der Werf et al., 2021).

Van der Werf and Tier, (2021) discusses statistical approaches to modeling G×E interactions, particularly in traits like maternal ability, and highlights the consequences of ignoring environmental heterogeneity in genetic evaluations. Mulder and Bijma, (2022) explored how G×E affects maternal traits and the need for environment-specific selection strategies to improve resilience and stability of genetic gains. Akanno et al (20210 highlighted the importance of modeling environmental effects in beef cattle, particularly for maternal and early growth traits, with emphasis on low-input production environments. Yao and Misztal, (2020) provided a statistical framework for modeling G×E using reaction norms, relevant to traits under maternal control in variable climates. Contextualizes G×E in African production systems, focusing on maternal performance under stress and the implications for breeding strategy design was discussed by Mwai, et al (2023).

Failure to account for G×E in statistical modeling frameworks can result in substantial underestimation of maternal genetic variance and biased covariance estimates, particularly in variable or low-input environments where stressors are pervasive. Models that assume homogeneous genetic expression across environments misallocate variance components and may incorrectly attribute environmental noise to additive genetic effects or overlook adaptive maternal contributions altogether. Such misestimating can misinform selection decisions, especially when breeding objectives prioritize robustness, adaptability, and maternal efficiency in resource-constrained systems.

Incorporating G×E interactions into genetic evaluation requires the implementation of reaction norm models or multi-environment animal models that allow for the estimation of environment-specific genetic parameters. These approaches enable the detection of genotype re-ranking across environmental gradients and facilitate the identification of resilient genotypes with stable maternal performance across production conditions. Moreover, integrating environmental descriptors as fixed or random covariates—such as temperature-humidity indices, forage availability scores, or disease prevalence—enhances model precision and the predictive accuracy of breeding values. Accounting for G×E is especially pertinent in tropical and subtropical livestock systems, where environmental heterogeneity is a major determinant of maternal trait expression and offspring survival.

Reliable estimation of covariance requires appropriate model specification and robust data structures. Small contemporary groups, incomplete pedigree information, and omission of key fixed effects—such as herd-year-season—can distort estimates by misattributing maternal effects to direct genetic components or vice versa (Toghiani et al., 2020). Multi-trait animal models with comprehensive fixed and random effects provide more accurate genetic parameter estimates.

- *Maternal Behavior and Phenotypic Expression and Covariance Between Direct and Maternal Genetic Effects*

Maternal behavior—shaped by both genetic predisposition and environmental influences—also affects covariance patterns. In sheep, for instance, mothering ability is influenced by flock dynamics and stress impacts lamb survival and growth, thus indirectly altering the observed covariance between maternal and direct effects (Carter et al., 2023). Including maternal behavior traits in models, when data permit, can enhance the precision of genetic evaluations.

The covariance between direct and maternal genetic effects in livestock is not purely a genetic phenomenon. Non-genetic factors—including climate, nutrition, management systems, G×E interactions, and maternal behavior—significantly influence both its magnitude and direction. Current evidence underscores the need for context-specific genetic evaluations and robust modeling approaches that incorporate environmental and management variables. Doing so helps avoid antagonistic selection outcomes and promotes sustainable genetic improvement across diverse livestock production systems.

- *Assumption of Zero Covariance Between Direct and Maternal Genetic Effects*

In animal breeding, it is commonly assumed that there is no covariance between an individual's direct genetic effects and the maternal genetic effects of its dam (i.e., setting ram=0r_{am} = 0ram=0), particularly when the pedigree is shallow or the data structure is limited. However, recent studies have challenged this assumption and offered more detailed guidance. Due to difficulties in accurately estimating direct–maternal correlations, some researchers have chosen to assume zero covariance (Splan et al., 2002). Although near-zero estimates have been observed in certain cases (Kaygisiz et al., 2010), this assumption can misrepresent the genetic architecture when negative covariance is significant, potentially skewing selection decisions (Moghbeli et al., 2021). Omitting covariance can also lead to bias in variance estimates (Koch, 1972). Despite the maternal influence on early growth traits, overlapping genetic contributions make precise estimation challenging (Assan & Makuza, 2015). David et al. (2015) found that setting a non-zero ramr_{am}ram to zero can still maintain the accuracy of total EBVs, even if direct or maternal components are inaccurately estimated, though it may slightly affect their genetic values. Recent broiler studies (Smith et al. 2023) have shown that while direct–maternal genetic covariance might be negative, the environmental covariance between dam and progeny is often positive. Ignoring these environmental factors can misrepresent the overall covariance structure.

Meyer (1992) and later simulation studies have shown that a high proportion of unrecorded dams and a mis-specified zero covariance assumption significantly increase bias and standard error in parameter estimates. In large-scale, multi-country genetic evaluations—such as those for Limousin cattle—assuming zero within-country and between-country r_{am} is common for simplicity. However, this assumption introduces greater bias in maternal and combined EBVs compared to direct effects, suggesting that it should be reconsidered when data connectivity is strong. Schaeffer (2019) demonstrated that having at least three generations of female records in the pedigree is crucial for reliable r_{am} estimation. In poorly connected datasets, the variance of estimates increases significantly, and assuming zero covariance may be more prudent to avoid misleading or unstable estimates. These insights suggest that while the default assumption of zero covariance can be justified under certain data constraints, accurate breeding decisions—and reliable EBVs—are best supported by explicitly estimating direct–maternal covariance when the data allows. Modeling both genetic and environmental pathways is particularly important in well-connected or international breeding programs.

- *Breed-Dependent Variation and Covariance Between Direct and Maternal Genetic Effects*

The relationship between direct and maternal genetic effects on growth traits is highly breed-dependent, reflecting distinct genetic architectures, selection histories, and environmental adaptations. The genetic covariance between these effects is not a fixed parameter across populations; rather, it varies in magnitude and direction depending on breed characteristics and the production system context. A positive covariance typically indicates complementarity, where superior direct genetic merit for growth is accompanied by favorable maternal contributions. Conversely, a negative covariance suggests antagonism, wherein selection for enhanced growth potential may inadvertently impair maternal ability, thereby complicating selection responses and necessitating a more nuanced breeding strategy.

Breed-specific dependencies in direct–maternal genetic relationships are a central consideration in the design of selection indices and genetic evaluation models. Variability in the timing and intensity of maternal effects—such as lactation curve shape, milk yield, and maternal care—further influences the expression and estimation of these covariances. For instance, Dodenhoff et al. (1999) and Meyer (2001) reported that many tropical breeds exhibit limited lactational capacity, which can reduce maternal environmental influence on early growth, altering the estimated direct–maternal covariance. Similarly, Mensah et al. (2024) emphasized that comparative assessments across temperate and tropical breeds must be interpreted within their specific environmental and genetic frameworks.

Recent empirical studies have reinforced the breed-specific nature of these relationships. Edea et al. (2021) documented variation in direct–maternal correlations for birth and weaning weights among Ethiopian indigenous cattle breeds. Van Marle-Köster et al. (2022) observed contrasting covariance estimates in South African Nguni and Bonsmara cattle, attributing these differences to divergent genetic backgrounds and environmental adaptability. In Mongolian native cattle, Togtokhbayar et al. (2023) found that uniform selection strategies failed to optimize maternal performance across breeds, leading to stagnated or even antagonistic responses. Likewise, Van der Westhuizen and Neser (2020) highlighted the need for breed-adapted genetic models in Namibian indigenous goats to accurately capture maternal effects and improve genetic progress.

Advancements in quantitative genetics have facilitated the development of robust statistical frameworks that allow for breed-specific modeling of maternal effects. Methods such as single-step genomic BLUP (ssGBLUP), Bayesian hierarchical models, and multi-breed animal models now enable more accurate partitioning of direct and maternal variance components while accounting for genotype-by-environment interactions. For example, Misztal et al. (2022) demonstrated that incorporating breed-specific maternal correlations into multi-breed genomic evaluations improved the predictive accuracy of breeding values in beef cattle. Similarly, Assan (2024) applied reaction norm models to assess maternal effect variability in Zimbabwean goats under different environmental stressors, providing deeper insight into breed-specific G×E responses.

These findings underscore the importance of tailoring genetic evaluations and selection strategies to the unique maternal effect profiles of indigenous breeds, particularly within low-input and smallholder systems. Neglecting this breed specificity can lead to erosion of valuable maternal traits through indiscriminate crossbreeding or generalized selection objectives. Yakubu and Alabi (2021) warned against the loss of maternal performance in Nigerian native chickens when crossed with exotic strains, while Wurzinger et al. (2023) emphasized participatory breeding approaches that integrate local knowledge and preserve maternal competencies specific to traditional systems.

In conclusion, the covariance between direct and maternal genetic effects is fundamentally influenced by breed-specific factors. Accurate estimation and strategic utilization of this dependency are vital for sustainable genetic improvement, particularly in the context of indigenous breeds adapted to resource-limited environments. Incorporating breed-specific parameters, environmental interactions, and maternal behavioral traits into modern evaluation systems will enhance the effectiveness and resilience of livestock breeding programs.

- *Impact of Management Systems and Covariance Between Direct and Maternal Genetic Effects*

Management practices significantly influence the expression of maternal effects. Swalve (1993) and Gutierrez et al. (1997) observed that negative covariance may result from suboptimal nutrition or management. Artificial rearing removes postnatal maternal environmental influence, leaving only prenatal and genetic contributions, which can lead to different covariance estimates compared to suckled animals (Okello et al., 2021). Moreover, reduced genetic variance from prolonged sire use and inbreeding in poorly managed systems can diminish additive genetic contributions and misrepresent covariance estimates (Tito et al., 2023).

- *Data Structure and Preparation and Covariance Between Direct and Maternal Genetic Effects*

The integrity of pedigree and performance records plays a crucial role in accurately estimating genetic covariances. Maniatis and Pollott (2003) highlighted the importance of including dams and maternal grand-dams with records for accurate estimation. Differences in data structure, such as partitioning or missing pedigree links, can bias covariance estimates (Assan, 2009; Pribyl et al., 2008). Additionally, limitations in data availability, especially in traditional systems with minimal record-keeping, compromise estimation accuracy (Campelo et al., 2004; Mathur et al., 1998). Recent studies confirm that quality of pedigree and family structure remain pivotal to accurate variance component estimation (Mbole-Kariuki et al., 2021).

- *Growth Trait Type and Maturation Stage and Covariance Between Direct and Maternal Genetic Effects*

The stage of growth significantly influences covariance estimates. Maternal effects are most critical at early ages but diminish as animals mature (Robinson, 1981). Breed maturity patterns further affect this trend—early-maturing breeds may lose maternal influence sooner than late-maturing ones (Meyer, 1995). Covariance values for weaning weight and average daily gain tend to be similar due to their linear interrelationship. However, selection for traits like yearling weight may alter growth curve dynamics and indirectly influence maternal effects (Archer et al., 1998; Zhang et al., 2020). Ignoring the influence of reproductive and maturation traits on growth trait covariances may lead to misinterpretation of selection responses (Chen et al., 2021).

➢ *Magnitude and Direction of Covariance Between Direct and Maternal Genetic Effects for Growth Traits*

Understanding the magnitude and direction of the covariance between direct and maternal genetic effects is fundamental to effective genetic evaluation and improvement of growth traits in livestock. Direct genetic effects refer to the influence of an animal's genes on its phenotype, while maternal genetic effects stem from the dam's genotype, primarily affecting early growth through maternal care, uterine environment, and milk production (Mrode, 2014; Akanno et al., 2013). The covariance between these effects can be either negative or positive, with important implications for selection strategies. A negative covariance often indicates antagonism, where selecting for improved individual performance may compromise maternal ability, potentially slowing genetic progress (Meyer, 1992; Oyeyemi et al., 2021). Conversely, a positive covariance suggests a complementary relationship that facilitates simultaneous improvement of both traits (Nephawe, 2004). Quantifying this covariance accurately is essential for designing breeding programs that balance short-term productivity with long-term sustainability, especially in systems where maternal influences are pronounced, such as in early weaning and extensive rearing environments (Van Vleck, 2006; Mulder et al., 2016).

- *Synergistic Relationships: Negative Covariance Between Direct and Maternal Genetic Effects for Growth Traits*

A negative covariance in animal breeding genetic evaluation means a genetic antagonism between maternal and direct effects. In the genetic evaluation of ruminant growth traits, the covariance between direct and maternal genetic effects is a critical parameter. Recent findings suggest that highly negative covariances between these two components are not only common but also biologically meaningful (Bakhshalizadeh et al., 2022; Safari et al., 2023). A large negative covariance implies a trade-off: animals that possess superior direct genetic potential for growth may be born to dams with lower maternal ability, and vice versa. This antagonistic relationship complicates genetic improvement strategies, particularly when selection emphasizes individual growth without considering maternal contributions.

A negative covariance implies a trade-off between direct and maternal genetic effects—where improvement in one component can inadvertently compromise the other. For instance, selecting for faster-growing offspring (high direct genetic merit) may result in dams with reduced maternal ability, ultimately limiting the benefits of selection at the population level. This antagonism complicates genetic evaluations and necessitates balanced selection strategies or the use of selection indices that account for both effects. Understanding this negative relationship is crucial, especially in species where early growth traits are maternally influenced, such as in cattle, sheep, and goats.

Strongly negative estimates of direct–maternal genetic covariance often result in inflated estimates of both direct and maternal heritabilities while simultaneously reducing the estimate of total heritability (Yusuf et al., 2023). This distortion can lead to erroneous selection decisions if the covariance is ignored or inaccurately estimated. Consequently, the assumption of zero covariance, although convenient, may be misleading and lead to biased breeding value predictions (Notter, 2021; Emamgholi Begli et al., 2020).

One proposed explanation for the negative covariance is physiological compensation by the dam, particularly for traits such as birth weight. For example, fetuses with high direct genetic potential for increased birth weight may trigger maternal mechanisms to limit excessive growth in utero—possibly a natural response to optimize calving ease and offspring survival (Togtokhbayar et al., 2020; Mandal et al., 2021). This interplay underscores the influence of maternal genetics and the uterine environment on fetal development, a dynamic that is often masked when maternal effects are excluded from genetic models.

Moreover, when maternal genetic effects are omitted in evaluation models, the ranking of animals can change substantially. Animals with favorable direct genetic values may be overestimated in their breeding potential if maternal influence is not concurrently considered (Boujenane & El-Hazzab, 2024). Accurate estimation of direct–maternal genetic covariance is therefore essential for proper animal ranking and reliable prediction of genetic merit.

In practical breeding programs, this antagonism has implications for trait selection. Strategies that incorporate both direct and maternal genetic effects yield greater genetic gains and are more robust than those focusing solely on direct effects (Safari et al., 2023). Intensive selection for growth traits, particularly early-life traits like birth and weaning weight, without considering maternal performance may inadvertently reduce dam productivity in future generations.

While biologically large negative covariances may seem counterintuitive for growth traits, they have been consistently reported across multiple ruminant populations. Recent studies have emphasized the need for high-quality pedigree data, appropriate model specification, and large datasets to accurately separate and estimate these effects, particularly under variable environmental and management conditions (Bakhshalizadeh et al., 2022; Yusuf et al., 2023).

- *Synergistic Relationships: Positive Covariance Between Direct and Maternal Genetic Effects for Growth Traits*

For positive covariance, the maternal and direct effects reinforce each other. Although antagonistic (negative) relationships between direct and maternal genetic effects have been widely documented in ruminant species, instances of positive genetic covariance have also been reported and deserve equal attention. In such scenarios, the genetic merit of an individual for growth traits is complemented rather than opposed by the maternal genetic contribution of the dam. This synergy enhances the cumulative genetic value of offspring, facilitating more efficient and sustainable selection strategies in livestock breeding programs.

A positive genetic covariance between direct and maternal effects indicates that the genetic influences contributing to the individual's performance (direct effects) are aligned with those affecting the performance of its offspring (maternal effects). This synergy facilitates concurrent genetic improvement, as selection for superior individuals inherently favors those that will also produce better-performing progeny. For example, in traits such as weaning weight, where both the calf's own growth potential and the dam's nurturing ability contribute to phenotype, a positive covariance simplifies breeding strategies and accelerates response to selection. This scenario is ideal in breeding programs aiming for rapid and sustainable improvement across generations.

Recent studies on indigenous and composite breeds of cattle, sheep, and goats have observed moderate to high positive correlations between direct and maternal genetic effects, particularly for early-life growth traits such as birth weight and weaning weight (Boujenane & El-Hazzab, 2024; Mulindwa et al., 2023). These findings challenge the general assumption of a universal negative correlation and suggest that the nature of the covariance may vary significantly depending on breed type, selection history, and production environment.

The biological interpretation of positive direct–maternal genetic covariance is grounded in the idea that animals with favorable alleles for growth are often born to dams who themselves possess superior maternal abilities. This alignment could arise due to past selection strategies that did not differentiate direct and maternal pathways but rather favored general performance, indirectly maintaining the positive correlation. Moreover, co-selection for growth and maternal traits in nucleus breeding herds or under natural selection pressures may enhance this alignment (Safari et al., 2023; Emamgholi Begli et al., 2020).

From a breeding perspective, positive covariance is advantageous, as it simplifies selection indices and facilitates genetic progress without compromising maternal performance. Selection for heavier offspring will concurrently improve maternal ability, thereby reducing the risk of indirect negative consequences on dam traits such as milk yield or mothering behavior (Yusuf et al., 2023). This synergistic relationship improves both short-term selection response and long-term population sustainability.

However, the stability and consistency of positive covariance estimates should not be taken for granted. The magnitude and direction of this parameter are highly sensitive to data structure, model specification, and environmental variability (Safari et al., 2023). Misestimation can result from model misspecification, particularly if random maternal environmental effects are confounded with genetic maternal effects. Thus, the use of multi-trait animal models, proper pedigree depth, and appropriate accounting for permanent environmental effects is imperative to ensure accurate parameter estimation.

In summary, while positive covariance between direct and maternal genetic effects may not be universally observed, its presence in certain populations highlights the need for population-specific breeding strategies. Capitalizing on this positive correlation can result in enhanced cumulative genetic merit and improved maternal efficiency, thereby advancing the goals of sustainable livestock production.

- *High and Low Magnitude of Between Direct and Maternal Genetic Effects for Growth Traits*

The term "high magnitude" indicates a significant genetic influence on phenotypic growth traits. When the magnitude of genetic covariance, whether positive or negative, is substantial, it has a pronounced impact on the phenotype. In instances of high positive covariance, it can facilitate rapid and efficient genetic progress. Conversely, a high negative covariance may significantly constrain selection response unless advanced mating strategies or genomic tools are employed to mitigate the unfavorable linkage. High magnitude covariance typically suggests that both maternal and direct effects are genetically significant contributors to the trait and must be jointly considered in genetic evaluations.

A low magnitude of covariance reflects minimal genetic interaction or influence on growth traits. It indicates a weak genetic connection between maternal and direct effects, suggesting that one or both components have limited genetic influence or that their interactions are negligible. While this may reduce the risk of antagonism, it also implies that selection targeting one component will have minimal indirect effects on the other. In such scenarios, breeding decisions can focus more directly on the primary trait without significant concern for correlated maternal effects, although this may slow cumulative genetic gain.

IV. IMPLICATIONS

The findings of this systematic review hold critical implications for genetic improvement strategies in ruminants, especially under the complex environmental and data-limited conditions prevalent in tropical production systems. Misestimating or disregarding the covariance between direct and maternal genetic effects introduces substantial bias into genetic evaluations, which compromises the accuracy of breeding value predictions and may lead to suboptimal or even counterproductive selection outcomes. This is particularly consequential for traits expressed early in life, where maternal influence is most significant.

Accurate genetic evaluations must reflect the interplay between an animal's own genetic potential and the maternal environment it provides or receives. Thus, animal breeding programs should prioritize the refinement of statistical models to accommodate population-specific and trait-specific covariance estimates. Such refinement enables more informed selection decisions, safeguards genetic diversity, and enhances the rate of genetic gain.

Moreover, integrating maternal attributes into breeding goals—especially in contexts where reproductive efficiency and early survival are vital for productivity—can reinforce resilience and sustainability. Adoption of genomic tools and longitudinal modeling techniques further presents an opportunity to capture complex genotype-by-environment interactions and to mitigate data quality challenges common in tropical systems.

V. CONCLUSION

This review elucidates the nuanced and often underappreciated relationship between direct and maternal genetic effects on growth traits in sheep, goats, and cattle, with a focus on the challenges and opportunities within tropical environments. The broad spectrum of reported correlations—from negative to positive—reflects the multifactorial influences shaping this relationship, including genetics, management practices, data structure, and model choice.

Crucially, the assumption of zero covariance between these effects, though commonly employed for simplicity, can distort genetic evaluations and diminish selection efficacy. As such, the explicit modeling of direct–maternal genetic covariance emerges as a foundational requirement for accurate genetic parameter estimation.

For breeding programs targeting resilient and productive ruminant populations in tropical regions, acknowledging and incorporating these covariance structures is not optional—it is indispensable. Future research must pivot toward advanced statistical and genomic methodologies that can better capture these complex relationships, ultimately guiding the development of balanced, efficient, and sustainable selection strategies that honor both individual growth potential and maternal contributions.

➢ *Key Takeaways Include:*

- Accurate separation of direct and maternal genetic effects requires robust data structures and appropriate modeling of environmental influences.
- The covariance between these effects is dynamic and may vary with age, trait, and production system, necessitating population-specific parameter estimation.
- Assumptions of zero covariance can lead to biased evaluations and misguided selection responses.
- Integrating reproductive and maternal traits with growth traits in selection indices may enhance overall breeding objectives and maternal efficiency.
- Selection programs must utilize models that explicitly account for direct–maternal covariance to avoid antagonistic responses and ensure sustainable genetic improvement.

Future research should focus on advanced modeling approaches, including genomic and random regression methods, to refine estimates of these genetic components and support balanced selection strategies that promote both individual performance and maternal capability.

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