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Review article

Magnitude of correlation between direct and maternal genetic effects for growth traits in ruminants

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A R T I C L E   I N F O

A B S T R A C T

This is a review paper that looks at the influence of sign and magnitude of the correlation between direct and maternal genetic effects for growth traits in sheep, goats and cattle. Considerable debate exists about the validity of results on the factors which influence the sign and magnitude of the correlation between direct and genetic effects of growth traits in sheep, goats and cattle. The current reports on sign and magnitude of the correlation between direct and maternal effects for growth traits in sheep, goats and cattle show that both positive and negative values are possible. It emerged that the use of an appropriate covariance of direct and maternal genetic effects for growth traits in sheep, goats and cattle has a bearing on the accuracy of selected programs. The importance of correlation between direct and maternal effects for growth traits in sheep, goats and cattle is based on the notion that ignoring the covariance of direct and maternal genetic effects for growth traits in sheep, goats and cattle may distort the ranking of individual animals in a population. The review paper therefore, concludes that the sign and magnitude of covariance of direct and maternal genetic effects for growth traits in sheep, goats and cattle, is dependent on various factors which include management, breed and data preparation process.

1. Introduction

Growth traits have been the most important criteria in the selection of sheep, goats and cattle for meat production. Genetic evaluation of growth traits has been obtained by considering weights at standard ages in domesticated animals (e.g. birth, weaning, yearling etc. and final or weight gains between two ages as different traits. Different interpretations have been given to the negative and/or positive covariance of direct and maternal genetic effects for growth traits in ruminants. An effort to improve genetic quality of sheep, goat and cattle through selection require accurate information on covariance of direct and maternal genetic effects. The progress of selection response can be understood if information of covariance of direct and maternal genetic effects is available.

Many studies have found negative covariance of direct and maternal genetic effects in sheep, goat and cattle. However, positive relationships have also been reported in sheep, goat and cattle by Nesser et al., (2001), Tilki et al., (2008) and Choi et al., (2000), respectively. Considering the aforementioned scenario the estimation of covariance of direct and maternal genetic effects has been a subject of controversy in animal breeding evaluation procedures. No conclusive reports given on the causes of different signs and magnitude of covariance between direct and maternal. This debate has been monopolized by researchers in the temperate region, despite animal production environmental variability.

Foulley and Lefort (1978) suggested that the estimation of maternal effects and their respective genetic parameters is inherently problematic and, due to the confusion of direct and maternal effect, subject to large sampling errors. Meyer (1994) attributed them also to a large extent, to sampling covariation. Whilst Shi et al., (1993) thought there could also be a covariance between direct and maternal environments. Robinson (1996b) showed a dramatic increase in the likelihood along with a substantial reduction in estimate of the covariance of direct and maternal when additional effects such as sire* herd effect or regression on maternal phenotypes were included in the model of analysis.

2. Factors influencing the magnitude of covariance of direct and maternal genetic effects

2.1 Non genetic factors

Until now different studies in domesticated animals showed negative covariance values for growth traits, but still lack comprehensive knowledge of the effects of modeling different non genetic factors in influencing covariance. Modeling of few non genetic factors have been reported with different results (Robinson (1996b). There has been an agreement between results from similar animal models differed in modeling of non genetic factors, and /or models accounting for the same non genetic factors observing similar genetic parameter results. However, agreement of results from different models, which could be easily explained by lack of covariance of direct and maternal genetic effects of growth traits. Meyer (1997) suggested that inflated estimates of covariance of direct and maternal genetic effects for growth traits might be caused to some extent by unaccounted sources of variation. It is necessary to take note of existence of very important environmental influences on growth traits and the need to adjust for them in order to improve the accuracy of genetic parameter estimation. Inclusion of the regression on maternal phenotypic for weaning weight in the animal model could explain that part of the covariance of direct and maternal genetic effects is environmental. However, maternal regression had little effect on estimates of genetic covariance showing that most of covariance was genetic.

2.2. Assumption of zero covariance of direct and maternal genetic effects

Considering the difficulties in obtaining reliable estimates of the correlation between direct and maternal genetic effects some researchers have assumed this correlation to be zero. Elsewhere near zero covariance of direct and maternal genetic effects have been reported (Splan et al., 2002; Kaygisiz et al., 2010). However this approach will only worsening the situation if the magnitude of covariance is present and of that matter is highly and negative. The ranking of animals in such a population may be incorrect. or distorted. When covariance of

direct and maternal genetic effects are assumed to be zero estimates of components seemed to be robust (Guiterrez et al., 1997). Koch (1972) emphasized the possibility of a negative direct and maternal genetic covariance if not modeled to bias the estimates of direct and maternal genetic variance. Even though pre-weaning growth traits can be clearly affected by the maternal influence, some times it is not easy to determine such influence due to the presence of genetic correlation between direct and maternal genetic effects.

2.3. Breed effect

An investigation conducted by Dodenhoff et al., (1999) on several breeds of beef cattle indicates that dependences between direct and maternal genetic effects are determined by breed. Meyer, (2001) reported the breed differences in the importance of maternal environmental effects are important and some breeds lower permanent environmental earlier, maternal effects due to decline of the lactation curve than other breeds. It is obvious that the potential for milk production is poorly developed in most livestock indigenous to the tropics. The more limiting milk in tropical breeds may influence a certain covariance of direct and maternal genetic effects. When direct effects are least important but decline sharply after weaning and at the highest age this effect is negligible depending on breed. However Dodenhoff et al., (1999) report fell short on the fact that it did not clearly show if this dependences may be different if the same breed is managed in a different environment(temperate vs tropics).

Cross sectional covariance estimates may not be very reliable. Imposing estimates derived from temperate domestic livestock on tropical animal's genetic evaluation as starting values may be inappropriate and misleading. Fairly high heritability arising from large genetic variance due to multibreed composition of herds could be expected to influence the covariance of direct and maternal genetic effects only if this effect is accounted for by the model of analysis. In the tropics, where there is harsh environmental condition for animal production, still many issues need to be investigated which may influence the magnitude of covariance of direct and maternal genetic effects.

2.4. Influence of management systems

Swalve (1993) suggested that the negative covariance between direct and maternal genetic effects may be the result of management system. Gutierrez et al., (1997) reported antagonism between direct and maternal genetic effects for weaning weight for Zebu cattle and suggested that this antagonistic relationship should be compensated by improving managerial practices and using supplemental feeding when necessary. Animals which are artificially fed remove maternal environment at birth, and any presence of maternal effects could only be explained as carryover effects from residual prenatal care of the dam or to the compound effects of the residual prenatal care plus additive and non additive effects in the dam which most of the cases are unaccounted for in most models fitted by researchers. In contrary the expectation on suckling young ones may be different from artificial fed young ones which definitely influence their covariance of direct and maternal genetic effects. Consistent with most studies done on suckling beef cattle is the presence of maternal effects, it is suffice to say that the nature of covariance of direct and maternal genetic effects on artificial or bucket fed and suckled population of any domesticated species may be different due to the difference in the exhibition of maternal genetic effects. It is correct to assume that the carryover concept may be partly genetically controlled due to the genotypic differences in the size of the dams and the uterine environment dams provide along with possible cytoplasmic effects, which play a role in influencing of maternal effects. On the other hand, there is close agreement between covariance between direct and maternal genetic effects for growth traits , but less for similar management in the temperate. These contradictory results suggest that estimates of covariance of direct and maternal genetic effects for temperate cattle breeds may be less precise. The deterioration in management resulting to poor nutritional status of animals, and same sire used for a number of years resulting in inbreeding and decrease in additive genetic variance may influence the covariance. Covariance of direct and maternal genetic effects seem to be equally important in different management systems as is evident from the estimates in different studies.

2.5. Data preparation influencing covariance of direct and maternal genetic effects

Apart from inconclusive reports on real differences among populations analyzed, differences in preparation of data could play an important role in influencing the sign and magnitude of covariance between direct and maternal genetic effects for growth traits in sheep, goat and cattle. Maniatis and Pollot (2003) reported that

estimation of the correlation between direct and maternal genetic effects is dependent on key pedigree relationships where a high proportion of both dams and maternal grand dams with their own records are essential. Moreover Pribyl et al., (2008) showed that editing the database plays a role in estimating genetic parameters and includes a more complex pedigree as well as produces slightly different results. From the reported results in literature researchers have not agreed on the minimum number of records to effectively estimate the covariance of direct and maternal genetic effect. However, it has been mentioned that the size of maternal genetic effects and their relationship among themselves and with direct genetic effects are less clear and far from being known (Meyer, 1993).

In another study by Assan (2009) in Tuli cattle, the covariance of direct and maternal genetic effects were small and positive (0.11) in males and 0.15 in female calves. However, a strong negative covariance was observed for pooled data. The positive covariance in males and females may have been caused by the changes in the structure in the data set which became small due to partitioning. The impact of data structure on separating maternal genetic and maternal environmental effects from combined and direct effects was demonstrated by Maniatis and Pollot (2003). Showed that the accuracy of estimation of maternal genetic effects depends on the family structure and demonstrated that the both the number of progeny per dam and the proportion of dams having their own records in the data considerably affects the variance components estimation. Hence, the partitioning of data for genetic evaluation may be found wanting in the sense that it distorts the family structure and reduces both the number of progeny per dam and the proportion of dams having their own records. The reduction of records in preparation of data may impose light differences in the estimation of covariance between direct and maternal genetic effects for growth traits in sheep, goats and cattle.

Reliable estimation of direct and maternal genetic parameters accounting for direct and maternal covariance requires data with a sufficient amount of reliable records and good pedigree records. This can be a major limitation in artificial insemination related programs because accessibility of pedigree information on artificial insemination sires may be difficult to compile. Data collected from cattle farmers with traditional rearing system and having incomplete record of production, identification and pedigree reduced inverse matrix of genetic correlation. Generally in developing countries with traditional rearing system, artificial insemination or using bull inter –cattle herds has not been done that caused weakness of genetic correlation among herds and produced genetic variance bias (Mathur et al., 1998; Campelo et al., 2004)

2.6. Growth traits considered

Stage of growth traits in question may generate different covariance due to their relation in the growth curve. Robinson (1981) suggested that maternal genetic effects generally are important for growth traits at young ages and diminishes with an increasing age. The tendency of maternal genetic effects to decline from birth to later ages my presumably be different in different breeds (early maturing vs late maturing) or temperate vs tropical breeds). This phenomenon may be directly related to their lactation curve. Weaning weight and average daily gain may show similar results between them in terms of covariance of direct and maternal genetic effects, assumption is that weaning weight is a linear combination between birth weight and average daily gain (Weaning=Birth + Age*Average Daily Gain). The covariance of direct and maternal genetic effects for weaning weight must be very close for average daily gain but slightly modified towards those for birth weight assuming other factors are the same for example management, breed, etc.

The selection based on different growth traits may affect the sign and magnitude of covariance. Selection for yearling weight may not change the scale of growth curve but can change the shape of the growth curve. It may be assumed that selection based on yearling weight can indirectly improve maternal ability which can influence increasing of maturing rates. Estimation of variance components of growth traits and maturity traits, Meyer (1995) reported significant positive maternal genetic effects on maturation rate in Hereford. Growth and maturation derived from a growth curve and their relationships with direct and maternal genetic effects of growth traits could be considered as additional information for use in genetic evaluation programs. Archer et al., (1998) argued that it was possible that the improved maternal ability increased rate of maturation, whereas the direct genetic effect might have decreased rate of maturation, with no resultant change in phenotypic rate of maturation. It seems failure to consider the influence of some other reproductive traits on growth may have negative consequence on the estimation of covariance of direct and maternal genetic effects.

3.Negative covariance of direct and maternal genetic effects

Meyer (1997) found that large, negative estimates of direct and maternal genetic covariance are associated with overestimating of additive direct and maternal variance. The highly negative covariance indicates important trade offs between direct and maternal genetic effects. The large negative covariance of direct and maternal genetic effects were associated with an increase in estimates of both direct and maternal heritability, and reduction in total heritability. The accuracy of covariance of direct and maternal genetic effects of growth traits was highly required in selection programs. This entails that the assumption of zero covariance may be misleading in genetic parameter estimation. Tosh and Kemp (1994) studying sheep suggested that the negative covariance may be due to natural selection for an intermediate optimum for birth weight. It is nature's own course to limit birth weight in ruminants. The negative covariance may act as a physiological compensatory effect of the dam to reduce the birth weight of offspring that have high direct genetic value of birth weight. The genetics of the physiological and physical capacities of a dam and its environment have the influences on the fetus and offspring as maternal effects.

The use of inappropriate magnitude of covariance of direct and maternal genetic effects may distort the ranking of individual animals in a population, because high and negative covariance cause heritability estimate to rise. Szwaczkowski et al., (2006) showed that the negative covariance between direct and maternal genetic effects indicates different rankings of individual animals when the maternal contributions is omitted in the genetic evaluation. Because of negative genetic correlation between direct and maternal genetic effects for growth traits, methods of selection accounting for both direct and maternal genetic effects would result in greater economic selection response than selection based only on direct genetic effect.

The highly negative covariance of direct and maternal genetic effects suggest a genetic antagonism between a heifer's prenatal growth potential and the subsequent quality of her uterine environment (Norris et at., 2004). This also indicates that the probable reduction in maternal performance due to intensive selection for individual growth may be substantial. The negative covariance for birth weight shows the importance of not relying totally on actual weight to determine the genetic potential of an individual.

Robinson (1996a) using Simmental data, showed that the covariance of direct and maternal genetic effects may be negative, not only because of genetic antagonism, but also because of additional sire* environmental variation or negative dam offspring covariance. However, using Angus field data from Australia, Robinson (1996a) reported that the negative dam offspring covariance was not important and most of the direct of covariance of direct and maternal genetic effects was genetic. Less than sufficient environment may impose a negative correlation between direct and maternal genetic effects (Meyer, 1993; Swalve, 1993). Koch, (1972) had earlier suggested that excess milk production by dams daughter also resulting in a negative dam offspring correlation. High weaning weights impede the milking potential of the developing animals. The high negative covariance of direct and maternal genetic effects seem biologically unlikely for growth traits.

4. Positive covariance of direct and maternal genetic effects

Positive covariance of direct and maternal genetic effects for growth traits have been observed in cattle (Beffa, 2005), in sheep (Saacti et al., 1999) and in goats (Gholizadeh et al., 2010). The reason for the positive relationship in previous studies on growth traits could not conclusively be explained by the authors (Dodenhoof et al., 1999). Nasholm and Danell (1996) concluded that selection for increased growth traits in sheep will also improve the maternal ability in the case of positive correlation between direct and maternal genetic effects.

5. Conclusion

Accounting for a direct and maternal genetic effects is necessary in any selection program for growth traits. Covariance of direct and maternal genetic effects can differ inter- species as influenced by management and the nature of the selection procedure. A good data structure in the population is necessary to allow the separation of both genetic effects. Again further research about modeling of different non genetic factors and their influence on the covariance of direct and maternal genetic effects need some attention. These arguments in the review suggested that the contribution of direct additive and maternal additive genetic effects to growth variation differed not only in expression in time, of covariance of direct and maternal effects, but also in action magnitude. It may suffice to say that any factors which affect the presence of direct additive and maternal additive genetic effects will influence the magnitude of the covariance giving room for manipulation of covariance of direct and

maternal genetic effects in selection programs. Covariance of direct and maternal genetic effects are population specific , hence it is inappropriate to use information generated elsewhere. Additional information such as reproductive traits can complement growth traits in selection programs. In order to decide upon a feasible selection strategy estimation of the genetic parameters and the covariance of direct and maternal genetic effects are necessary. Selection programs for improving growth traits should be based on models where the covariance of direct and maternal genetic effects have been well taken care of.

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