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Genetic analysis of maternal behavior and its effect on lamb survival

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Genetisk analys av modersbeteende och dess effekt på lammöverlevnad

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Abstract

Improvement of lamb survival rates is an important topic for production and welfare in the sheep industry. Maternal behavior affects lamb survival and vigor during the neonatal period. A measurement used in the literature for maternal behavior is MBS, which measures the distance between ewe and lamb during handling of the lamb. MBS displays low to moderate heritability and repeatability. Genetic correlations with litter survival are considered to be low. Small genetic improvement for lamb survival is expected but the advance would be slow. The aim of this current review was to investigate the genetic value of incorporating maternal behavior as an indirect selection trait for lamb survival in breeding programs. With the low genetic parameters found it is suggested that selection for maternal behavior to improve lamb survival would have slow genetic progress. Other correlated traits might be more efficient to improve lamb survival. The evaluation of differences between breeds in this review indicates that more intensively bred breeds have lost more maternal ability than those who have been extensively bred. This could imply that our current, intense breeding for production traits without including maternal behavior is resulting in a decline of ewes expressing good maternal care. If further research can strengthen this theory, maternal behavior should be included in breeding programs for sheep.

Sammanfattning

Hur man kan förbättra lammöverlevnad är en viktig fråga som påverkar både produktion och djurvälfärd inom fårindustrin. Modersbeteende påverkar lammöverlevnad och livskraft under den neonatala tiden. En metod som används i litteraturen för att mäta modersbeteende är MBS som mäter avståndet mellan lamm och tacka medan lammet hanteras. MBS visade låg till måttlig avbarhet och repeterbarhet. Korrelationer med lammöverlevnad anses vara låga. Ett litet genetiskt framsteg för lammöverlevnad förväntas men utvecklingen skulle gå långsamt. Syftet med denna studie var att undersöka det genetiska värdet av att inkorporera modersbeteende som en indirekt egenskap för lammöverlevnad i avelsprogram. Med de låga genetiska parametrarna som hittades, antas det genetiska framsteget bli lågt. Andra korrelerade egenskaper skulle kunna vara mer effektiva för att öka lammöverlevnaden. Utvärderingen av skillnader mellan raser i denna litteraturstudie, visar att intensivt avlade raser har tappat mer modersegenskaper än de som genomgått en mer lågintensiv avel. Detta kan indikera att vår nuvarande, intensiva avel för produktionsegenskaper som inte inkluderar modersbeteende, resulterar i en minskning av tackor som uttrycker goda modersegenskaper. Om fortsatt forskning kan stärka denna teori bör modersbeteende inkluderas i avelsprogram för får.

Introduction

High lamb mortality results in reproductive inefficiencies of the herd and a financial loss for the farmer. It can also be considered a welfare problem for the sheep industry. There is a broad variety in death rates between both herds and countries. The average lamb mortality rate in Sweden is 9% from birth to weaning (*Svenska fåravelsförbundet*, 2013). In the United

Kingdom (UK) the average lamb mortality from scanning to 3 days of age is 10–25% (*NADIS*, 2016). A review written by Hinch & Brien (2014) points to a great variation in lamb survival in Australia. They conclude that average mortality rates for single born lambs were 10% and 30% for twins.

Sheep are naturally relatively shy and nervous animals but are also known for being well abled mothers. After parturition the ewe normally licks the lamb tenderly and stands still to enable the lamb to suckle. During the first few hours a bond is established between the mother and her lamb, which is highly dependent on smell and vocalization (Nowak, 1990; Sjödin *et al.*, 2008). If the lamb smells of another ewe there is a risk that it might be rejected by its own mother. The connection between ewe and lamb is upheld by bleating (Sjödin *et al.*, 2008). Maternal behavior and rearing performance of the ewe influences the survival rate of the neonate (O'Connor *et al.*, 1985). An improvement by selection of good mothers might lead to reduced lamb mortality. Maternal ability is affected by genotype but also by age, or rather previous lambing experience of the ewe. Older, multiparous ewes are more attentive and caring towards their lambs (Lambe *et al.*, 2001; Everett-Hincks & Cullen, 2009; von Borstel *et al.*, 2011). Ewes that rear multiple lambs also tend to show greater maternal care than ewes with singles (Lambe *et al.*, 2001; Everett-Hincks *et al.*, 2005).

The purpose of the present paper is to review the possible genetic gain of including traits for maternal behavior in sheep breeding programs as a mean to improve lamb survival. This review will attend to questions concerning the heritability of ewe rearing performance and the variation between breeds. The effect of maternal behavior on lamb survival and its possible role as indirect selection criteria will also be viewed.

Maternal ability

Maternal behavior score

Several studies use a maternal behavior score (MBS) to measure the rearing performance of the ewe (Dwyer & Lawrence, 1998; Lambe *et al.*, 2001; Everett-Hincks *et al.*, 2005; Brien *et al.*, 2010; Hatcher *et al.*, 2010; Plush *et al.*, 2011). This measurement will be the main focus for discussion of genetic parameters in this article. The method is based on observations of the proximity of the ewe to her lambs during handling and tagging by the farmer. Ewes are in most cases scored on a 1-5 scale similar to the method described by O'Connor *et al.* (1985). In O'Connor *et al.* (1985) tagging occurs within 24 hours after birth. The time of MBS observation differs slightly between trials. If the mother flees when the handler is approaching and does not return to her lamb(s), a MBS score of 1 is given. The highest score, 5 is given to ewes that stay within close proximity of her lamb during tagging or handling. Methods for scoring in-between numbers vary somewhat but are based on the distances between the dam and her young.

Maternal behavior

Alternative maternal behaviors that can be recorded are interaction with the lambs early postpartum. Other behavioral patterns taken into account are caring behaviors such as licking, nosing, aiding suckling, and rejecting behaviors like not allowing suckling, retreating from the lambs, aggressiveness and abandonment (McGlone & Stobart, 1986; Dwyer & Lawrence, 1998, 2000b; Pickup & Dwyer, 2011). A separation test is also a method to determine the ewes' mothering ability. The lamb is separated from the ewe during a fairly short period of time within 12-24 hours after birth. Behavior and vocalization during separation and after reuniting is observed (von Borstel *et al.*, 2011).

Genetic parameters for maternal behavior score

Heritability and correlations

The MBS shows a relatively low direct heritability and repeatability in most studies displayed in Table 1. In the study executed by Everett-Hinks *et al.* (2005) on a Coopworth flock selected for maternal ability. The mean MBS was 3.3 and litter survival calculated as a percentage of lambs weaned, correlated positively with MBS. The negative correlation in Table 1 is the genetic correlation between MBS and lamb survival as a trait of the lamb (Everett-Hincks *et al.*, 2005). In the article by Brien *et al.* (2010) 80% of the ewes were Merino and 20% Border Leicester × Merino and MBS is used as a trait for the lamb instead of the ewe. The estimated genetic correlation (r_g) and phenotypic correlation (r_p) of MBS with lamb survival was estimated for 3 days of age and up to weaning and were negative (Brien *et al.*, 2010). Lambe *et al.* (2001) measured MBS on Scottish Blackface ewes on a six-point scale instead of five. Genetic correlations were estimated for MBS with lamb survival to marking (ca 42 days) and to weaning (110-120 days). However the standard errors were large and the results may not be reliable (Lambe *et al.*, 2001). Hatcher *et al.* (2010) studied a flock of Merino ewes of different strains. Genetic and phenotypic correlation was estimated for MBS and lamb survival from birth to 7 days and to 110 days (weaning). Plush *et.al* (2011) used a flock of Merino sheep selected for meat and wool traits. A MBS similar to the one described in O'Conner *et al.* (1985) was measured, but referred to as ewe mothering temperament (EMT). Their results showed that EMT had a moderately high heritability compared to the MBS heritabilities mentioned above. Genetic correlation and phenotypic correlation of EMT with litter survival was calculated only from birth to weaning (Plush *et al.*, 2011). Brown *et al.* (2016) combined data from several flocks consisting of Merino, Poll Dorset, White Suffolk, Border Leicester and Coopworth. Genetic correlation estimates was -0.25±0.07 between MBS and number of lambs weaned per ewe. Everett-Hincks & Cullen (2009) also combined several breeds, predominantly Romney, Coopworth and Texel. They estimated correlations between MBS and litter survival to weaning (100 days), but also at birth which was $r_p = 0.05 \pm 0.02$ and $r_g = 0.20 \pm 0.41$.

While the values for heritability vary between experiments, they are all low to moderate. This suggests that genetic gain from breeding will be slow. The genetic and phenotypic correlations with MBS to lamb survival were low or even negative in some studies. The low

to moderate repeatability indicate that the dams may not have the same MBS every lambing year. The span of the early estimated correlations between litter survival and MBS is so large that it is not possible to compare the estimates correctly but indicates that the different time measurements are correlated (Brien et al., 2010).

Table 1 Estimates (±s.e.) of direct genetic parameters for MBS and genetic (r_g) and phenotypic (r_p) correlation between MBS and litter survival early (3-42 days) and at weaning (100-120 days)

		Early		Weaning	
Heritability	Repeatability	r_g	r_p	r_g	r_p
[1]0.09±0.09	0.09±0.09	---	---	-0.74±0.26	---
[2]0.20±0.03	---	-0.27±0.24	-0.06±0.01	-0.24±0.24	-0.08±0.01
[3]0.13±0.03	0.32	0.60±0.19	0.03	0.89±0.71	0.001
[4]0.20±0.02	0.49±0.02	0.12±0.15	0.02±0.01	0.16 ±0.15	0.01±0.010
[5]0.35±0.02	---	---	---	0.18±0.08	0.17±0.02
[6]0.20±0.02	0.24±0.01	---	---	---	---
[7]0.13±0.03	0.38±0.03	---	---	-0.09±0.29	0.08±0.02

[1](Everett-Hincks *et al.*, 2005), [2](Brien *et al.*, 2010), [3](Lambe *et al.*, 2001), [4](Hatcher *et al.*, 2010), [5](Plush *et al.*, 2011), [6](Brown *et al.*, 2016), [7](Everett-Hincks & Cullen, 2009).

Variation

Low estimates for genetic and permanent environmental variances for maternal behavior score and litter survival have been recorded in Everett-Hincks *et al.* (2005). They also estimated the total phenotypic variance for MBS which was 3.62±0.34. The variation appears to be mostly due to temporary environmental effects. The low variation might be due to the fact that the flock was intensively selected for maternal ability. Lambe *et al.* (2001) reported estimates of genetic variance and permanent environmental variance for MBS which were larger than those reported in Everett-Hincks *et al.* (2005). The genetic variances were still considered to be small but significant. As in Everett-Hincks *et al.* (2005) the environmental variation seem to be the major source of variance. Brown *et al.* (2016) estimated a phenotypic variance of 0.68±0.01 for MBS and moderate to high genetic variance. The direct genetic variance which equals the heritability, is estimated to account for 20% of the phenotypic variance in Hatcher *et al.* (2010).

Breed differences

Comparisons between the intensively selected Suffolk and the more extensively bred Scottish Blackface have shown that Scottish Blackface ewes appear to be more affiliative and caring towards their young (Dwyer & Lawrence, 2000a; Pickup & Dwyer, 2011). Von Borstel *et al.* (2011) also had the hypothesis that the more intensively selected breeds would be poorer and less active mothers. However, in collation two out of five German breeds in the study did not abide by the theory. The authors reason that it might be due to a small and non-representative

observational group, or that the separation method measured the temperament of the dams instead of maternal behavior which was intended (von Borstel *et al.*, 2011).

It has also been found that Australian Superfine Merino ewes have a much poorer rearing ability than the Medium-wool Merino ewes. Within the first four weeks after birth the superfine ewes lost 29% of the lambs and the medium-wool ewes only 4%. The reason for the difference in lamb mortality was related to the inferior rearing performance of the superfine ewes and their lambs' lower birthweights. The reason for the severe difference in maternal ability is however unclear (Kuchel & Lindsay, 1999). Another Australian study tested the difference between four breeds; Border Leicester (BL), Glen Vale Border Leicester (GV, 18% Merino genes), crosses between the two mentioned above (XB) and Medium-fine-wool Merino (M). The maternal behavior was measured with several tests, amongst them; reactivity of ewes during tagging, early post-partum behavior and ewes with multiples also underwent a separation test. GV ewes performed best in most of the tests and thereafter followed the crosses XB as well abled mothers. BL was inferior to the GV in rearing ability but the poorest ability was found in the Merino ewes (Alexander *et al.*, 1990).

Selection strategies

Current selection

Breeding goals vary depending on breeds, production systems and countries. The goals are often directly related to production and reproduction. Sheep are often bred for temperament but not always for other behavioral traits (Boon *et al.*, 2008; Jansson, 2012; Meat & Livestock Australia & Australian Wool Innovation, 2013). In Sweden maternal traits are only calculated as a measure of the weight of the lambs and might not reflect the behavior per se (Jansson, 2012). In recommendations for the UK, maternal ability is an important estimated breeding value (EBV) for several breeds. It mostly reflects maternal care in form of supplying milk to the lamb and is also measured by weight of the lambs (Boon *et al.*, 2008). An ocular observation of expression of maternal care is only mentioned as a mean to select replacement ewes, no EBV is calculated (Boon *et al.*, 2008). Sheep Genetics Australia estimates breeding values for number of lambs weaned and maternal weaning weight as a measure of ewe maternal ability. This as well, does not directly include any behavioral measurements (Meat & Livestock Australia & Australian Wool Innovation, 2013).

Direct selection for lamb survival

Litter survival is estimated to have a low heritability so direct selection for the trait would not be able to reach a high genetic gain (Everett-Hincks *et al.*, 2005; Everett-Hincks & Cullen, 2009; Brien *et al.*, 2010; Plush *et al.*, 2011). Brien *et al.* (2010) still believe that litter survival could be used as a selection trait among progeny-tested sires and give a small genetic gain. The study also concluded that lamb survival may genetically decline if traits to reduce lamb mortality are not included in breeding programs (Brien *et al.*, 2010). The progress in breeding programs would most likely be slow and costly. That is why other indirect traits such as maternal performance are interesting for improvement of lamb survival.

Indirect selection

Maternal behavior score

All studies reviewed here report low to moderate genetic parameters for MBS (Table 1). Despite this some of them still argue that it might be of interest to include MBS as an indirect selection criterion for litter survival in breeding programs (Lambe *et al.*, 2001; Brown *et al.*, 2016). However, some authors do not agree that maternal behavior will have value as an indirect selection trait (Everett-Hincks *et al.*, 2005; Hatcher *et al.*, 2010; Plush *et al.*, 2011). Other authors claim that further research on the subject is needed to give a justified answer (Everett-Hincks & Cullen, 2009; Brien *et al.*, 2010).

Traits correlated to maternal behavior

Näsholm & Danell (1996) found that maternal ability has a positive correlation with lamb birth weight and mature ewe weight. Lambe *et al.* (2001) also recorded that higher (improved) MBS gave heavier lambs, the relation was however not significant. Maternal care in Merino sheep and wool quality and length were not significantly correlated. This indicates that selection for maternal ability will not affect wool traits (Plush *et al.*, 2011). Positive relations were found between MBS and litter number, indicating that maternal behavior is greater for more experienced ewes (Lambe *et al.*, 2001; Everett-Hincks & Cullen, 2009; von Borstel *et al.*, 2011). MBS was higher for ewes rearing multiples than ewes with single born lambs (Lambe *et al.*, 2001; Everett-Hincks *et al.*, 2005). However, it has also been suggested that selection for improved maternal care could result in more nervous ewes (Plush *et al.*, 2011).

Alternative selection traits

Matheson *et al.* (2012) investigated if lamb survival could be improved by selection of neonatal fitness and behavior as a trait of the lamb. The results revealed moderate heritability for these traits and appeared to have no detrimental effect on production traits. This suggests that selection would not only be possible but also efficient. Cloete *et al.* (2009) researched survival of lambs descended from divergent lines selected for rearing ability of multiples. The results indicate that selection for an indirect trait such as rearing ability of multiples could give genetic gain for improved lamb survival. Rectal temperature of the lamb, time taken for the lamb to bleat after being held by the farmer and length measurement from the nape of the neck to the tail base of the lamb have been estimated to have moderate to high correlation with lamb survival. These traits were estimated to improve accuracy of predicted genetic gain for lamb survival (Brien *et al.*, 2010).

Marker-assisted selection

Shumbosho *et al.* (2013) assessed the benefits of using genomic selection in breeding programs for small ruminants, as an alternative to traditional based on pedigree and phenotypic values. The prediction was constructed by using data to model breeding scenarios of traditional and genomic selection. The genomic selection scenario with best annual genetic gain (AGG) was 17.9% greater than the traditional selection for meat breeding programs.

AGG increased in all scenarios when genomic selection was incorporated (Shumbosho *et al.*, 2013). Further development of accuracy for genomic selection and prediction of genomic EBV is under investigation (Auvray *et al.*, 2014). Mapping of behavioral associated quantitative trait locus (QTL) based on single nucleotide polymorphism (SNP) markers have recently been executed by Hazard *et al.* (2014). Wang *et al.* (2015) examined mutations in the prolactin receptor gene (PRLR) in Hu sheep. PRLR is important for induction of maternal behavior. The study found significant differences in some maternal behavioral traits depending on PRLR genotype of the ewe.

Discussion

Maternal behavior score

Since the estimates of heritability and repeatability vary between studies as listed in Table 1, it is difficult to determine whether MBS would have a valuable role as indirect selection criterion for litter survival. However, all estimates for heritability and repeatability are favorable and some genetic gain for MBS is to be expected. Most estimates for genetic and phenotypic correlation between MBS and litter survival in Table 1 are small but positive, except for estimates recorded by Brien *et al.* (2010) and Everett-Hincks & Cullen (2009). A few authors do believe that despite the slow progress it might be of relevance to include either litter survival as a direct selection trait or maternal ability as an indirect trait (Lambe *et al.*, 2001; Brown *et al.*, 2016).

The genetic variation for MBS vary between moderately low to high (Lambe *et al.*, 2001; Hatcher *et al.*, 2010; Brown *et al.*, 2016). The very low variation in Everett-Hincks *et al.* (2005) was most likely reduced due to selection on maternal ability in the flock. The results could therefore be disregarded since it may not reflect average sheep populations. If the genetic variance for MBS is moderate to high it would suggest that selection of the trait would be beneficial and improvement of maternal behavior feasible. However, the low heritability in other studies (Table 1) contradicts this possibility. The main source of variation seem to be environmental (Lambe *et al.*, 2001; Everett-Hincks *et al.*, 2005).

To discuss whether or not to include maternal ability score as an indirect selection trait for lamb survival we must first consider what effects it could have on other traits. To design a sustainable breeding program all traits should be investigated for possible correlation, to enable a prediction of genetic response. Positive correlations have been found between MBS and lamb birth weight (Näsholm & Danell, 1996; Lambe *et al.*, 2001). Great birth weights could have negative effects on lambing ease and might increase lamb mortality at birth. However, positive correlations between MBS and ewe weight were also found. This could suggest that bigger lambs will be born to larger ewes and might not cause problems at parturition. Selection for MBS could also lead to ewes having more lambs per litter which might have detrimental effects on lamb survival if the litters become too large. The low to moderate repeatabilities for MBS (Table 1) could be due to multiparous ewes, having gained experience show improved maternal behavior (Lambe *et al.*, 2001; Everett-Hincks & Cullen,

2009; von Borstel *et al.*, 2011). It was found that higher MBS gave more nervous ewes (Plush *et al.*, 2011). This may depend on how the maternal behavior was measured. MBS could also measure reactivity to humans and not maternal ability, this would however give the opposite result.

The genetic progress is estimated to be slow and inefficient but nonetheless positive. The lack of financial benefits could be considered as the main issue in including MBS in breeding programs to increase litter survival. It would not be economically viable to include a trait that might cost more to incorporate than the economic benefits it could have on future productivity. It could also be difficult to implement a time consuming measurement such as MBS on commercial farms under practical conditions.

Breeds

Variation in expression of maternal ability is found within and between breeds. Merino ewes for example seem to exhibit poor maternal care towards their offspring (Alexander *et al.*, 1990; Kuchel & Lindsay, 1999). Maternal behavior was better for medium wool ewes compared with superfine Merino. This could indicate that more intensively bred strains or breeds show poorer expression in maternal behavior. Von Borstel *et al.* (2011) sought to confirm the detrimental effects on maternal ability of intense breeding but two out of five breeds did not support the hypothesis. Results to strengthen the theory is found in comparisons between Suffolk and Scottish Blackface (Dwyer & Lawrence, 2000a; Pickup & Dwyer, 2011). This suggests that current breeding programs may need to adjust for improved maternal ability and investigate possible unfavorable correlations. Further research on this subject is needed to confirm the theory. It is however clear that inclusion of maternal ability in breeding selection is more relevant in certain breeds than in others.

Breeding possibilities

Since studies indicate that MBS might not be an efficient selection trait for lamb survival other correlated traits could be more successful. Lamb vigor and behavior showed better results on improving lamb survival (Matheson *et al.*, 2012). Selecting for the ability of ewes to rear multiples also resulted in genetic progress for lamb survival (Cloete *et al.*, 2009). Other possible lamb traits are rectal temperature, length from crown to rump and time taken for the lamb to bleat. They all correlated with lamb survival but need to be researched further for possible use in breeding programs (Brien *et al.*, 2010).

Today selection based on genomic information for sheep is very limited but might be relevant in the near future. The possible use of genomic information for selection in sheep breeding programs is under development (Shumbosho *et al.*, 2013; Auvray *et al.*, 2014). The mapping of behavioral associated QTL might be a step towards including behavioral traits such as maternal behavior in genomic selection for sheep (Hazard *et al.*, 2014). Wang *et al.* (2015) believe that their findings of SNPs and mutation on the PRLR gene will further advance the possible use of marker-aided selection for maternal behavior of Hu sheep. Genomic selection

would increase the annual genetic gain and accelerate the genetic progress (Shumbosho *et al.*, 2013).

Conclusions

Heritability and repeatability for MBS were low to moderate and correlations with litter survival were also low. Modest genetic gain in selecting for MBS is to be expected but the progress will be slow. Research on the benefits of including maternal behavior in sheep breeding programs is relatively scarce and further research is needed. Investigation of other possible selection traits to increase litter survival would also be of interest. Another unsubstantiated theory that is lifted in this review is the possibility that current intense breeding leads to a decline in maternal behavior. An existing difference in maternal behavior between breeds can be concluded. Genomic based selection may simplify the inclusion of behavioral traits in future sheep breeding.

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