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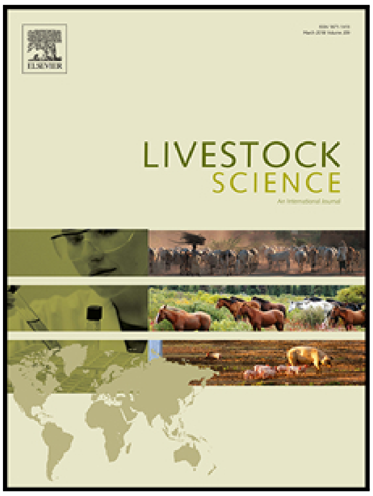

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Genetic associations of ewe body condition score and lamb rearing performance in extensively managed meat sheep

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Highlights

- New traits for lifetime resilience in maternal sheep breeding programmes studied
- BCS found to be heritable at certain points throughout the year and over time
- Relationships with traits associated with ewe maternal performance complex
- BCS and changes in condition can affect ability of ewes to conceive and rear lambs

Abstract

Many small ruminant production systems are relatively low input and rely heavily on animals grazing pastures often in extensive and harsh environmental conditions, unsuitable for any other type of agriculture. New breeding goal traits for lifetime resilience for maternal sheep breeding programmes have been investigated, focusing on body tissue mobilisation phenotypes and their genetic relationships with maternal production traits. Performance records of 8,355 Scottish Blackface ewes, from 2 extensively reared hill sheep flocks, collected over a 20-year period, were used to quantify relationships between body condition score (BCS) and the ewe's ability to successfully rear lambs. Between 14,000 and 25,000 data records per trait were available, measured across the annual sheep reproductive cycle. The pedigree file used for the analyses included sire and dam information for 50,207 animals. Most heritability estimates for the BCS traits - measured at key time points within the annual production cycle, or considering BCS changes between time points - were low, but significantly different from zero, ranging between 0.07 and 0.17. The heritability estimate for the number of lambs at pregnancy scanning was 0.09. Heritabilities for foetal loss from pregnancy scanning to lambing, lamb loss from lambing to weaning and number of lambs weaned were 0.02, 0.02 and 0.06, respectively. These estimates indicate that genetic control over the reproductive and lamb survival traits (expressed as a trait of the dam), is lower than that for BCS (and BCS changes) over the reproductive cycle. The genetic relationships amongst the BCS of ewes at pre-mating, pregnancy scan and at pre-lambing, with litter size at pregnancy scan and number of lambs weaned, were consistent. They indicate that ewes of higher body condition score (potentially over-fat, within the range recorded in these flocks) conceive, and rear, fewer lambs, with genetic correlations ranging between -0.18 and -0.58. However, post-weaning, animals with genetic propensity for greater gain in BCS from weaning to pre-mating produce larger litters and rear more lambs. In addition, the selection of ewes that lose less condition during pregnancy will reduce foetal losses. The results from this study paint a complex picture that should be interpreted in the context of specific management practices for extensively managed hill sheep, at critical times in their reproductive cycle. The traits relating to body tissue mobilisation, as assessed using BCS, are mostly heritable and their inclusion in future breeding programmes, to aid future selection for resilience, should be considered.

Keywords:

Body condition score; Lifetime resilience; Genetic parameters; Maternal sheep; Lamb production.

1. Introduction

Many small ruminant production systems are relatively low input and rely heavily on animals grazing pastures often in extensive and harsh environmental conditions, unsuitable for any other type of agriculture. With agriculture facing numerous challenges, including those associated with climate change and the rising costs of inputs, production from these grazing environments is predicted to become increasingly important in the future (Friggens et al., 2017, O'Mara, 2012). Despite the importance of these production systems, in terms of social, economic and environmental aspects, the overall small ruminant sector has been deemed vulnerable (Belanche et al., 2021). The challenges that the sector faces to improve its sustainability are numerous. Genetic breeding programmes associated with UK hill sheep production in these environments are already available to farmers, (Conington et al., 2001; Signet Sheepbreeder, 2023), with improved productivity and financial gains having been observed as a result of genetic selection based on these selection indices (Conington et al., 2006; Lambe et al., 2014). However, with the increasing challenges outlined above, future breeding strategies would benefit from the ability to identify and breed from robust and resilient animals to improve the sustainability of these systems further (Friggens et al., 2017; Sánchez-Molano et al., 2020).

Colditz and Hine (2016) and Berghof et al. (2019) highlight several definitions and interpretations of resilience and resilience-associated concepts, including robustness, in the literature. Young & Thomson (2014) suggest that the concept of both robustness and resilience should be considered in pastoral systems since ewes will inevitably encounter environmental challenges, but the severity and timing of these can be unpredictable. Ewes require a level of robustness, to deal with short-term challenges, but also a degree of resilience, to allow them to survive and remain productive in the medium to longer term. Hill ewes (such as Scottish Blackface ewes) must often deal with limited food availability and poor (and increasingly unpredictable) weather conditions for several months each year, particularly during periods of high energy demand (pregnancy and early lactation). The extensive nature of these environments means there is less opportunity for farmers to make changes in management to reduce the impact of poor environmental conditions, therefore it's important that ewes are resilient to face these challenges. To do this, many will mobilise body tissue reserves to meet the nutritional requirements of both her own needs and the demands of reproduction (Lambe et al., 2003; Lambe et al., 2005).

A simple and low-cost method of assessing these changes is body condition scoring (BCS), a subjective measure of fat and muscle cover in the loin region, based on a scale of 0 - 5 (Jefferies, 1961; Russel et al., 1969). Whilst traditionally used as a flock management tool for nutritional management, BCS has been found to be heritable at specific time points throughout the year and over time (Kenyon, et al., 2014; Walkom & Brown, 2017; Mace et al., 2018). However, the number of studies reporting genetic parameters remains relatively low. The influence that the ewe's BCS has on maternal production traits linked to fertility and productive longevity, such as lamb survival and the number of lambs she successfully rears, are also important relationships to consider, in terms of welfare and productivity. Previous studies, in cattle, have found BCS to be heritable and have also observed BCS, and BCS changes between events, to influence reproductive performance (Pryce et al., 2001; Roch et al., 2009).

The main objectives of this study were to a) investigate genetic parameters associated with body tissue mobilisation, based on body condition score traits, throughout the annual production cycle, b) assess genetic parameters for traits associated with ewe fertility and productive performance, and c) investigate the genetic and phenotypic relationships between body condition score traits and ewe fertility and productive performance, to help assess the potential for body condition related traits to be included in future hill sheep breeding programmes.

2. Materials and methods

2.1. Animals and Data Collection

All procedures involving animals for data collection were approved by an animal ethics committee at Scotland's Rural College (SRUC) and were performed under the United Kingdom Home Office licence following the regulations of the Animals Act 1986.

Data were available from 8,335 individual Scottish Blackface ewes reared on two extensively managed hill farms between 1999 and 2019. The ewes were reared under typical UK hill farm conditions on Castlelaw farm, in the Pentland hills, in Midlothian (n = 4,635 individual ewes) and on Kirkton farm, in the West Highlands, in Perthshire (n = 3,700 individual ewes). Both flocks have been performance recorded as part of a genetic improvement scheme since 1991 and 1996 respectively. The flocks are genetically linked through the use of common sires, as previously demonstrated by McLaren et al. (2012). More detailed descriptions of both the farms and flocks are given by Conington et al. (2006) and McLaren et al. (2012).

2.2. Ewe body condition score traits

BCS data were collected at each farm at pre-mating (PMBCS) in November; pregnancy scanning (SBCS) in February; pre-lambing (LBCS) in April; mid-lactation (MBCS) in June; and weaning (WBCS) in August. BCS was assessed on a 0-5 scale, as described by Russel et al. (1969), by different scorers on each farm. The data collected at each event were also used to assess the change in body condition between events. The traits investigated were the gain between pre-mating and pregnancy scanning (PM-S); between pregnancy scanning and pre-lambing (S-L); between pre-lambing and mid-lactation (L-M); between pre-lambing and weaning (L-W); and between weaning and the next pre-mating (W-PM). An additional period, between pre-mating and pre-lambing (PM-L) was also considered. There were no LBCS or MBCS data collected at Kirkton farm after 2006, with the exception of LBCS data collected in 2015. Ewes that were less than BCS 2 at pre-mating did not go on to be mated that year.

2.3. Ewe maternal performance

The traits relating to ewe maternal performance included those associated with the number of foetuses the ewe was carrying at pregnancy scanning (PScan); the number of foetuses lost between pregnancy scanning and lambing (FLoss); the number of lambs lost between lambing and mid-lactation (LLoss) and the number of lambs reared to weaning (LWean). All barren and the small number of triplet rearing ewes were removed from the Loss trait analyses.

2.4. Genetic analysis

The pedigree file used in the analyses had sire and dam information for 50,207 animals. Using ASReml 3.0 (Gilmour et al., 2009) variance components for each trait (genetic and phenotypic variances and heritability) were estimated using univariate analyses. Analyses were based on the following model:

$$y = Xb + Za + Wpe + e$$

Where *y* is the vector of phenotypic observations; *b* is the vector of fixed effects, consisting of ewe age, farm, year, lambs carried/reared, plus the interactions between farm and year and between farm and ewe age; *a* is the vector of random animal effects; *pe* is the vector of permanent environment effects; e is the vector of random residual effects, and X, Z and W are incidence matrices relating observations to their respective effects. Ewe age was the age of the ewe, in years (6 levels: 2 to $\geq$7) and farm was where the ewes were based (2 levels: Castlelaw and Kirkton). Number of lambs carried/reared was the number of feotuses the ewe was carrying from pregnancy scanning to lambing (4 levels: 0 to 3) or the number of lambs reared from lambing (3 levels: 0 lambs to 2 lambs). Number of lambs carried/reared was not fitted in the PMBCS model. Year was the year in which the data were collected (21 levels: 1999 to 2019). Interactions between farm and year and farm and ewe age were also fitted. For the change traits, a similar model was used with BCS at the initial event also included as a covariate. Each fixed effect was significant for the majority of traits and, to remain consistent, the same models were fitted across the different traits. However, to allow convergence, no *pe* random effect was fitted for WBCS or L-W. Additionally, the interaction between farm and ewe age was removed from the model used to analyse W-PM. Summary statistics for each BCS trait and covariates are given in Table 1.

Genetic and phenotypic correlations were then estimated between each BCS trait and the traits associated with ewe rearing performance (PScan, FLoss, LLoss and LWean), using bivariate models in ASReml 3.0 (Gilmour et al., 2009). The animal models used for the BCS traits were the same as described above. Analyses of the ewe rearing performance traits were based on the following model:

$$y = Xb + Za + Wpe + e$$

Where *y* is the vector of phenotypic observations; *b* is the vector fixed effects, consisting of ewe age, farm, year, initial lamb number, plus the interactions between farm and year and between farm and ewe age; *a* is the vector of random animal effects; *pe* is the vector of permanent environment effects; e is the vector of random residual effects, and X, Z and W are incidence matrices relating observations to their respective effects. All of the fixed effects were the same as those described previously for the BCS associated traits, with the exception of the initial lamb number, which was the number of lambs the ewe originally had (e.g. number of feotuses at pregnancy scanning for FLoss and the number of lambs born for for LLoss) (2 levels: 1 lamb or 2 lambs). The models for PScan and LWean did not include any lamb number effect. The PScan model included the ewe's pre-mating weight and PMBCS as covariates, however PMBCS was not fitted in the biviariate model associated between PScan and PMBCS. (Summary statistics are given in Table 1).

3. Results

3.1. Data summaries

Summaries of the data analysed, and the relevant covariates fitted in the models, are given in Table 1. The highest average raw body condition score value recorded across the flocks was at PMBCS recording event (2.91). The average fell to the lowest point at LBCS (2.66) before increasing towards the next pre-mating BCS (2.83) (Figure 1). The period between pregnancy scanning and pre-lambing had the highest BCS loss, (S-L = -0.14), with the most condition gained during the period between weaning and the next pre-mating (W-PM = 0.15). The overall averages for PSCAN and LWean were 1.28 and l.9 lambs respectively.

3.2. Genetic parameters

The univariate parameters for the BCS and maternal performance traits are given in Table 2. With the exception of WBCS and L-W (which had heritability estimates close to zero), low heritability estimates were observed for the remaining BCS traits ranging from 0.07 to 0.17, with permanent environment effects ranging from 0.04 to 0.16. The highest heritability estimates were associated with SBCS and W-PM (both 0.16). The heritabilities for the ewe maternal performance traits were also low, ranging from 0.02 to 0.09.

3.3. Relationships between body condition scores recorded at each event

Genetic and phenotypic correlations estimated between each BCS event are given in Table 3. High genetic correlations (≥0.88) were observed between each event, apart from those associated with WBCS, which were low and associated with high standard errors. The highest genetic correlation was observed between SBCS and LBCS (0.98). Phenotypic correlations were low to moderate (0.30 to 0.54), again with the exception of those associated with WBCS (which were all 0.01).

3.3. Relationships between body condition score traits and ewe maternal performance

The genetic and phenotypic correlations estimated between the BCS and ewe maternal performance traits are given in Table 4. Genetic correlations observed with PScan were low to moderate with the strongest relationships observed between PScan and LBCS (-0.48), PMBCS (-0.45) and W-PM (0.42). The lowest genetic correlations with PScan were associated with PM-S and PM-L (0.02). The phenotypic relationships between PScan and the BCS traits were low ranging from -0.38 (LBCS) to 0.10 (PMBCS).

For FLoss, the strongest genetic correlation was associated with PMBCS (0.40). The only other correlation with FLoss that was significantly different from zero was for PM-L (-0.28). Most of the remaining genetic correlations with FLoss were low and negative, ranging from -0.11 (LBCS) to -0.23 (MBCS) but associated with high standard errors. The correlations of FLoss with SBCS, WBCS and L-W were positive (0.04 - 0.29), but also associated with high standard errors. Phenotypic correlations with FLoss ranged from -0.08 to 0.09, with the negative correlations associated with BCS data collected from PMBCS through to L-M.

The genetic correlations estimated with LLoss were all positive (ranging from 0.03 to 0.34) apart from the negative correlation observed with W-PM (-0.25). The highest correlation was associated with PMBCS (0.34). Phenotypic correlations with LLoss were all close to zero, ranging from -0.01 to 0.05.

The strongest genetic correlations estimated for LWean were with PMBCS (-0.58) and W-PM (0.30). The strongest phenotypic correlation with LWean was observed for W-PM (-0.31), with the remaining estimates ranging from -0.09 to 0.09.

4. Discussion

4.1. Body tissue mobilisation throughout the productive year

The changes observed in BCS throughout the productive year are logical when considering the different environmental conditions and nutritional demands hill ewes experience throughout pregnancy through to when the lambs are weaned and then on to the next mating. The decrease in BCS from pre-mating to pregnancy scanning and then on to pre-lambing, has been observed in a number of previous studies, including those of Walkom and Brown (2017) and Mace et al. (2018). Similar changes were also seen when tissue changes were assessed using computer tomography, with both carcass and internal fat depots of hill ewes being depleted during pregnancy, and muscle levels also being mobilised to some extent once fat reserves had fallen to very low levels (Lambe et al. 2003). The mobilisation of body tissues from mating to lambing is due to the negative energy balance associated with this physiological phase. The often-harsh environmental conditions associated with this time period (winter) and reduced grazing availability and quality, when combined with the gradual increase in nutrient demand to support the development of the foetus(es), all impact on the tissue reserves of the hill ewe. In addition, Flay et al. (2021) and Morgan-Davies et al. (2008) highlight the importance of the ewe's BCS at pre-mating and pregnancy scanning respectively, with those at the lower end of the scale at a greater risk of premature culling and mortality. The average rate of depletion was greater between pregnancy scanning and lambing, when compared to the rate observed between pre-mating and pregnancy scanning. This is likely influenced by the fact that as the pregnancy progresses, the size, and therefore demands, of the feotus(es) grows, particularly in the later stages before parturition.

The lowest average BCS was recorded at pre-lambing, but the subsequent averages at mid-lactation and weaning were only up to 0.02 of a score different from the pre-lambing value. When compared to the averages observed by Mace et al. (2018), although the pre-lambing BCS was similar in both studies (approximately 2.6), the changes in BCS from lambing up to weaning were slightly different. There were also differences in terms of breed and management, grazing type and grazing availability throughout the year (particularly during the summer months during which the vegetation can be affected by drought conditions). The drought conditions experienced may have had an influence on the timing of when the lambs were weaned (Mace study = lambs weaned in late June, current study = lambs weaned in August) (Mace et al., 2018; Gonzalez-Garcia et al. 2014). However, when assessed by computer tomography, Lambe et al. (2003) also observed a similar pattern to Mace et al. (2018) for most tissue types, with the lowest point often associated with mid-lactation (in June), but the ewes associated with this study were from Castlelaw farm only (and not Kirkton) therefore different management practices between the farms could also be influential (McLaren et al. 2012). Walkom and Brown (2017) and Tait et al. (2018) did not have any records available for mid-lactation, but both observed the lowest average BCS at weaning, potentially influenced by the effects of dry and hot summer conditions experienced in Australia and New Zealand.

The recovery in body condition between weaning and the next mating was on average less in the present study when compared to the average observed by Mace et al. (2018), but as highlighted earlier, this could be influenced by factors such as the length of recovery time (ewes in the present study had approx. a month less recovery time) and grazing quality and availability during this period. Typically, grass growth tends to slow down and the quality reduces in the hill areas during late autumn in Scotland whereas the rangelands in France tend to regreen in the autumn months, after a period of no growth during the hot and dry summer months (Gonzales-Garcia et al., 2014). However, as highlighted above, it is important to note that when comparing results from different studies at similar events, particularly those after lambing, care should be taken as they may not actually be directly comparable due to the differences in timing and in the age of the lambs (for example when they are weaned).

4.2. Genetic parameters

The results from this study have confirmed that many of the traits associated with body tissue mobilisation in Scottish Blackface ewes, as assessed by BCS, were heritable. Notable exceptions were those associated with WBCS and L-W, which were found to have no significant genetic component, with heritability estimates close to zero. This suggests that any phenotypic variation in these traits was not due to genetics but influenced by other environmental factors. In fact, the phenotypic variances for these two traits were slightly higher than the other BCS traits, which suggests increased non-genetic influences on variation in these traits associated with BCS at weaning. The heritabilities of the remaining BCS collected at each recording event ranged from 0.10 to 0.17, similar to those estimated by Everett-Hincks and Cullen (2009), but lower than those observed by Shackell et al. (2011) and Walkom and Brown (2017) (0.21 to 0.30). The repeatability of these traits ranged from 0.22 to 0.27, slightly lower than previous estimates by Shackell et al. (2011) and Walkom and Brown (2017), but nonetheless suggest there is a low level of consistency within each ewe across the different reproductive seasons. The genetic correlations estimated between each BCS event were all $\geq$0.88, with the highest estimate between SBCS and LBCS (0.98), very similar to the correlation of 0.95 observed by Everett-Hincks and Cullen (2009) and close to the range of values observed by Walkom and Brown (2017). The high genetic correlations indicate the different BCS traits are under similar genetic control. The BCS change traits range of heritabilities were also low (0.07 to 0.16), similar to those observed by Mace et al. (2018) but higher than those observed by Walkom and Brown (2017) (0.03 to 0.06). W-PMchange was associated with the highest repeatability (0.32) with the remaining change traits less repeatable (0.11 to 0.19). For the traits associated with ewe maternal performance, heritability estimates observed for LLoss and LWean were very similar to those previously estimated by Conington et al. (2001) and Lambe et al. (2008), using earlier data recorded from the same population. Those associated with PScan and FLoss have not been estimated before for this population, but the estimates were in close agreement with those observed by Brown et al. (2021) (for both PScan and Floss) and Hickey et al. (2022) (for PScan). Results from both the present study and that of Brown et al. (2021) found an average foetal loss of 7% after scanning, but the genetic component to this was very small.

4.1. Relationships between body condition and ewe maternal performance

When assessing the relationships between the BCS traits and PScan, the genetic correlations indicated that ewes that have genes associated with gaining more condition between weaning and pre-mating also had a similar genetic tendency for higher pregnancy scan results and higher numbers of lambs subsequently weaned. Few studies have looked at the genetic component relating to BCS change between weaning and pre-mating, although Mace et al. (2019) did observe a positive, though not significant, relationship between this trait and prolificacy. However, the negative genetic correlations estimated between PMBCS and PScan suggest higher pregnancy scan results are associated with ewes with lower condition scores at pre-mating. Even though this appears to be counter-intuitive, it does suggest that within the constraints of acceptable BCS levels for management of hill sheep (i.e. with the majority of animals having >BCS 2+), at the genetic level, more prolific ewes have the genetic propensity to be leaner. Similar observations were seen between PMBCS and LWean, suggesting the relationship between PMBCS and overall lambs reared is consistent. Negative genetic relationships were also observed with BCS at scanning and pre-lambing (SBCS and LBCS) and the number of lambs at both pregnancy scanning and weaning. The relationships associated with BCS at marking and weaning (MBCS and WBCS) were low and positive, but not significantly different from zero. The negative relationships observed in the current study (associated with PMBCS, SBCS and LBCS) differ from the positive relationships observed previously by Walkom (2014) and Walkom and Brown (2017), as well as the relationships with SBCS and LBCS estimated by Everett-Hincks and Cullen (2009). However, studies by Lambe et al. (2005, 2008) also observed negative genetic correlations between fat levels of Scottish Blackface animals (when measured by computer tomography) at pre-mating and both litter size at birth and LWean. The genetic relationship between ewe condition and traits associated with numbers of lambs produced by the ewe therefore seems to be complex. The results from the present study suggest that when considering the Scottish Blackface breed, careful management of genetically over-fat animals at pre-mating, and throughout pregnancy, is required, otherwise lower lamb numbers will persist. The phenotypic correlations estimated between PMBCS and both PScan and LWean were small but positive and confirms previous findings observed by Gunn et al. (1991) and Kenyon et al. (2014), although both highlight that this relationship can be dependent on specific ranges of BCS, depending on the breeds involved. Kenyon et al. (2014) provide evidence of studies which have found that both low and high BCS can influence a number of factors including reducing ovulation rate, increasing ova and embryonic loss and reducing conception rates, all of which ultimately lead to whether the ewe becomes pregnant or not and, if she has become successfully pregnant, whether she manages to maintain the pregnancy until parturition.

However, once the ewe has lambed, the correlations observed in the present study suggests those that have higher BCS change (L-M and L-W), genetically, have higher litter sizes and rear more lambs due to the positive relationships observed with LWean (and PScan). This differs to the estimates observed by Mace et al. (2019), who found no significant genetic relationship between BCS change between lambing and suckling and prolificacy, and Walkom and Brown (2017) where the relationship between L-W and LWean (and lamb survival) was strongly negative. The negative relationship indicates that selecting ewes that gain condition during this period will reduce the number of lambs weaned. The variation between the present study and those by Mace et al. (2019) and Walkom and Brown (2017) may be influenced by environmental characteristics during the summer months, particularly the hot and dry Mediterranean-type climate, as highlighted earlier. Walkom and Brown comment that there was a range of environmental conditions across the eight research sites in their study, including some that also experienced hot and dry summers, similar to those experienced by Mace et al. (2018). This would suggest that ewes that genetically lose condition during this period of restricted grazing availability, mobilise more energy to successfully rear their lambs to weaning, when faced with this type of climatic conditions. In the present study, however, the Northern European, temperate climate, meant that that summer months coincided with improved grass growth and grazing quality, therefore ewes that manage to increase their tissue levels during this period also manage to successfully rear more lambs.

The relationships with the lamb Loss traits (expressed as a trait of the ewe) imply ewes with a genetic tendency to gain condition between weaning and mating also tended to lose less lambs between pregnancy scanning and lambing and between lambing and weaning. There was also a similar relationship observed between PM-L and FLoss, with those gaining (or losing less) body condition during pregnancy losing less foetuses. Observations by McCoard et al. (2020)

indicated that avoiding BCS loss during pregnancy was important to support lamb survival. In the present study, this would agree with the relationship between PM-L and FLoss. However, the relationship with lamb survival, once born (LLoss), was less clear. Phenotypically, the relationship was similar to the that observed with FLoss, but the genetic relationship was positive, indicating that those gaining (or losing less) BCS during pregnancy also had a tendency to lose more lambs after they were born. However, the positive correlation estimated was not significantly different to zero, so caution should be taken when interpreting this particular result. When considering lamb survival as a proportion of those reared to weaning compared to those born, Mace et al. (2019) observed a moderately strong negative genetic correlation with W-PM.

5. Conclusion

Overall, this study has found that traits relating to body tissue mobilisation, as assessed using BCS, are mostly heritable and their inclusion in future hill sheep breeding programmes, to aid future resilience, should be considered. However, the results and some of the relationships observed with traits associated with productive longevity and fertility, in terms of the number of lambs conceived and reared to weaning and lamb survival traits (associated with lamb losses, expressed as a trait of the ewe), are complex. The genetic relationships observed amongst BCS of ewes at pre-mating, pregnancy scanning and pre-lambing, with litter size at pregnancy scan and the number of lambs weaned were consistent, indicating that ewes of higher body condition (potentially over-fat) conceive, and rear, fewer lambs. However, after lambing, selecting ewes who gain BCS, particularly during the period between weaning to pre-mating, will result in higher litter sizes and more lambs. In addition, the selection of ewes that lose less condition during pregnancy will result in reduced feotal losses. These results should be interpreted in the context of specific management practises for extensively managed hill sheep, in temperate climates, at critical times in their reproductive cycle.

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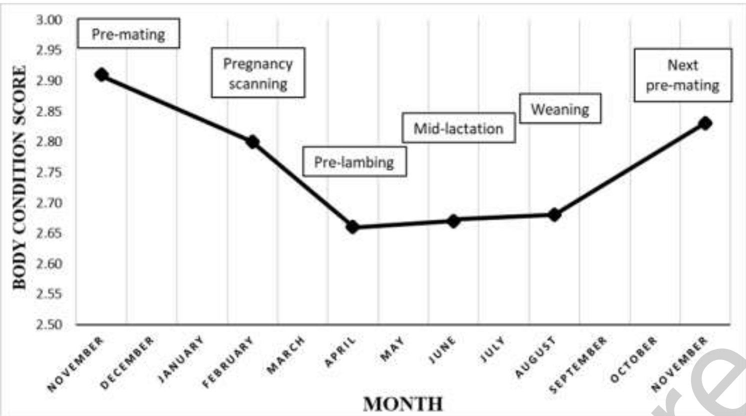

Figure 1. Average raw body condition scores (BCS), across both farms, at each event

Table 1 Summary of the body condition score (BCS) and ewe maternal performance traits included in the analyses.

Trait	Description	Count	Min.	Max.	Mean	S.D.
Body condition score						

PMBCS	Pre-mating (score)	23,816	1.0	5.0	2.91	0.36
SBCS	Pregnancy scan (score)	20,691	1.25	5.0	2.80	0.33
LBCS	Pre-lambing (score)	14,936	1.0	4.0	2.66	0.34
MBCS	Mid-lactation (score)	14,895	1.25	4.5	2.67	0.43
WBCS	Weaning (score)	23,031	1.0	5.0	2.68	0.48
Body condition score change						
PM-S	Pre-mating to Pregnancy scan (score)	20,590	-2.0	2.0	-0.12	0.35
S-L	Pregnancy scan to Pre-lambing (score)	14,265	-2.25	1.0	-0.14	0.32
PM-L	Pre-mating to Pre-lambing (score)	14,865	-2.25	1.5	-0.28	0.42
L-M	Pre-lambing to Mid-lactation (score)	14,105	-1.50	2.0	-0.05	0.39
L-W	Pre-lambing to Weaning (score)	14,343	-2.25	2.75	0.04	0.55
W-PM	Weaning to next Pre-mating (score)	13,827	-2.75	3.0	0.15	0.57
Ewe maternal performance traits						
PScan	Pregnancy scan result (count)	25,068	0	3	1.28	0.66
FLoss	Foetal loss: Pregnancy scan to lambing (count)	22,293	0	2	0.07	0.31
LLoss	Lamb loss: Lambing to Mid-lactation (count)	22,105	0	2	0.17	0.41
LWean	Lambs reared to weaning (count)	23.938	0	2	1.09	0.67
Additional covariates						
PMWT	Pre-mating live weight	24,051	28.0	83.0	52.04	7.12

Table 2 Direct additive genetic (σ^2_a), permanent environment (σ^2_{pe}) and phenotypic (σ^2_p) variances**,** heritabilities (h^2) and permanent environment effects (*pe*) for each trait investigated. Standard errors in parentheses

Trait	σ^2_a	σ^2_{pe}	σ^2_p	h^2	*pe*
PMBCS	0.01 (0.001)	0.008 (0.001)	0.10 (0.001)	0.14 (0.01)	0.08 (0.01)

SBCS	0.01 (0.001)	0.007 (0.001)	0.08 (0.001)	0.17 (0.01)	0.09 (0.01)
LBCS	0.01 (0.001)	0.01 (0.001)	0.08 (0.001)	0.16 (0.02)	0.12 (0.01)
MBCS	0.01 (0.001)	0.01 (0.001)	0.11 (0.001)	0.10 (0.01)	0.13 (0.02)
WBCS	0.0004 (0.0004)	-	0.18 (0.002)	0.002 (0.002)	-
PM-S	0.006 (0.001)	0.003 (0.001)	0.06 (0.001)	0.11 (0.01)	0.04 (0.01)
S-L	0.004 (0.001)	0.003 (0.001)	0.06 (0.001)	0.07 (0.01)	0.05 (0.01)
PM-L	0.008 (0.001)	0.005 (0.001)	0.07 (0.001)	0.12 (0.01)	0.07 (0.01)
L-M	0.007 (0.001)	0.004 (0.001)	0.09 (0.001)	0.07 (0.01)	0.04 (0.01)
L-W	0.001 (0.001)	-	0.19 (0.002)	0.004 (0.004)	-
W-PM	0.02 (0.002)	0.02 (0.001)	0.10 (0.001)	0.16 (0.02)	0.16 (0.02)
PScan	0.03 (0.004)	0.02 (0.004)	0.39 (0.004)	0.09 (0.01)	0.06 (0.01)
FLoss	0.002 (0.0005)	0.0003 (0.001)	0.09 (0.001)	0.02 (0.005)	0.003 (0.01)
LLoss	0.003 (0.0007)	0.0007 (0.001)	0.14 (0.001)	0.02 (0.01)	0.01 (0.01)
LWean	0.03 (0.003)	0.003 (0.003)	0.42 (0.004)	0.06 (0.01)	0.01 (0.01)

PMBCS = Pre-mating BCS; SBCS = Pregnancy scan BCS; LBCS = Pre-lambing BCS; MBCS = Mid-lactation BCS; WBCS = Weaning BCS; PM-S = Pre-mating to Pregnancy scan BCS change; S-L = Pregnancy scan to Pre-lambing BCS change; PM-L = Pre-mating to Pre-lambing BCS change; L-M = Pre-lambing to Mid-lactation BCS change; L-W= Pre-lambing to Weaning BCS change; W-PM = Weaning to Pre-mating BCS change; PScan = Pregnancy Scan result; FLoss = Foetal loss (Pregnancy scan to Lambing); LLoss = Lamb loss (Lambing to Weaning); LWean = Number of lambs weaned

Table 3 Genetic (above diagonal) and phenotypic (below diagonal) correlations estimated between each Body Condition Score recorded at Pre-mating (PBCS), Pregnancy Scanning (SBCS), Pre-lambing (LBCS), Mid-lactation (MBCS) and Weaning (WBCS). Standard errors in parentheses

Trait	PBCS	SBCS	LBCS	MBCS	WBCS

PBCS		0.91 (0.01)	0.88 (0.02)	0.92 (0.02)	0.16 (0.22)
SBCS	0.50 (0.01)		0.98 (0.01)	0.92 (0.02)	0.23 (0.21)
LBCS	0.41 (0.01)	0.54 (0.01)		0.93 (0.01)	0.06 (0.24)
MBCS	0.30 (0.01)	0.37 (0.01)	0.44 (0.01)		0.36 (0.21)
WBCS	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	

Table 4 Genetic (r_g) and phenotypic (r_p) correlations estimated between traits associated with body condition score (BCS) and ewe maternal performance. Standard errors in parenthesis.

Trait	PScan		FLoss		LLoss		LWean	
	r_g	r_p	r_g	r_p	r_g	r_p	r_g	r_p
PMBCS	-0.45 (0.05)	0.10 (0.01)	0.40 (0.08)	-0.03 (0.01)	0.34 (0.09)	-0.01 (0.01)	-0.58 (0.04)	0.09 (0.01)
SBCS	-0.18 (0.05)	0.03 (0.01)	0.04 (0.09)	-0.04 (0.01)	0.14 (0.09)	-0.02 (0.01)	-0.26 (0.05)	0.03 (0.01)
LBCS	-0.48 (0.05)	-0.38 (0.01)	-0.11 (0.11)	-0.08 (0.01)	0.22 (0.10)	-0.03 (0.01)	-0.18 (0.06)	0.03 (0.01)
MBCS	0.05 (0.07)	-0.05 (0.01)	-0.23 (0.12)	0.09 (0.01)	0.08 (0.12)	0.04 (0.01)	0.12 (0.08)	-0.09 (0.01)
WBCS	0.37 (0.29)	-0.01 (0.01)	0.11 (0.38)	0.00 (0.01)	0.46 (0.47)	-0.01 (0.01)	0.19 (0.28)	-0.03 (0.01)
PM-S	0.02 (0.06)	-0.01 (0.01)	-0.20 (0.10)	-0.03 (0.01)	0.03 (0.11)	-0.01 (0.01)	0.07 (0.01)	0.03 (0.01)
S-L	-0.14 (0.08)	-0.14 (0.01)	-0.13 (0.13)	-0.02 (0.01)	0.20 (0.14)	-0.02 (0.01)	-0.03 (0.08)	0.03 (0.01)
PM-L	0.02 (0.06)	-0.13 (0.01)	-0.28 (0.11)	-0.03 (0.01)	0.17 (0.11)	-0.03 (0.01)	0.14 (0.07)	0.05 (0.01)

L-M	0.22 (0.07)	0.02 (0.01)	-0.21 (0.13)	-0.05 (0.01)	0.06 (0.13)	0.05 (0.01)	0.23 (0.08)	-0.08 (0.01)
L-W	0.41 (0.27)	0.00 (0.01)	0.29 (0.40)	0.00 (0.01)	0.25 (0.40)	-0.01 (0.01)	0.35 (0.29)	-0.01 (0.01)
W-PM	0.42 (0.05)	-0.01 (0.01)	-0.19 (0.10)	0.04 (0.01)	-0.25 (0.11)	-0.01 (0.01)	0.30 (0.07)	-0.31 (0.01)

PMBCS = Pre-mating BCS; SBCS = Pregnancy scan BCS; LBCS = Pre-lambing BCS; MBCS = Mid-lactation BCS; WBCS = Weaning BCS; PM-S = Pre-mating to Pregnancy scan BCS change; S-L = Pregnancy scan to Pre-lambing BCS change; PM-L = Pre-mating to Pre-lambing BCS change; L-M = Pre-lambing to Mid-lactation BCS change; L-W= Pre-lambing to Weaning BCS change; W-PM = Weaning to Pre-mating BCS change; PScan = Pregnancy Scan result; FLoss = Foetal loss (Pregnancy scan to Lambing); LLoss = Lamb loss (Lambing to Weaning); LWean = Number of lambs weaned

Disclosures

The authors declare there are no conflicts of interest.

Declaration of Competing Interest

The authors declare there are no conflicts of interest.

Sample CRediT author statement

Ann McLaren: Writing - Original Draft, Formal analysis, Investigation, Methodology **Nicola Lambe**: Writing - Review & Editing, Supervision, Conceptualization, **Joanne Conington**: Writing - Review & Editing, Conceptualization, Supervision, Funding acquisition, Project administration.

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