GRAPHICAL MODELLING OF THE RELATIONSHIP BETWEEN BODY RESERVES AND YEARLING REPRODUCTION IN MATERNAL SHEEP

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SUMMARY

The underlying causal relationship between traits associated with energy reserves and yearling reproduction is often a cause of conjecture within the sheep industry in part due to anecdotal evidence often mistaking phenotypic associations with genetic. The use of graphical models to disentangle the underlying causal relationships between traits associated with energy reserves and yearling reproduction showed that selection for sires with high post-weaning fat and muscle will have little impact on the reproductive performance of the resulting progeny as yearling dams.

INTRODUCTION

Body weight and traits associated with body composition and energy reserves (fat and muscle) are important components of breeding objectives in sheep. These traits influence the amount of saleable meat and therefore have a direct economic value to the production system. However, the economic value placed on fat to produce a leaner carcase is at odds with the desired direction of change in fat as an indirect selection criterion for other traits, primarily reproductive performance and maternal efficiency. Previous studies have illustrated that body weight and body composition traits are associated with reproductive performance. The relationship between these traits and reproduction can be moderate at the phenotypic level but is often lower at the genetic level (Walkom *et al.* 2014; Walkom and Brown 2016).

Mixed effects models (often solved using REML) have been commonly used to estimate the associations between the traits at both a phenotypic and genetic level. However, such estimates indicate a correlation between traits rather than discover or define underlying causality. An alternative way to model the association between multiple traits is using graphical models (Valente *et al.* 2011). Graphical models, such as structural equation models and Bayesian networks including Incremental Association Markov Blankets (IAMB) (Tsamardinos *et al.* 2003), attempt to model all possible pathways in which two traits are associated. Hence, they provide insight into possible causal relationships that may exist, rather than association indicated by correlation alone (Valente *et al.* 2011). In this study, we use a graphical model to explore the underlying causal relationship between traits associated with energy reserves and yearling reproduction at both the phenotypic and genetic levels.

MATERIALS AND METHODS

Data used for the study were provided by maternal sheep breeders to Sheep Genetics as part of the routine LAMBPLAN genetic evaluation (Brown *et al.* 2007). The analysis focussed on six core traits: post-weaning weight (PWT), post-weaning ultrasound fat (PCF*) and eye muscle depth (PEMD*), yearling conception (YCON), yearling number of lambs born (YNLB) and yearling number of lambs weaned (YNLW) (Table 1).

Statistical Analysis. For each trait phenotypic, residual and genetic variances were estimated from univariate animal models. A series of bivariate analyses where then used to estimate correlations between traits. The initial genetic analyses were conducted using ASReml (Gilmour *et al.* 2009)

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using a pedigree 22 generations deep and containing 674,028 animals. The model fitted to the post-weaning traits had fixed effects of contemporary group (as per Brown and Swan 2016), birth and rearing type group (SS, MS, MM), dam age (years), and linear and quadratic age terms. Unlike the model for standard Sheep Genetics traits, weight was not fitted as a covariate for the scan traits (represented by *). The permanent environment of the dam was also fitted as a random effect. Yearling reproduction traits were adjusted for a contemporary group, which was formed based on site, flock, year grouping and developmental factors as discussed by Bunter *et al.* (these proceedings).

Table 1. Summary of records available and genetic parameters from a univariate animal model for maternal sheep breeds. Phenotypic variance (σ^2_p), direct additive variance (σ^2_a), maternal permanent environment variance (σ^2_c), residual variance (σ^2_e) and heritability (h^2)

Trait	Records	Mean	SD	σ^2_p	σ^2_a	σ^2_c	σ^2_e	h^2
PWT	279,872	45.70	8.98	25.1	5.18	2.27	17.63	0.29 ± 0.01
PCF*	282,251	3.20	1.31	0.61	0.13	0.02	0.46	0.27 ± 0.01
PEMD*	263,555	26.70	4.14	6.20	1.42	0.32	4.45	0.32 ± 0.01
YCON	68,669	0.90	0.35	0.06	0.01	-	0.06	0.08 ± 0.01
YNLB	68,085	1.20	0.70	0.33	0.02	-	0.31	0.07 ± 0.01
YNLW	51,496	0.90	0.72	0.37	0.02	-	0.35	0.05 ± 0.01

Graphical Modelling. A subset of the data were used in the graphical model analyses, restricted to animals with a phenotype for all 6 traits (20,093 animals). For the 'genetic' graphical model sires with single trait breeding values, calculated from the univariate analysis, for all 6 traits were used (2,261 sires). The graphic models in Figures 1 and 2 provide a graphical representation of Bayesian networks at the phenotypic and genetic (sire) levels, respectively, and were developed using the bnlearn package implemented in R (Scutari 2010). The networks were estimated using a constraint-based structure learning algorithm based on the Markov blanket detection algorithm, which is based on a two-phase selection scheme (a forward selection followed by an attempt to remove false positives) (IAMB, Tsamardinos *et al.* 2003). The need for every animal to have an observation for all traits resulted in the use of YNLB and YNLW instead of the component traits as per Bunter *et al.* (these proceedings). The probability of the connections (strength & direction) between the trait nodes was estimated using bootstrap sampling with the IAMB learning algorithm (Friedman *et al.* 1999).

RESULTS AND DISCUSSION

Phenotypic association. The phenotypic correlations from the bivariate analysis are shown in Table 2. Moderate to strong phenotypic correlations exist between the post weaning traits (PWT, PCF*, PEMD*) and between the reproduction traits (YCON, YNLB, YNLW). However, the correlations between the two trait groups were weak.

The graphical model based on the phenotypic associations, using raw phenotypes, an indication of the observed variation, is represented in Figure 1. PCF* has a causal effect on PWT. Thus, changes in PCF* will cause a change in the PWT, but changes in PWT can occur without a responding change in PCF*. The relationship for PCF* on PEMD* is also causative, with PCF* having both a direct and indirect association via PWT on PEMD*. The graphical model identifies no direct causative effect of PCF* or PEMD* on the yearling reproduction traits. The graphical model shows that once you condition on PWT (remove variation associated with PWT), changes in PCF* or PEMD* had no impact on yearling reproduction.

Table 2. Estimates of phenotypic (above diagonal) and genetic correlations (below diagonal) between body composition and yearling reproduction traits

	PWT	PCF*	PEMD*	YCON	YNLB	YNLW
PWT		0.48 ± 0.01	0.63 ± 0.01	0.07 ± 0.01	0.11 ± 0.01	0.09 ± 0.01
PCF*	0.42 ± 0.01		0.49 ± 0.01	0.05 ± 0.01	0.06 ± 0.01	0.04 ± 0.01
PEMD*	0.58 ± 0.01	0.51 ± 0.01		0.06 ± 0.01	0.07 ± 0.01	0.07 ± 0.01
YCON	0.04 ± 0.04	0.09 ± 0.04	0.06 ± 0.04		0.60 ± 0.01	0.43 ± 0.01
YNLB	0.06 ± 0.04	0.07 ± 0.04	-0.03 ± 0.04	0.69 ± 0.03		0.64 ± 0.01
YNLW	0.17 ± 0.06	0.09 ± 0.06	0.08 ± 0.05	0.70 ± 0.05	0.78 ± 0.04	

The ability to achieve conception (YCON) has a causal effect on values for NLB and NLW, as expected (Figure 1). The relationship from YCON and YNLW to PWT indicates that there is a phenotypic association between these traits. However, the direction of the relationship shows that the mechanisms behind increasing fertility and number of lambs weaned is associated with heavier PWT but increasing PWT will not necessarily cause a response in YCON or YNLW. The causative relationship of PWT on YNLB suggests increased weight, possibly as an indicator of maturity, is leading to increased litter sizes.
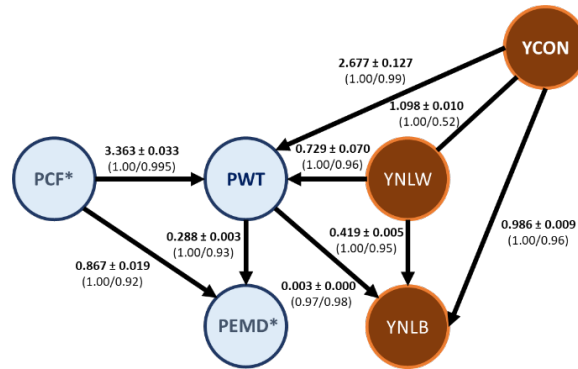

Figure 1. Graphical model of the phenotypic relationship between body composition and yearling reproduction. Size of the effect in bold with the probability of the relationship and then direction of causation using bootstrap techniques shown in parentheses

Genetic Association. The genetic correlations between the post weaning traits and the reproduction traits were weak in maternal breeds (Table 2), which relative to other breeds (eg. Merino) are heavier and fatter at young ages. This suggests that genetic selection for post-weaning body composition is likely to have a limited impact on yearling reproduction. The graphical model of the genetic association between the traits (Figure 2) is very different to Figure 1, indicating that the relationships are different at the genetic level. As observed in the phenotypic model (Figure 1) the association between the post-weaning traits remains strong but the causative direction between the traits could not be determined. A causative association between PWT and YNLW was detected and whilst the association was highly probable, the observed effect was very small, with a 1 kg increase in the sires's PWT breeding value (EBV) associated with an increase of only 0.002 in the sire's YNLW breeding value. An indirect association, via PWT, between PCF* and NLW would only see an extra 0.000128 lambs weaned per ewe joined for every extra (genetic) mm of PCF*. Variation in genetic merit for post-weaning traits is largely independent of genes which affect ovulation rate, litter size or lamb survival (Bunter *et al.,* these proceedings). The causative nature of YNLB and YCON on YNLW also means that the association between post-weaning traits and YNLW is due to the litter survival component of YNLW and not the variation associated with

fertility or litter size. This may be related to known associations between lamb birth weight (which affects survival) and post-weaning development traits (Bunter *et al.,* these proceedings).
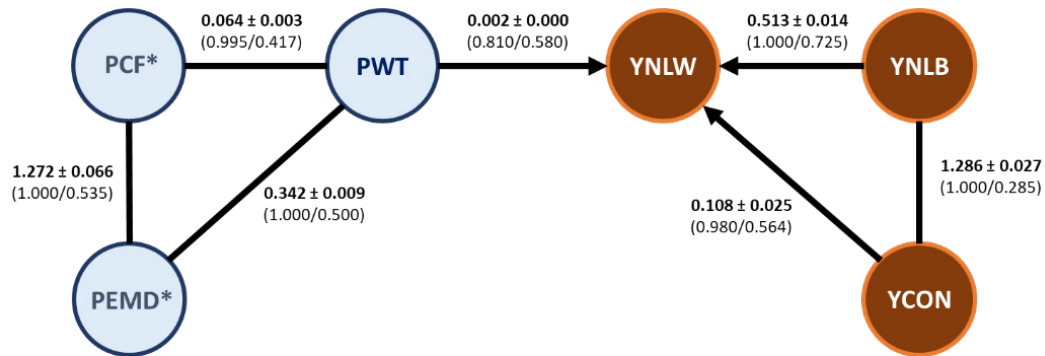

Figure 2. Graphical model of the genetic (sire breeding values) relationship between body composition and yearling reproduction. Size of the effect in bold with the probability of the relationship and then direction of causation using bootstrap techniques shown in parentheses

CONCLUSIONS

This study shows that modelling the relationship between body composition and yearling reproduction can be complex and not simple to interpret and the association between traits, and the causative associations between the traits, are strongly associated with the ability to disentangle the environmental and genetic components. In both phenotypic and genetic graphical models the effect of PCF* and PEMD* appears to be moderated through PWT. As has been shown from the genetic correlations and the graphical modelling, selection for higher PCF* and PEMD* sires will have little direct genetic impact on the reproductive performance of the resulting progeny as yearling dams, although it may influence the ease with which target weights are met pre-joining.

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