

CONTRIBUTIONS FROM GENETIC GROUPS AND OUTCROSSING TO COMPONENTS OF REPRODUCTION IN MATERNAL SHEEP BREEDS

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SUMMARY

Industry data for traits included in the new multi-trait genetic evaluation for reproductive traits provided by Sheep Genetics were used to investigate variation due to sub-populations (genetic groups) and due to outcross ewe genotypes in maternal sheep breeds. Substantial variation due to genetic groups (gg^2 : typically 11-30% of the phenotypic variance) for traits reflecting development (*eg* weight, condition score, muscle depth) were not accompanied by comparable variation for reproductive traits (gg^2 : 0-8%). Variation due to outcross ewe genotypes ranged from 0 to 8% across traits, being highest for adult ewe weight (8%) and yearling conception (6%) traits, which are expected to be affected by heterosis. Accommodating these sources of variation appropriately may be important for the genetic evaluation of data affected by admixture of populations.

INTRODUCTION

Two key issues for genetic evaluation of reproductive traits for maternal sheep breeds (referred to as the MATL evaluation) are the extent of variation between sub-populations described by genetic groups, as well as fair comparison of 'homebred' ewes with outcrossed contemporaries. The diversity of breeds and breed composition within the MATL evaluation is increasing. Breeds occur in sub-populations (*eg*. Australia vs New Zealand) and have also contributed to outcrossing and composite populations, increasing diversity of breed composition and expression of heterosis. Further, outside introductions can be accompanied by absence of pedigree and therefore creation of additional genetic groups. Preliminary investigation of breed composition demonstrated considerable variability in the genetic architecture of individual flocks (*eg*. composite vs pure-breeding) and the breed choice of outcross or introduced sires. Therefore, a general strategy to accommodate variation in the effects of heterosis is required. In this paper, we provide estimates of genetic parameters for traits included in the new single-step, multi-breed analyses used to produce breeding values for ewe reproductive performance traits (Bunter *et al.* 2019), including variances for genetic group effects and flock-outcross ewe genotypes.

MATERIALS AND METHODS

Data included in these analyses commenced in 2000, with pedigree and genetic groups extended back to 1998. Briefly, component traits were defined annually for conception of ewes joined (CON: 0=failed to conceive, 1=conceived) along with litter size (LS: 1 to n lambs born) and ewe rearing ability (ERA: lambs surviving/lambs born) for pregnant ewes. Pregnancy scan data was a secondary data source to define CON or LS when lambs were not recorded individually. Additional traits included maternal behaviour score of the ewe (MBS: scored from 1: good to 5: poor) as well as pre-joining weight (WT) and condition score (CS) recorded within the 30 days prior to joining. Data describing development of the young ewes and/or their male relatives was obtained for the subset of flocks included in reproductive analyses and included scanned post-weaning carcass fat (PFAT) and eye muscle depth (PEMD), along with post-weaning (PSC) or yearling (YSC) scrotal circumferences.

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Based on previous analyses (Bunter and Brown 2013), yearling and adult performances of CON, LS and ERA were treated as separate traits. Models for reproductive traits accounted for the systematic effects of CG + age, where CG refers to joining (CON, LS) or lambing (ERA) contemporary groups (based on site-year-timegp-mgp details) and age refers to age at recording in years (adult ewes). Time group (timegp) was assigned based on lambing dates, to accommodate evidence of gaps between joining events, and management groups (mgp) were as specified by breeders. Contemporary groups for reproductive traits were further refined to include: 1) month of birth and dam age group (yearling, adult, unknown) in the CG for yearling traits, and 2) previous status of the ewe (no lamb, lambed and lost or weaned, or unknown) in the CG for 2-year-old traits, enabling flock specific differences with respect to these factors. Additional model terms included birth-rearing type group for yearling but not adult reproductive traits and litter size group (1, 2 and 3 or more) at birth for ERA, since litter size alters the rearing challenge for ewes (Bunter *et al.* 2018). For the remaining traits (PFAT, PEMD, PSC and YSC), contemporary groups were as previously defined for these traits (Brown *et al.* 2007), and additional model terms included regressions on age, but not weight, where $P < 0.05$.

Specific model comparisons were made using univariate analyses. Trait dependent base models (model A) included animal genetic effects for all traits, permanent environmental effect of the dam (subset of traits), and permanent environmental effects to accommodate repeated records for adult ewes. Additional random effects subsequently added to base models included genetic groups (GG), defined as per Swan *et al.* (2016), and a flock \times outcross term intended to represent a pure- or crossbred (PC) genotype for the individual ewe. Genetic groups were as assigned for the genetic evaluation of maternal breeds, which are currently kept constant across all relevant analyses and trait sets. Ewes were considered an outcross if their sire was identified by a different flock code; different types of outcrosses (*ie* sire breeds) were not distinguished. The full model (model GGPC) was only fitted for traits where each of these terms significantly ($P < 0.05$) improved model fit.

RESULTS AND DISCUSSION

Estimates of heritabilities for early in life development traits (PFAT, PEMD, YWT, YCS) and scrotal measures (PSC, YSC) were generally consistent with expectation and are not discussed further. Model comparisons for pre-joining weight and condition score or maternal behaviour score are currently hindered by relatively low record numbers, but heritabilities were moderate.

Yearling vs adult expressions of reproductive traits. The order of magnitude for heritability estimates was $YERA < YLS < YCON$ for yearling ewes (Table 1) and $CON < ERA < LS$ for adult ewes (Table 2). Heritability for ERA was consistently lower than for litter size, reflecting an increase in environmental contributions to ERA. The relatively higher heritabilities for YCON vs CON and LS vs YLS support the strong influence of age at puberty, which is a moderately heritable trait, on YCON for yearling but not adult ewes, and an increased expression of genetic differences for litter size in adult compared to yearling ewes.

Genetic group effects. Pedigree is generally well known for current animals included in MATL analyses. Therefore, genetic groups predominantly represent within flock base populations and missing historical pedigree. Estimates of variances due to genetic group effects for early development traits ranged from negligible (PCF) to substantial (YWT) and the ratio of genetic group to additive (rgga) variance increased in magnitude from 0.20 (PCF) $< YCS < PEMD < 3.96$ (YWT). Considerable variance due to genetic groups was also evident for AWT and CS of adult ewes (Table 2), but rgga were lower (< 1.5) than for corresponding yearling traits. With respect to reproductive traits, the range in rgga from GG models was much lower (0.06 to 1.83) across both yearling and adult ewes, and this ratio was largest when flock-outcross variances were present and not accounted for (Model GG vs GGPC). This result implies that the ratio of genetic group variance (gg^2) is potentially inflated due

to the effects of multi-breed outcrossing. The ratio gg^2 was substantial for YCON but not CON, but generally negligible for all other reproductive traits. The ratios of genetic group to additive variances were somewhat similar to those reported by Swan *et al.* (2016) within trait groups.

Table 1. Parameter estimates for post-weaning fat (PCF), muscle depth (PEMD), post-weaning (PSC) and yearling (YSC) scrotal circumference, yearling conception (YCON), litter size (YLS) and ewe rearing ability (YERA), along with pre-joining weight (PWT) and condition score (PCS). The number of records is presented in brackets

| Trait | Model | Variances | | | | | | Ratios | | | | |
|------------------|-------|--------------|-----------------|-----------------|------------------|--------------|--------------|--------|--------|--------|---------|--------|
| | | σ_a^2 | σ_{gg}^2 | σ_{pc}^2 | σ_{ped}^2 | σ_e^2 | σ_p^2 | h^2 | gg^2 | pc^2 | ped^2 | $rgga$ |
| PCF (302747) | A | 0.135 | - | - | 0.020 | 0.460 | 0.614 | 0.22 | - | - | 0.03 | - |
| | APC | 0.135 | - | 0.005 | 0.020 | 0.466 | 0.625 | 0.22 | - | 0.01 | 0.03 | - |
| | GG | 0.134 | 0.027 | - | 0.020 | 0.467 | 0.647 | 0.22 | 0.04 | - | - | 0.20 |
| PEMD (301908) | A | 1.41 | - | - | 0.31 | 4.49 | 6.21 | 0.23 | - | - | 0.05 | - |
| | APC | 1.37 | - | 0.18 | 0.32 | 4.50 | 6.36 | 0.22 | - | 0.03 | 0.05 | - |
| | GG | 1.31 | 2.66 | - | 0.32 | 4.54 | 8.84 | 0.21 | 0.30 | - | 0.05 | 2.03 |
| PSC (69400) | GGPC | 1.32 | 2.44 | 0.11 | 0.31 | 4.52 | 8.71 | 0.21 | 0.28 | 0.02 | 0.05 | 1.85 |
| | A | 1.60 | - | - | 0.31 | 3.59 | 5.50 | 0.29 | - | - | 0.06 | - |
| | APC | 1.60 | - | 0.15 | 0.30 | 3.58 | 5.50 | 0.28 | - | 0.03 | 0.05 | - |
| YSC (42637) | GG | 1.59 | 0.001 | - | 0.31 | 3.59 | 5.49 | 0.29 | 0.00 | - | 0.06 | 0 |
| | A | 1.19 | - | - | 0.14 | 2.45 | 3.79 | 0.31 | - | - | 0.04 | - |
| | APC | 1.16 | - | 0.07 | 0.15 | 2.46 | 3.85 | 0.30 | - | 0.02 | 0.04 | - |
| YCON (24826) | GG | 1.16 | 0.64 | - | 0.14 | 2.46 | 4.41 | 0.31 | 0.14 | - | 0.04 | 0.55 |
| | GGPC | 1.15 | 0.49 | 0.05 | 0.15 | 2.47 | 4.30 | 0.30 | 0.11 | 0.01 | 0.04 | 0.42 |
| | A | 0.021 | - | - | - | 0.151 | 0.172 | 0.12 | - | - | - | - |
| YLS (58068) | APC | 0.021 | - | 0.010 | - | 0.151 | 0.181 | 0.12 | - | 0.05 | - | - |
| | GG | 0.018 | 0.033 | - | - | 0.153 | 0.204 | 0.10 | 0.16 | - | - | 1.83 |
| | GGPC | 0.016 | 0.011 | 0.011 | - | 0.153 | 0.191 | 0.09 | 0.06 | 0.06 | - | 0.69 |
| YERA (41955) | A | 0.016 | - | - | - | 0.233 | 0.249 | 0.06 | - | - | - | - |
| | APC | 0.016 | - | 0.001 | - | 0.233 | 0.249 | 0.06 | - | 0.00 | - | - |
| | GG | 0.016 | 0.001 | - | - | 0.233 | 0.250 | 0.06 | 0.00 | - | - | 0.06 |
| YWT (4515) | A | 0.005 | - | - | - | 0.123 | 0.128 | 0.04 | - | - | - | - |
| | APC | 0.005 | - | 0.001 | - | 0.123 | 0.128 | 0.04 | - | 0.00 | - | - |
| | GG | 0.005 | 0.003 | - | - | 0.123 | 0.130 | 0.04 | 0.02 | - | - | 0.60 |
| YCS (2803) | A | 10.4 | - | - | 4.17 | 9.44 | 24.0 | 0.43 | - | - | 0.17 | - |
| | APC | FTC | - | - | - | - | - | - | - | - | - | - |
| | GG | 5.66 | 22.4 | - | 5.01 | 11.8 | 44.9 | 0.25 | 0.50 | - | 0.22 | 3.96 |
| YCS (2803) | A | 0.028 | - | - | 0.001 | 0.149 | 0.178 | 0.16 | - | - | 0.01 | - |
| | APC | 0.028 | - | 0.001 | 0.001 | 0.148 | 0.178 | 0.16 | - | 0.01 | 0.01 | - |
| | GG | 0.022 | 0.034 | - | 0.001 | 0.151 | 0.207 | 0.11 | 0.16 | - | 0.00 | 1.70 |

Variances due to additive genetic (σ_a^2), genetic group (σ_{gg}^2), flock-outcross (σ_{pc}^2), and maternal permanent environment (σ_{ped}^2) effects, along with the residual (σ_e^2) and phenotypic variances (σ_p^2). Variance ratios are heritabilities ($h^2: \sigma_a^2 / \sigma_p^2$), variance due to genetic groups ($gg^2: \sigma_{gg}^2 / \sigma_p^2$), flock-outcross ($pc^2: \sigma_{pc}^2 / \sigma_p^2$) or permanent environmental effects of the dam ($ped^2: \sigma_{ped}^2 / \sigma_p^2$), excluding σ_{gg}^2 from σ_p^2 for ratios not involving σ_{gg}^2 in GG and GGPC models, and $rgga = \sigma_{gg}^2 / \sigma_a^2$; FTC: failed to converge.

Flock-outcross effects. There is likely little advantage for accuracy of selection in correcting for differences in retained heterosis within stabilised composites. However, fair comparison of outcross with homebred ewes is warranted. Ratios of variances due to flock-outcross terms (pc^2) were largest for fertility (YCON: 6%, CON: 3%) and ewe weight traits (AWT: 8%). For comparison, heterosis for fertility (17-21%), lamb survival (2-8%) but not litter size, was previously observed in structured

data involving divergent maternal breeds by Fogarty *et al.* (1984). The absence of substantial ratios for pc² for many traits implies that across the wide range of flocks and crosses, alternative ways to model heterosis may be required.

Table 2. Parameter estimates for adult conception (CON), litter size (LS) and ewe rearing ability (ERA), along with maternal behaviour score (MBS), pre-joining weight (WT) and condition score (CS). The number of records is presented in brackets

| Trait | Model | Variances | | | | | | | Ratios | | | |
|-----------------|-------|--------------|-----------------|-----------------|-----------------|------------------|--------------|--------------|----------------|-----------------|-----------------|------|
| | | σ_a^2 | σ_{pc}^2 | σ_{gg}^2 | σ_{pc}^2 | σ_{ped}^2 | σ_c^2 | σ_p^2 | h ² | gg ² | pc ² | rgga |
| CON (144803) | A | 0.002 | 0.004 | - | - | - | 0.073 | 0.079 | 0.03 | - | - | - |
| | APC | 0.002 | 0.004 | - | 0.002 | - | 0.073 | 0.081 | 0.03 | - | 0.03 | - |
| | GG | 0.002 | 0.004 | 0.001 | - | - | 0.073 | 0.080 | 0.03 | 0.01 | - | 0.50 |
| LS (685962) | GGPC | 0.002 | 0.004 | 0.001 | 0.002 | - | 0.073 | 0.082 | 0.02 | 0.01 | 0.03 | 0.53 |
| | A | 0.019 | 0.012 | - | - | - | 0.304 | 0.335 | 0.06 | - | - | - |
| | APC | 0.019 | 0.012 | - | 0.002 | - | 0.303 | 0.336 | 0.06 | - | 0.01 | - |
| ERA (536320) | GG | 0.018 | 0.013 | 0.015 | - | - | 0.304 | 0.350 | 0.06 | 0.04 | - | 0.83 |
| | GGPC | 0.018 | 0.013 | 0.018 | 0.002 | - | 0.304 | 0.354 | 0.05 | 0.05 | 0.01 | 1.00 |
| | A | 0.001 | 0.003 | - | - | - | 0.081 | 0.085 | 0.02 | - | - | - |
| MBS (10293) | APC | 0.001 | 0.003 | - | 0.001 | - | 0.081 | 0.086 | 0.01 | - | 0.01 | - |
| | GG | 0.001 | 0.003 | 0.001 | - | - | 0.081 | 0.086 | 0.01 | 0.01 | - | 1.00 |
| | A | 0.101 | 0.074 | - | - | - | 0.501 | 0.676 | 0.15 | - | - | - |
| AWT (10709) | APC | 0.101 | 0.074 | - | 0.001 | - | 0.501 | 0.677 | 0.15 | - | 0.00 | - |
| | GG | 0.100 | 0.075 | 0.021 | - | - | 0.501 | 0.696 | 0.15 | 0.03 | - | 0.21 |
| | A | 18.2 | 3.04 | - | - | 2.53 | 25.7 | 49.5 | 0.37 | - | - | - |
| CS (14959) | APC | 18.1 | 2.99 | - | 11.2 | 2.41 | 25.6 | 60.3 | 0.30 | - | 0.19 | - |
| | GG | 16.7 | 3.72 | 21.0 | - | 2.57 | 25.6 | 69.6 | 0.34 | 0.30 | - | 1.25 |
| | GGPC | 16.6 | 3.68 | 18.8 | 11.1 | 2.48 | 25.6 | 78.3 | 0.28 | 0.24 | 0.08 | 1.13 |
| CS (14959) | A | 0.043 | 0.017 | - | - | 0.002 | 0.177 | 0.239 | 0.18 | - | - | - |
| | APC | 0.043 | 0.017 | - | 0.001 | 0.002 | 0.177 | 0.240 | 0.18 | - | 0.00 | - |
| | GG | 0.041 | 0.018 | 0.028 | - | 0.002 | 0.177 | 0.266 | 0.17 | 0.11 | - | 0.68 |

Variance due to repeated records (σ_{pc}^2); accompanying ratios ranged between 0.03 and 0.11. All other abbreviations as per Table 1. Range for ped²: 0.01 to 0.05.

CONCLUSIONS

Admixture of populations within data used by Sheep genetics for MATL breed analyses requires strategies to accommodate variance due to genetic groups and outcrossing within flocks. For reproductive traits without a long and effective selection history within flocks, variances due to genetic groups were generally lower than or similar to estimates of additive variances. Variation in performance due to outcrossing explained relatively little variation for all traits except AWT and YCON. Alternative ways to model heterosis may be required.

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