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YEARLING AND ADULT EXPRESSIONS OF REPRODUCTION IN MATERNAL SHEEP BREEDS ARE GENETICALLY DIFFERENT TRAITS

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SUMMARY

Reproductive data (N=19335 ewes recorded) from maternal breeds recorded in industry flocks were used to estimate genetic parameters for the number of lambs born (NLB) and weaned (NLW) per ewe joined, along with their component traits fertility (FERT), litter size (LSIZE) and lamb survival (LSURV). Data were analysed as different traits for ewes in different age groups (yearlings, two year olds, and 2+ year olds). Yearling performance was characterised by low FERT (54%), low LSIZE, reflecting an increased frequency of single births, and increased lamb losses relative to older ewes bred in the same flock-years. Heritability (h^2) estimates were highest for yearling FERT (h^2=0.16) and declined for this trait with ewe age group (h^2~0.07). In contrast, heritabilities and variance increased with ewe age for LSIZE (h^2: 0.05 to 0.11). Genetic correlations (rg) between yearling and later records within traits were significantly <1 (range 0.10 to 0.54). The exception was LSIZE where the genetic correlation between ewe age groups was consistently high (rg: 0.85 to 1.0). Trait values affected by fertility outcomes (FERT, NLB and NLW) had significant service sire effects, whereas service sire effects were insignificant for LSIZE and LSURV. Service sire recording was incomplete more frequently for infertile ewes. Yearling reproductive performance should be treated as genetically different to adult expressions of the same traits for genetic evaluation purposes, and the different genetic architecture of component traits towards NLB and NLW can then be appropriately accommodated.

INTRODUCTION

Reproductive performance of ewes joined to lamb as yearlings is low relative to that of maiden two-year old or multiparous mature ewes (Afolayan *et al.* 2008). Both lower fertility and prolificacy (litter size), and fewer offspring weaned per ewe lambing, are characteristic outcomes from the first joining of polyovulatory species such as sheep and pigs. This reflects variation amongst individuals in attributes like age at puberty and sufficient expression of behavioural estrus, adequate weight or body condition pre-breeding, along with differences in ovulation rate, foetal survival and pre-weaning survival. Such characteristics are all under genetic control to varying degrees. Some genetic evaluation systems treat first parity performance as a genetically different trait to performance in later parities for sheep (SIL, Walker 2008) and pigs (PIGBLUP, Crump and Henzell, 2000). Since 2012, Sheep Genetics (Brown *et al*. 2007) has also analysed yearling number of lambs born (NLB) and weaned (NLW) per ewe joined separately to the same traits recorded for older ewes. The aim of this study was to estimate genetic correlations using industry data for NLB and NLW, along with the component traits of fertility (FERT), litter size (LSIZE) and lamb survival (LSURV), when considered as different traits for ewes in different age groups. A secondary goal was to examine the importance of service sire effects for these traits.

MATERIAL AND METHODS

Reproductive data were derived from industry records submitted to Sheep Genetics. The data subset analysed included only those flocks and years where significant numbers of yearling ewes

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were recorded. The resulting data (N=19335 ewes) represented nineteen flocks and five breeds (Border Leicester, Coopworth, White Suffolk and two Maternal synthetic flocks). Most flocks had few years in which yearling ewes were recorded. Flock-years with 100% fertile ewes were excluded from analyses as these reflected incomplete recording. All yearling ewes were naturally joined whereas older ewes were either naturally joined or bred using artificial insemination (AI). A complete pedigree for the combined breeds was used for parameter estimation (N=1240091).

Traits were defined by ewe age group (yearlings, two year olds, and 2+ year olds) and included fertility of joined ewes (FERT: pregnant or not, 1/0), fecundity (LSIZE: lambs born per ewe lambing), lamb survival (LSURV: lambs weaned per ewe lambing) and number of lambs born (NLB) or weaned (NLW) per ewe joined. The fixed effect models for the yearling traits accounted for flock-year of lambing (45 levels), dam age group (6 levels: 1yo, 2yo, 3yo, 4yo, 5-8yo, 8+ yo), ewe age (in days) and month of birth fitted as linear and quadratic covariates, along with service sire age group (5 levels: 1yo, 2yo, 3-7yo, 7+ yo, and unknown). Fixed effect models for older ewes included flock-year combined with conception method (2 levels: natural or AI), along with the linear effect of ewe age and the service sire age group, as described above. Breed was confounded with flock and was not explicitly fitted in models for analysis. Ewe parity at joining was not fitted in models for two or 2+ year old ewes. Parameters were estimated for all traits under linear animal models, treating each ewe as the animal and the service sire at joining as an additional random effect (i.i.d). Ewes had only one record used per ewe age group (repeated records in the 2+ age group were not used due to low N). Estimates of heritabilities and genetic correlations were obtained under an animal model using ASREML (Gilmour et al. 2009) from a series of univariate and bivariate analyses. Where the service sire effect was only marginally significant in univariate analyses, it was removed from models for the relevant trait(s) in bivariate analyses. No covariance between service sire effects was fitted.

RESULTS AND DISCUSSION

Raw data means for each trait by ewe age group show lower fertility, prolificacy, lamb survival and therefore NLB and NLW for yearling compared to older ewes recorded in the same flock-years (Table 1). The larger trait standard deviation shows that fertility was more variable between flock-years for yearling relative to older ewes. In contrast, LSIZE was less variable for yearling ewes, resulting from a smaller range in trait values and a relatively high frequency of single births for yearling ewes (not presented). Because of low fertility, the number of yearling ewes with subsequent records for LSIZE and LSURV was low.

Table 1. Means, standard deviations (SD) and record count, by ewe age group (Y: yearling; 2yo: two-year old; 2+: older than 2 years old), for fertility (FERT), litter size (LIZE) and lamb survival (LSURV), along with lambs born (NLB) or weaned (NLW) per ewe joined

	Mean (SD)			Counts of records				
	Yearling	2yo	2+	Yearling	2yo	2+	Y/2yo	Y/2+
FERT	0.54 (0.50)	0.91 (0.28)	0.94 (0.23)	12153	9315	6657	4931	2405
LSIZE	1.40 (0.51)	1.62 (0.58)	1.74 (0.63)	6548	8487	6313	2253	1122
LSURV	1.08 (0.62)	1.39 (0.63)	1.52 (0.66)	6544	8485	6290	2220	1208
NLB	0.75 (0.79)	1.47 (0.72)	1.65 (0.73)	12153	9315	6657	4931	2405
NLW	0.58 (0.70)	1.26 (0.72)	1.44 (0.73)	12153	9315	6657	4931	2405

Estimates of heritability and service sire effects differed with ewe age class (Table 2). Fertility was most heritable (h^2=0.16) and service sire variance (s^2=0.23) was largest for yearling ewes, with both parameter estimates (h^2~0.07, s^2~0.06) and phenotypic variation decreasing in magnitude for FERT with increasing ewe age. In contrast, heritability and variability in LSIZE increased with ewe age. Around 15% of yearling ewes lambed and lost, increasing the phenotypic variance for LSURV relative to LSIZE. However, this effect was smaller for older ewes where only 6% failed to rear any lambs. Within older ewe age groups, the heritability estimates for LSURV were typically lower than the corresponding estimates for LSIZE and residual variance was increased. Poor fertility and an increased incidence of lamb deaths for yearlings also affected parameters and variances for NLB and NLW, relative to LSIZE and LSURV, because these trait distributions become zero enriched when either fertility is low or a significant proportion of ewes rear no lambs. Genetic correlations between yearling and adult performance for FERT, LSURV, NLB and NLW were significantly less than unity, supporting the concept that genetically yearling reproductive performance differs from adult expressions for the same traits. However, genetic correlations between ewe age groups for LSIZE did not differ from unity (rg: 0.85 - 1.0).

Table 2. Estimates of heritability and the proportion of service sire effects, along with genetic correlations, by ewe age group (Y: yearling; 2yo: two-year old; 2+: older than 2 years old), for fertility (FERT), litter size (LIZE), lamb survival (LSURV), and lambs born (NLB) or weaned (NLW) per ewe joined

Parameter	Age1*	Age2*	FERT	LSIZE	LSURV	NLB	NLW
Heritability	Y		0.16±0.02	0.05±0.02	0.07±0.02	0.13±0.02	0.08±0.01
	2yo		0.07±0.02	0.10±0.02	0.07±0.02	0.10±0.02	0.08±0.02
	2+		0.07±0.02	0.11±0.02	0.06±0.02	0.09±0.02	0.06±0.02
Service sire effect	Y		0.23±0.02	0.02±0.01	0.02±0.01	0.11±0.01	0.14±0.02
	2yo		0.16±0.02	0.01±0.01	0.01±0.01	0.05±0.01	0.04±0.01
	2+		0.06±0.01	0.01±0.01	B	0.02±0.01	0.01±0.01
Phenotypic Variance	Y		0.15	0.25	0.36	0.39	0.35
	2yo		0.073	0.31	0.38	0.45	0.47
	2+		0.044	0.36	0.42	0.46	0.49
Genetic Correlation	1yo	2yo	0.44±0.12	1.0±0.21	0.38±0.20	0.33±0.11	0.40±0.14
	1yo	2+	0.10±0.15	1.0±0.18	0.54±0.24	0.33±0.15	0.42±0.20
	2yo	2+	0.28±0.21	0.85±0.12	0.65±0.22	0.91±0.12	0.95±0.21

Age*: for trait 1 or traits 1 & 2 (univariate vs bivariate analyses); B: converged to zero boundary

Few studies have reported parameter estimates for reproductive traits of ewes recorded in different age classes. Heritability estimates from combined parity data for naturally joined crossbred ewes bred in the Maternal Central Test project were 0.11±0.04 for FERT, 0.19±0.05 for LSIZE, 0.03±0.02 for LSURV, 0.17±0.04 for NLB and 0.11±0.04 for NLW (Afolayan *et al.* 2008), consistent generally with estimates from this study. Comparable estimates from combined parity Merino data tend to be lower (Safari *et al.* 2007). Newton *et al.* (2013) reported heritabilities of 0.20±0.05 and 0.16±0.05 for yearling NLB and NLW, recorded on maternal-cross ewes in the Sheep CRC INF flock. Service sire effects accounted for 21, 17 and 8% of variation in FERT, NLB and NLW in Safari *et al.* (2007); a similar pattern was observed in this study. Since service sire effects were negligible for LSIZE or LSURV, this suggests that for NLB and NLW, some service sire variation arose from an auto association between the incidence of ewe infertility and the reporting of a service sire as unknown. The percentages of records without service sires reported was 17.7% in yearling data, compared to 3.7% and 3.9% of records for older ewes. This reduced to <3% of unknown service sires for lambed ewes in any age group. However, this phenomenon would not have influenced the comparable results of Safari *et al.* (2007). In addition, since each service sire defined a joining group, other factors could also contribute to estimates of service sire variation for FERT – for example group size and paddock attributes. Approximately

50% of the variation attributed to the service sire effect for fertility can be removed by fitting additional fixed effects in models for analyses, such as joining group size (results not presented). These results suggest that the implications of service sire effects for the accurate genetic evaluation of ewe fertility should be investigated further with more complete recording of service sires for all ewes joined. The relative magnitude of service sire effects is expected to be lower for NLB and NLW because of contributions to these trait values from LSIZE and LSURV, which are unaffected by service sire effects.

Low fertility of adult ewes typically reflects a service sire failure rather than genetic inferiority of all of the ewes for fertility *per se*. Consequently, low fertility groups of ewes are typically removed from the Sheep Genetics genetic evaluation system to reduce the possibility of bias introduced by service sire failures. However, no such editing was applied to this data on the basis of yearling performance levels because in this age group low fertility of the group joined does not necessarily represent service sire failure. The extent to which genetic correlations between parities are influenced by the threshold for fertility applied to edit data needs to be examined further for yearling ewes. Service sire effects were not important for LSIZE or LSURV in these data. Genetic evaluation for these traits might be more accurate than for the compound traits of NLB or NLW when service sires are not fully reported in Industry data.

CONCLUSIONS

The relative contributions of component traits such as fertility, litter size and lamb survival to trait values for NLB and NLW varies with ewe age. This is accompanied by differences in heritabilities and phenotypic variances for fertility in particular, where performance differences between yearling and older ewes are large. Relatively low genetic correlations indicate that reproductive traits of yearling ewes should generally be treated as genetically different traits to the same traits recorded on older ewes, with the exception of LSIZE. The contribution of service sire effects to variation in reproductive performance warrants further investigation for fertility traits in particular, since this will also influence NLB and NLW. Current parameter estimates for service sire effects using Industry data may be partially influenced by incomplete recording of service sires more often when ewes are infertile, or might be eliminated by optimising management of yearling ewes at joining.

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