

PHENOTYPIC TRADE-OFFS BETWEEN LAMBS AND WOOL REFLECT WEAK ANTAGONISTIC GENETIC CORRELATIONS BETWEEN REPRODUCTIVE AND WOOL TRAITS

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SUMMARY

Rearing lambs while producing wool is an annual source of competition for available nutritional resources supplied to breeding ewes. Genetic correlations between wool and reproductive traits were estimated from industry data, comparing models that did or did not account for the effects of reproductive level on wool traits recorded at different wool age stages (yearling, hogget, adult). Small to moderate antagonistic correlations between wool and reproductive traits tended to decrease in magnitude when birth-rear type of the individual (yearling and hogget stages) or reproductive output (adult ewes) were accounted for in models for wool traits. Increased recording of reproductive performance would make it possible to more accurately compare young animals for wool traits as well as genetically improve both trait sets (ewe reproduction and wool traits) for Merinos.

INTRODUCTION

For breeding ewes, reproductive performance and wool production are annual outputs that compete for access to common, potentially limiting, nutritional resources. In addition, progeny born as singles have, on average, superior wool attributes relative to twins (Hocking-Edwards *et al.* 2011). In the Australian Merino industry, the majority of animals are recorded for wool traits as yearlings or hoggets (i.e. between 12 and 18 months of age), prior to their first joining. Data for adult wool traits is subsequently predominantly from breeding ewes. At both time points, variability introduced by litter size at birth-rearing (progeny) or reproductive status (ewe) could potentially affect estimates of the genetic correlations between wool and reproductive traits. Derivation of component traits for reproductive performance (Bunter *et al.* 2021) enable these associations to be investigated further across industry flocks. This paper examines how birth-rear type of offspring and previous reproductive status of ewes affect wool trait values and estimates of genetic correlations between these trait groups.

MATERIALS AND METHODS

Data and pedigree recorded from 2000 onwards for greasy fleece weight (GFW) and fibre diameter (FD) were extracted from the Sheep Genetics database for the subset of flocks that had some reproductive data for conception (CON), litter size (LS) and ewe rearing ability (ERA) traits. Wool and reproductive records were merged by animal-year of recording. Wool records were classified by age-stage groupings (Y: yearling; H: hogget and A: adult). Wool and ewe reproductive data were concurrent for the adult wool stage data only. Reproductive performance in the year prior to the adult stage shearing was derived from reproductive data, or described as unknown. The complete pedigree contained about 740k animals.

Contemporary groups for wool traits within stage were defined by flock-year-date of shearing-breeder subgroup (Brown *et al.* 2007), and contemporary groups for reproductive traits were as previously described by Bunter *et al.* (2021). Age at recording for wool traits was accounted for

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using linear regression (Y, H stages) or by fitting age in years as a class effect (A stage). Animals over 6 years old at the time of recording were grouped in the 7yo age group. Sex was accounted for to accommodate wool records for males. An additional model term for Y, H and A stage wool traits was birth-rear type group (BTRTG: SS, MS, MM, SU, MU or UU, where S=single, M=multiple and U=unknown). Previous reproductive outcome (RSTAT: 4 levels for ewes: 0, 1 or 2+ lambs reared, or unknown) was fitted for ewe A stage wool traits only. Models containing these additional terms were compared to base models without these terms. Least squares means for BTRTG and RSTAT for each wool trait were obtained using the GLM procedure of SAS software (2002-2012). Heritabilities were estimated assuming an animal model for the alternative systematic effect models in univariate analyses. Additional random effects included maternal effects for wool traits (all stages) and a permanent environmental effect to accommodate repeated records for adult reproductive and wool traits. Correlations between wool and reproductive traits were estimated from a series of bivariate analyses using ASREML (Gilmour *et al.* 2014).

RESULTS AND DISCUSSION

Approximately 82% (70%) of animals had sires (dams) known and 6% of adult shearing records for ewes had previous reproductive status known. Data characteristics and heritabilities (Table 1) were generally consistent with expectation, with the exception of higher heritabilities for reproductive traits relative to the data sample of Bunter *et al.* (2021), which contained more flocks characterised by less historical pedigree and data. Maternal effects were about 2% for FD and ranged between 6-9% for GFW across stages, and were consistent within trait stage across models.

Table 1. Estimates of additive genetic (h^2) and permanent environmental effects (pe^2) relative to the phenotypic variance (σ_p^2) for reproductive (CON, LS, ERA) or wool traits under the Base model, or after accounting for birth-rear type group (+ BTRTG) or previous reproductive status (RSTAT)

Trait	N	Mean(SD)	Base model			Base + BTRTG			Base + RSTAT		
			h^2	pe^2	σ_p^2	h^2	pe^2	σ_p^2	h^2	pe^2	σ_p^2
CON	48899	0.91 (0.28)	0.09	0.09	0.075	-	-	-	-	-	-
LS	89165	1.34 (0.49)	0.09	0.02	0.206	-	-	-	-	-	-
ERA	51781	0.82 (0.35)	0.03	0.05	0.117	-	-	-	-	-	-
YGFW	370089	3.24 (1.12)	0.28	na	0.319	0.31	na	0.309	-	-	-
YFD	375031	16.6 (1.86)	0.60	na	1.23	0.60	na	1.22	-	-	-
HGFW	170254	4.50 (1.25)	0.37	na	0.401	0.38	na	0.396	-	-	-
HFD	201061	17.9 (1.90)	0.61	na	1.50	0.62	na	1.49	-	-	-
AGFW	196896	5.04 (1.49)	0.35	0.20	0.529	0.36	0.19	0.524	0.36	0.19	0.523
AFD	167028	17.9 (2.42)	0.69	0.05	1.56	0.69	0.05	1.55	0.69	0.05	1.55

-: not fitted; all $se < 0.01$; CON: conception; LS: litter size; ERA: rearing ability; greasy fleece weight and fibre diameter for yearling (YGFW, YFD), hogget (HGFW, HFD) and adult (GFW, FD) stages

Systematic effects. Lambs born and reared as singles (SS) had heavier fleeces than MM lambs at Y (GFW: 3.21 ± 0.004 vs 2.93 ± 0.005 kg), H (GFW: 4.54 ± 0.01 vs 4.36 ± 0.01 kg) and A stages (GFW: 5.30 ± 0.03 vs 5.16 ± 0.03 kg). Single born lambs also had lower FD than MM lambs at Y (16.8 ± 0.01 vs 16.9 ± 0.01), H (17.9 ± 0.01 vs 18.1 ± 0.01) and A stages (18.0 ± 0.06 vs 18.2 ± 0.06). Animals born as multiples and reared as single were intermediate. These effects result from permanent changes to lamb development arising from competition for resources during gestation and lactation. Phenotypic selection for increased fleece weight and finer micron would therefore favour SS over MM lambs, in the absence of accounting for BTRTG, particularly when based on yearling wool data. Clark and Thompson (2021) showed that BTRTG affects classing results, due to the effects of BTRTG on both weight and wool traits.

Across parities, ewe fleece weights were reduced by about 150g per additional lamb weaned in the previous year (i.e. GFW LSM: no lambs: 4.95±0.03 kg; one lamb: 4.80±0.03 kg; two lambs: 4.65±0.03 kg) but FD did not significantly differ ($p=0.07$) with the previous years' reproductive performance. These effects result from the trade-off between ewe wool growth and partitioning of ewe resources (feed intake) towards successful gestation and lactation outcomes (Freer *et al.* 1997). Hocking-Edwards *et al.* (2011) suggested that appropriate nutritional management of twinning ewes during pregnancy can offset detrimental effects for wool traits for both ewes and their offspring.

Genetic parameters. The significant effects of birth-rear type on fleece weights (FW) or fibre diameter (FD: ewes and rams) and previous reproductive status (adult ewes) on AGFW suggest that correlations between wool and reproductive traits are antagonistic. However, ewe BTRTG categories are cross-classified with lamb BTRTG categories, enabling separation of genetic from non-genetic effects for wool traits associated with litter size in multiple generation data.

Model comparisons. Variance in wool traits explained by BTRTG decreased with age/stage (ie A < H < Y stages) and was collectively proportionally more collectively for FW (2-7%) relative to FD (0-2%) (Table 1). Sheep born as multiples have lighter fleeces and broader micron, on average, due to permanent developmental effects (Hocking-Edwards *et al.* 2011). In contrast, RSTAT explained very little variance for adult wool traits (Table 1) and did not alter estimates of genetic correlations with reproductive traits (Table 2). This could be because RSTAT was unknown for the majority of ewe A stage wool records. For other trait combinations, the models fitted for wool traits affected estimates of genetic correlations between wool with reproductive traits.

Genetic (ra) correlations between wool and reproductive traits. Genetic correlations were unfavourable (ra: -0.22) between GFW and CON, but this was less evident for Y and H fleece weights (Table 2). A more effective correction for RSTAT may be important for accurate estimates of the genetic correlation between GFW and CON. Genetic correlations between GFW at all stages and LS were negligible, providing BTRTG was included in wool trait models. Genetic correlations between GFW at any stage and ERA were negligible under all models. Fibre diameter at all stages had low positive genetic correlations with LS and ERA (ra: 0.15 to 0.22); antagonistic correlations of FD with CON were evident for HFD only. Overall, breeding objectives that aim to increase fleece weight (less so) and reduce fibre diameter (more so) have detrimental implications for ewe reproductive performance and lambs reared. However, genetic correlations were relatively low, indicating scope for concurrent improvement in both reproductive performance and wool traits with appropriate data recording and selection criteria. Safari *et al.* (2007) previously reported an antagonistic genetic correlation for NLW with CFW (-0.26±0.05), negligible with FD (0.06±0.04). Results here suggest genetically broader FD sheep are more likely to have higher genetic merit for LS and ERA, which is consistent with lower litter size and lamb survival typically observed for fine- relative to medium- or strong-wool sheep (Hatcher *et al.* 2009).

Positive residual (not shown) and phenotypic correlations were evident between YGFW and LS, suggesting that unidentified non-genetic factors increasing ewe YGFW increased future litter size. Negative correlations between permanent environmental effects for ewe wool and reproductive traits (not shown) indicate that persistent high reproductive performance has negative consequences for FD and GFW within individual ewes. Overall, parameters derived for Y & H stage wool data, recorded prior to any joining event provide consistent results: wool traits are affected by reproductive performance levels but the genes that control these trait groups are largely independent, with the absolute magnitude of genetic correlations typically less than 0.2.

CONCLUSIONS

Merino breeders would benefit from recording reproduction accurately, as knowledge of birth-rear type is important for accurate comparisons of young animals (e.g. YGFW, YFD) and comparison of adult ewe fleeces are also affected by variation in reproductive output. In each case,

animals with or resulting from low reproductive output would be favoured for fleece or weight traits if this information were unknown. However, genes affecting reproductive traits are largely independent of genes affecting greasy fleece weight or fibre diameter (ra: magnitude negligible or generally $\leq \pm 0.2$), making it possible to change both trait sets with accurate recording of reproduction. Where correlations were not negligible, they were low and antagonistic, suggesting indirect selection pressure against improved reproduction from selection on uncorrected weight or fleece attributes.

Table 2. Additive genetic (ra), residual (re) and phenotypic (rp) correlations between wool (Trait 1) and reproductive (Trait 2) traits when BTRTG (Y & H stages) and previous reproductive performance (RSTAT, A stage only) are added to Base models for wool traits

Trait 1*	Trait 2**	Base model			Base + BTRTG			Base + BTRTG + RSTAT		
		ra	re	rp	ra	re	rp	ra	re	rp
YGFW	CON	-0.09	-0.01	-0.02	-0.07	-0.00	-0.01	-	-	-
	LS	-0.33	0.16	0.06	-0.03	0.10	0.07	-	-	-
	ERA	0.01	0.02	0.01	0.04	0.02	0.02	-	-	-
HGFW	CON	0.04	-0.06	-0.04	0.06	-0.07	-0.04	-	-	-
	LS	-0.10	0.03	0.00	0.04	-0.00	0.01	-	-	-
	ERA	0.06	-0.03	-0.02	0.06	-0.03	-0.01	-	-	-
AGFW	CON	-0.21	0.10	-0.05	-0.21	0.10	-0.05	-0.21	0.10	-0.05
	LS	-0.10	0.04	0.00	-0.03	0.04	0.01	-0.02	0.04	0.01
	ERA	-0.04	0.05	-0.02	-0.02	0.05	-0.02	-0.02	0.04	-0.02
YFD	CON	0.06	0.01	0.02	0.06	0.01	0.02	-	-	-
	LS	0.19	0.01	0.05	0.14	0.03	0.05	-	-	-
	ERA	0.22	0.02	0.04	0.23	0.02	0.04	-	-	-
HFD	CON	0.14	-0.00	0.03	0.13	-0.00	0.03	-	-	-
	LS	0.21	-0.07	0.01	0.14	-0.04	0.01	-	-	-
	ERA	0.22	0.03	0.05	0.20	0.04	0.05	-	-	-
AFD	CON	0.02	0.03	0.01	0.02	0.03	0.01	0.02	0.03	0.01
	LS	0.18	0.02	0.03	0.15	0.02	0.03	0.15	0.03	0.06
	ERA	0.19	0.03	0.02	0.18	0.03	0.02	0.18	0.03	0.02

Estimates $ra > 2 \times SE$ from 0 are in bold; *greasy fleece weight and fibre diameter for yearling (YGFW, YFD), hogget (HGFW, HFD) and adult (AGFW, AFD) stages; **conception (CON), litter size (LS) and rearing ability (ERA) traits for adult ewes

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