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Heritability estimates and genetic and phenotypic correlations of skin thickness and skin temperature with key production traits in FocusPrime, Texel, Romney, and Highlander sheep

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Abstract

Skin thickness was found to be moderately heritable and genetically associated with lamb survival in a previous study on Romney sheep. The aims of this study were to estimate the heritabilities of skin thickness and skin temperature at around 5 and 11 mo of age and determine genetic and phenotypic correlations between them and with production traits such as fat depth, loin-eye muscle depth and width, live weights at weaning, scanning, and 12 mo, and 12-mo fleece weight, in FocusPrime (n = 2,088), Texel (n = 732), Romney (n = 825) and Highlander (n = 1,801) sheep breeds. Heritability estimates of skin thickness at 5-mo old were moderate in FocusPrime (0.39 ± 0.12) and low in Texel and Highlander (0.11 ± 0.15 and 0.13 ± 0.09, respectively). Heritability estimates of skin thickness at 11-mo old were moderate in all breeds (ranging from 0.19 ± 0.07 to 0.29 ± 0.15). Heritability estimates of skin temperature were high in FocusPrime (0.39 ± 0.11), low in Texel (0.17 ± 0.11) and Highlander (0.12 ± 0.06) and almost zero in Romney (0.04 ± 0.03). A tendency in all breeds for negative and favorable correlations was found between skin thickness and skin temperature at 11-mo old sheep. Skin thickness at 11-mo tended to have a positive genetic correlation with fat depth in all breeds except in Texel where the correlation tended to be negative (−0.10 ± 0.34). Genetic correlations of skin thickness at 11-mo old with the weight traits were variate. There tended to be a positive correlation with weaning weight in Texel (0.14 ± 0.34) and Highlander (0.29 ± 0.22). However, there tended to be negative correlations with live weight at scanning and at 12-mo of age in FocusPrime (−0.03 ± 0.18 and −0.13 ± 0.22, respectively) and tended to be positive in Romney (0.09 ± 0.25 and 0.10 ± 0.24, respectively) and Highlander (0.26 ± 0.22 and 0.39 ± 0.21, respectively). Moreover, genetic correlations of skin thickness at 11-mo of age with FW12 tended to be positive in both Romney (0.20 ± 0.22) and Highlander (0.55 ± 0.19). Further studies on the genetic correlations of skin thickness and skin temperature with lamb survival in these breeds are warranted.

Lay Summary

This study aimed to estimate the heritabilities of skin thickness and skin temperature, while also estimating the genetic and phenotypic correlations between them and with several production traits of economic importance in 5- and 11-mo-old FocusPrime, Texel, and Highlander sheep. Skin thickness showed wide phenotypic variation with moderate heritability across breeds for 11-mo skin thickness, confirming that genetic selection in this trait is feasible. Negative favorable correlations between 11-mo skin thickness and skin temperature were observed. Skin thickness at 11 mo tended to be positively correlated with fleece weight and fat depth. Genetic association of skin thickness with Romney lamb survival has been reported in an earlier study and similar research on the association of skin thickness and skin temperature on lamb survival in these breeds is warranted. If the similar association is evinced in these breeds, skin thickness and skin temperature may potentially be used as an indicator trait for improving lamb survival.

Key words: genetic and phenotypic correlations, genetic parameters, sheep, skin temperature, skin thickness

Abbreviations: Birth_rearing type, born as single, twin or triplet, and reared as single, twin or triplet; BirthYear_flock, contemporary group; EMD, loin-eye muscle depth; EMW, loin-eye muscle width; FD, fat depth; FW12, fleece weight at 12-mo of age; h^2, heritability; LW12, live weight at 12-mo of age; LWS, live weight at scanning; ST11, skin thickness at 11-mo of age; ST5, skin thickness at 5-mo of age; Stemp, skin temperature; WWT, weaning weight

Introduction

Lamb mortality is a significant financial and welfare issue for sheep farmers internationally, where losses in the range of 10% to 25% have been recorded (Alexander, 1984; Haughey, 1993) and hence, increased lamb survival has been the objective of many research studies, especially in extensive outdoor production systems (Riggio et al., 2008; Brien et al., 2010). Recent reports state that lamb survival has been upscaled into

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the list of breeding priorities in some production systems, where this move should result in increased revenue through additional lamb sales (Bohan et al., 2019). Further, the addition of live lambs at weaning will increase selection intensity (Forrest et al., 2006).

In countries such as New Zealand and Australia, where lambing mostly occurs outdoors, the thermoregulatory capacity of the lamb and its ability to conserve heat is critical for survival since exposure to cold and/or starvation can cause lamb deaths (Haughey, 1993; Mellor and Stafford, 2004). It is known that the skin plays a vital role in increasing body insulation and reducing heat loss from the body surface (Alexander, 1978), and some studies have observed that new-born lambs with thicker skin were more resistant to cold stress (Samson and Slee, 1981; Stott and Slee, 1987; Slee et al., 1991). Skin thickness has been found to be a moderate to highly heritable trait (Gregory, 1982a; Slee et al., 1991; Janssens and Vandepitte, 2004; Tait et al., 2015; Soltani-Ghombavani et al., 2017), and has a positive genetic correlation with lamb survival from birth to weaning, ranging from 0.16 to 0.35 (Soltani-Ghombavani, 2021), it appears possible to improve lamb survival by indirect selection for skin thickness. Soltani-Ghombavani (2021) also reported that thick-skinned lambs, subjected to cold stress, had lower overall skin temperature, therefore a greater ability to maintain body temperature when exposed to cold, as opposed to thin-skinned contemporaries. Furthermore, skin thickness can be ultrasonically measured, simultaneously with other routinely measured ultrasound traits such as fat depth (FD) and muscle depth at around 5 to 12 mo of age. Therefore, adding skin thickness to the already recorded ultrasound measurements, or infrared measurements of skin temperature (as an indicator of resistance to cold stress), would be a low-cost and non-invasive phenotype for ram breeders to use in a genetic improvement program. Thus, the knowledge of whether skin thickness and skin temperature are heritable across New Zealand breeds would be of benefit. It is also important to understand how selection based on these traits (i.e., ultrasonic skin thickness and infrared-measured skin temperature) would be associated with production traits before making selection choices. To date, this has not been undertaken for breeds such as FocusPrime, Texel, and Highlander. Therefore, the aims of this study were to estimate the h^2 of skin thickness (at around 5 and 11 mo of age) and the skin temperature, plus the genetic and phenotypic correlations between them and with production traits of FD, loin-eye muscle depth (**EMD**) and loin-eye muscle width (**EMW**), live weights (at weaning, scanning, and 12 mo) and fleece weight at 12-mo of age in FocusPrime, Texel, Romney, and Highlander sheep breeds.

Materials and Methods

Animals and data collection

The study protocol was approved by Massey University Animal Ethics Committee (MUAEC), protocol number 18/63. The study included lambs from 4 breeds: FocusPrime, Texel, Romney, and Highlander. These animals were part of 3 Focus Genetics breeding farms in New Zealand: the Waikite farm for FocusPrime and Texel (Reporoa, 38°18'17.3"S 176°18'24.9"E), Goudies farm for Romney (Reporoa, 38°31'07.4"S 176°28'46.1"E) and Waipuna farm for Highlander (Wanganui, 39°49'23.9"S 175°16'38.7"E). The FocusPrime breed is a merge of 2 terminal composites, LambSupreme and Primera (Pickering et al., 2018). LambSupreme sheep were bred from the crossbreed progeny of Poll Dorset, Wiltshire, Romney-Dorset, Coopworth, Texel, and Romney, whereas Primera sheep were bred from the progeny of Suffolk, Poll Dorset, Australian White Suffolk, Dorper, Hampshire, and Dorset Down (Brito et al., 2017). FocusPrime and Texel are terminal breeds selected for meat and growth production traits, while Highlander and Romney are maternal breeds with selection based on a self-replacement system (Pickering et al., 2018).

Skin thickness of each lamb was measured ultrasonically during August 2018 in 2017-born lambs (i.e., approximately 11 mo old; ST11), and around January/February 2020 in 2019-born lambs (i.e., approximately 5 mo old; ST5). A commercial scanning operator undertook these measurements in both years, using a Mindray DP 50 ultrasound system (BCF Ultrasound Australasia, Auckland, New Zealand), with a 40 mm probe at 3.5 MHz set on the left dorsal loin region of the lambs around the 12th rib. It was set up such that 1 mm of skin depth measured 1 cm on screen, and measurements were to a tenth of mm. In the case of the 2017-born lambs only, on the same day of skin thickness measurement, skin temperature measurements (Stemp) of the left dorsal loin region were also obtained through infrared thermography using an infrared camera (FLIR T650sc; Teledyne FLIR, Wilsonville, OR, USA), mounted on a tripod at a fixed distance (1.2 m at an angle of 50°). Prior to obtaining the infrared image, the wool at the site was parted to either side using a metal rod so as to capture an accurate recording of the exposed skin. Using FLIR Research IR Max software (Teledyne FLIR, Wilsonville, OR, USA), the exposed skin area on the infrared image for each lamb was delimited and utilized to provide an average of the lamb's skin temperature. Subcutaneous FD, EMD, and EMW around the 12th rib region were measured ultrasonically at around 5 mo of age in all lambs by another commercial operator, utilizing SONOACE R3 ultrasound machine (Samsung Medison Co. Ltd, Seoul, South Korea), with a probe at 3.5 to 4.5MHz set to a depth of 220 mm. On the same day that FD, EMD, and EMW were measured, the live weight of the lamb at scanning (LWS) was recorded.

Measurements and records of all traits for the Romney breed came only from ram lambs born in 2017. In 2017, ST11 and Stemp of the remaining breeds were measured on both ewe and ram lambs (Table 1). In 2019, ST5 was measured on ram lambs only. Ultrasound traits, (FD, EMD, and EMW) of all breeds were only measured on ram lambs for both years. Pedigreed data, fixed effect information, and other phenotypes were obtained from the Sheep Improvement Limited (www.sil.co.nz) and Focus Genetics databases (www.focusgenetics.com), and they included: date of birth, sex (ewe/ram), birth flock, recording mob (regarding the same flock but under different paddocks at the time of measurement) for each trait at the time of measurement, birth rank, rearing rank, dam age, dam and sire identities, weaning weight (WWT at approximately 3 mo of age), liveweight at 12-mo of age (LW12) and fleece weight at 12-mo of age (FW12, only available for Romney and Highlander breeds).

Data editing

Lambs of unknown parentage in the pedigree dataset (n = 83), and lambs that had incomplete records of birth rank-rearing

Table 1. Records available for each trait based on birth year, flock and sex for FocusPrime, Texel, Romney, and Highlander sheep

Breed	Year	Flock	Sex	Trait									
				ST5	ST11	Stemp	FD	EMD	EMW	WWT	LWS	LW12	FW12
FocusPrime	2017	Flock 1	F	0	343	296	0	0	0	340	0	343	0
			M	0	459	400	458	454	458	455	457	459	0
		Flock 2	F	0	322	303	0	0	0	317	0	322	0
			M	0	103	100	103	103	103	102	103	103	0
	2019	Flock 1	F	0	0	0	0	0	0	0	0	0	0
			M	861	0	0	861	857	858	860	861	445	0
Texel	2017	Flock 1	F	0	255	251	0	0	0	254	0	254	0
			M	0	231	203	230	229	229	229	230	231	0
	2019	Flock 1	F	0	0	0	0	0	0	0	0	0	0
			M	246	0	0	264	246	246	244	264	162	0
Romney	2017	Flock 1	F	0	0	0	0	0	0	0	0	0	0
			M	0	825	813	822	820	822	824	824	823	809
Highlander	2017	Flock 1	F	0	435	376	0	0	0	430	434	434	433
			M	0	236	236	236	236	236	233	236	236	236
		Flock 2	F	0	313	257	0	0	0	313	0	313	308
			M	0	180	180	177	176	176	175	177	180	176
	2019	Flock 1	F	0	0	0	0	0	0	0	0	0	0
			M	637	0	0	637	637	637	634	637	0	0

EMD, loin-eye muscle depth; EMW, loin-eye muscle width; F, data available for females; FD, fat depth; FW12, fleece weight at 12-mo of age; LW12, live weight at 12-mo of age; LWS, live weight at FD, EMD, and EMW scanning; M, data available for males; ST11, skin thickness at 11-mo of age; ST5, skin thickness at 5-mo of age; Stemp, skin temperature; WWT, weaning weight.

rank (n = 35) were excluded from the final analysis. Dam ages of 6-yr-old or more were all considered as 5-yr-old (n = 254), due to relatively low numbers. Similarly, lambs with a birth rank of 4 (n = 36) were considered as triplets and those with a rearing rank of 4 (n = 28) were classified as lambs with a rearing rank of 3, due to relatively low numbers. Outlier observations (i.e., values that were outside of the mean ± 4 standard deviation (**SD**) range) were removed so all traits according to each breed followed a normal distribution. After editing, the data set for each breed included records for 2,088 FocusPrime lambs (born to 68 sires and 1501 dams), 732 Texel lambs (born to 37 sires and 505 dams), 825 Romney lambs (born to 58 sires and 762 dams) and 1,801 Highlander lambs (born to 56 sires and 1302 dams). A number of records available for each trait per breed and sex are available in Table 1.

Statistical analysis

Following data editing, the mean and SD for each trait by breed were obtained using the MEANS procedure of SAS 9.4 (SAS Institute Inc. 2013, Cary, NC, USA). Using the same software, analyses of variance for each dependent trait were performed using the GLM procedure. The linear model included the fixed effects of the contemporary group, which was defined as the group of lambs that were born in the same flock and year (BirthYear_flock, 1 to 3 levels depending on the trait/breed), sex (ewe/ram), Birth_rearing type (born as single, twin or triplet, and reared as single, twin or triplet, 6 to 8 levels depending on the trait/breed), the age of the dam (1 to 5 yr old, 4 to 5 levels depending on the trait/breed) and the recording mob for each trait at measurement (1 to 17 levels depending on the trait/breed). Additionally, for FD, EMD, and EMW analyses, LWS was included as a covariate. Live weight at scanning was tested as a covariate for ST11 and ST5, however, there was no significant effect and due to convergence problems for bivariate analysis, it was not used as a covariate. All the above-mentioned fixed effects and covariates were included in each model for each breed according to the availability of the records per trait. Least squares means and standard errors were estimated for each class of the fixed effects and were used for multiple mean comparisons using Fisher's least significant differences. Means were considered significantly different when $P < 0.05$.

Estimation of variance components and heritability

A single-trait animal model was used for the estimation of the variance components in order to calculate the h^2 of each skin trait within each breed. These calculations were undertaken using the statistical package ASReml-R version 4.2 (Butler et al., 2023). The single-trait animal model was represented as follows:

$$\mathbf{y} = X\mathbf{b} + Z\mathbf{a} + \mathbf{e}$$

where $\mathbf{y}$ is the vector of phenotypic traits; $\mathbf{b}$ is the vector of the fixed effects of the contemporary group, sex, birth-rearing type, the age of the dam and the recording mob; $\mathbf{a}$ is the vector of animal genetic effects; $\mathbf{e}$ is the vector of random residual effects; X and Z are the design matrices relating to the records of fixed and animal additive genetic, respectively.

The distributional properties of this model are the following:

$$\mathrm{E}\begin{bmatrix}\mathbf{y}\\ \mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}X\mathbf{b}\\ 0\\ 0\end{bmatrix}$$

$$\mathrm{var}\begin{bmatrix}\mathbf{u}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}A\sigma_a^2 0\\ 0 \quad I\sigma_e^2\end{bmatrix}$$

where $\boldsymbol{A}$ is the numerator relationship matrix between all the animals in the pedigree, $\boldsymbol{I}$ is an identity matrix of order equal to the number of ewes with records, σ_a^2 is the animal genetic additive variance and σ_e^2 is residual error variance.

Estimation of genetic and phenotypic correlations

A bivariate-trait animal model was utilized for the estimation of (co)variance components required for the estimation of genetic and phenotypic correlations between the traits by breed, using the same statistical package (ASReml-R version 4.2) as the heritabilities estimations. The model included the same fixed effects and covariates as the ones detailed above in the statistical analysis.

In matrix notation, the bivariate model can be represented as:

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}X_1 0\\ 0 \quad X_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix}+\begin{bmatrix}Z_1 0\\ 0 \quad Z_2\end{bmatrix}\begin{bmatrix}\mathbf{a}_1\\ \mathbf{a}_2\end{bmatrix}+\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}$$

where $\mathbf{y}_1$ and $\mathbf{y}_2$ is the vector of phenotypic measures for 2 traits under analysis; X_1 and X_2, and Z_1 and Z_2 constitute the design matrices pertaining to the fixed and random effects, respectively, on the phenotypes; $\mathbf{b}_1$ and $\mathbf{b}_2$ are the vectors of the fixed effects; $\mathbf{a}_1$ and $\mathbf{a}_2$ are the vectors of random effects of animal for each trait; and $\mathbf{e}_1$ and $\mathbf{e}_2$ are the vectors of random residual errors for each trait. The distributional properties of the model with E and V indicating the expectation and variance were as follows:

$$\mathrm{E}\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}X_1 0\\ 0 \quad X_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix}$$

and

$$\mathrm{V}\begin{bmatrix}\mathbf{a}_1\\ \mathbf{a}_2\\ \mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}=\begin{bmatrix}A\sigma_{a1}^2 & A\sigma_{a1a2} 0 & & 0\\ A\sigma_{a1a2} A\sigma_{a2}^2 & & 0 & 0\\ 0 & 0 & I_1\sigma_{e1}^2 & I_3\sigma_{e1e2}\\ 0 & 0 & I_3\sigma_{e1e2} I_2\sigma_{e2}^2 & \end{bmatrix}$$

where $\boldsymbol{A}$ is the numerator relationship matrix of order equal to the total number of animals in the pedigree file, according to the breed being analyzed; σ^2_{a1}, σ^2_{a2}, and σ_{a1a2} are the animals' (co)variance components for the 2 traits considered; $\boldsymbol{I}_1$ is an identity matrix of order equal to the number of records for trait 1; $\boldsymbol{I}_2$ is an identity matrix of order equal to the number of records for trait 2; $\boldsymbol{I}_3$ is an identity matrix of order equal to the number of records for trait with the highest number of records; and σ^2_{e1}, σ^2_{e2} and σ_{e1e2} are the residual (co) variance components for the traits.

Genetic and phenotypic correlations regarding ST5 with all other traits were not calculable due to the small size of the dataset.

Results

Descriptive statistics

The number of records, mean and SD and measurement ranges (Minimum and Maximum) for each trait by breed are presented in Table 2.

Factors affecting ST5, ST11 and Stemp

The contemporary group BirthYear_flock had a significant effect ($P < 0.05$) on ST11 only in the FocusPrime (F value = 6.73) and Highlander (F value = 9.92) breeds. The effect of sex was significant ($P < 0.05$) only on ST11 in FocusPrime (F value = 14.45), Texel (F value = 29.61), and Highlander (F value = 5.10). FocusPrime and Texel ewe lambs had 0.28 ± 0.02 and 0.58 ± 0.11 mm lower ST11 than respective ram lambs, whereas Highlander ewe lambs had 0.09 ± 0.04 mm higher ST11 than respective ram lambs. Birth_rearing type was significant ($P < 0.05$) only on ST5 in FocusPrime (F value = 3.09) and Highlander (F value = 3.07). The effect of age of the dam was significant ($P < 0.05$) only on ST11 in FocusPrime (F value = 3.93) lambs. For this breed, 1-, 2-, and 4-yr-old dams were associated with 0.23 ± 0.07, 0.10 ± 0.05, and 0.18 ± 0.06 mm less skin thickness, respectively, when compared to a 5-yr-old dam. The effect of the recording mob was significant ($P < 0.05$) on ST5 in FocusPrime (F value = 364.83) only, and on ST11 in Texel (F value = 4.74) and Highlander (F value = 183.72).

Regarding Stemp, only sex had a significant effect ($P < 0.05$) in FocusPrime (F value = 149.50) and Texel (F value = 108.47), where ewe lambs in the 2 breeds had 1.12 ± 0.09 and 1.22 ± 0.12 ^{0}C higher Stemp, respectively, than the respective ram lambs for each breed.

Heritabilities

Estimates of variance components (genetic, residual, and phenotypic) and h^2 for each skin trait per breed, are presented in Table 3. The h^2 estimates for ST5 were moderate for FocusPrime (0.39 ± 0.12) and low for Texel (0.11 ± 0.15) and Highlander (0.13 ± 0.09), whereas estimates for ST11 were moderate for all breeds. Estimates for Stemp were mostly low, reaching a value of almost zero in Romney (0.04 ± 0.03) and a high value in FocusPrime (0.39 ± 0.11).

Estimates of variance components and h^2 for each production trait per breed, are presented in Table S1.

Genetic and phenotypic correlations

Genetic and phenotypic correlations between ST11 and Stemp, and with the production traits are presented in Tables 4 and 5.

Skin thickness at 11-mo

Genetic and phenotypic correlations of ST11 with Stemp tended to be negative in all breeds, although linked to high standard errors. Genetic correlations of ST11 with FD tended to be positively correlated except in Texel (−0.10 ± 0.34). Genetic correlations of ST11 with EMD and EMW were variate; close to zero in FocusPrime, tended to be positive in Texel (0.42 ± 0.43 and 0.72 ± 0.41, respectively) as well as in Romney (0.44 ± 0.22 and 0.07 ± 0.31, respectively), but negative in Highlander (−0.55 ± 0.21 and −0.47 ± 0.33, respectively). Genetic correlations of ST11 with WWT were close to zero in FocusPrime and Romney, whereas Texel (0.14 ± 0.34) and Highlander (0.29 ± 0.22) tended to be positive. Genetic correlations of ST11 with LWS and LW12 were mixed: tended to be negative in FocusPrime (−0.03 ± 0.18 and −0.13 ± 0.22, respectively) and positive in Romney (0.09 ± 0.25 and 0.10 ± 0.24, respectively) and Highlander (0.26 ± 0.22 and 0.39 ± 0.21, respectively), while in Texel (−0.05 ± 0.42 and 0.69 ± 0.26, respectively) there was no consistent pattern of association.

Table 2. Descriptive statistics Mean ± SD, minimum and maximum values, and number of records for each trait in FocusPrime, Texel, Romney, and Highlander sheep

Trait	FocusPrime					Texel					Romney					Highlander				
	No. of records	Mean	SD	Min	Max	No. of records	Mean	SD	Min	Max	No. of records	Mean	SD	Min	Max	No. of records	Mean	SD	Min	Max
ST5 (mm)	861	3.22	0.41	2.10	4.40	246	3.41	0.36	2.50	4.90	.	.	.	.	.	637	3.15	0.40	2.10	4.30
ST11 (mm)	1,227	3.61	0.56	2.08	5.41	486	3.64	0.59	2.00	5.39	825	4.08	0.45	2.85	5.78	1,164	4.66	0.57	2.85	6.71
Stemp (°C)	1,099	37.47	1.53	31.40	41.20	454	37.24	1.44	32.70	40.40	813	37.84	1.32	32.40	41.10	1,049	36.15	1.97	28.90	41.00
FD (mm)	1,422	3.78	1.00	1.00	7.00	476	3.64	1.06	1.00	6.00	822	3.17	0.97	1.00	6.00	1,050	3.83	1.19	1.00	7.00
EMD (mm)	1,414	30.42	3.03	21.00	38.00	475	29.08	3.36	18.00	37.00	820	22.84	2.30	17.00	29.00	1,049	26.58	3.03	18.00	36.00
EMW (mm)	1,419	73.24	6.05	54.00	89.00	475	69.75	6.74	45.00	85.00	822	62.00	5.28	49.00	79.00	1,049	64.46	5.61	49.00	83.00
WWT (kg)	2,074	38.21	7.10	14.20	61.00	727	33.86	6.18	15.80	50.00	824	28.71	5.35	15.60	43.20	1,785	28.50	4.78	14.60	45.60
LWS (kg)	1,421	47.38	7.35	23.00	68.50	476	42.76	6.85	21.60	59.50	824	35.98	4.93	23.50	53.00	1,485	38.62	6.25	18.80	63.00
LW12 (kg)	1,672	64.32	11.98	32.80	97.00	647	59.80	9.04	35.00	83.00	823	67.57	6.30	50.00	83.50	1,163	52.75	8.50	34.00	79.00
FW12 (kg)	0	.	.	.	.	0	.	.	.	.	809	3.14	0.38	2.00	4.20	1,153	2.32	0.61	1.30	4.60

EMD, loin-eye muscle depth; EMW, loin-eye muscle width; FD, fat depth; FW12, fleece weight at 12-mo of age; LW12, live weight at 12-mo of age; LWS, live weight at FD, EMD, and EMW scanning; ST11, skin thickness at 11-mo of age; ST5, skin thickness at 5-mo of age; Stemp, skin temperature; WWT, weaning weight.
A dot is displayed where no records were available. The Romney dataset, in addition to FD, EMD, and EMW measurements in all breeds, did not include ewe lambs' data.

Table 3. Estimates of variance components (additive genetic, residual, and phenotypic) and heritabilities (±SE) for each skin trait in FocusPrime, Texel, Romney, and Highlander sheep

Trait	Breed	Variance			
		Genetic	Residual	Phenotypic	Heritability
ST5	FocusPrime	0.05 ± 0.02	0.07 ± 0.01	0.12 ± 0.01	0.39 ± 0.12
	Texel	0.01 ± 0.02	0.11 ± 0.02	0.12 ± 0.01	0.11 ± 0.15
	Romney	.	.	.	.
	Highlander	0.02 ± 0.02	0.14 ± 0.02	0.16 ± 0.01	0.13 ± 0.09
ST11	FocusPrime	0.07 ± 0.03	0.22 ± 0.02	0.28 ± 0.01	0.24 ± 0.08
	Texel	0.09 ± 0.05	0.22 ± 0.04	0.31 ± 0.02	0.29 ± 0.15
	Romney	0.06 ± 0.02	0.14 ± 0.02	0.20 ± 0.01	0.28 ± 0.10
	Highlander	0.05 ± 0.02	0.20 ± 0.02	0.25 ± 0.01	0.19 ± 0.07
Stemp	FocusPrime	0.80 ± 0.25	1.25 ± 0.21	2.05 ± 0.10	0.39 ± 0.11
	Texel	0.28 ± 0.19	1.37 ± 0.18	1.66 ± 0.12	0.17 ± 0.11
	Romney	0.07 ± 0.05	1.82 ± 0.10	1.76 ± 0.09	0.04 ± 0.03
	Highlander	0.48 ± 0.23	3.41 ± 0.24	3.87 ± 0.17	0.12 ± 0.06

ST5, skin thickness at 5-mo of age; ST11, skin thickness at 11-mo of age; Stemp, skin temperature.
A dot is displayed where no records were available for the trait.

Genetic correlations of ST11 with FW12 tended to be positive in both Romney (0.20 ± 0.22) and Highlander (0.55 ± 0.19). Additionally, overall phenotypic correlations of ST11 with all other traits were mostly positive and low.

Skin temperature

Genetic and phenotypic correlations of Stemp with FD were generally negative in all breeds. Genetic correlations of Stemp with EMD and EMW tended to be positive in FocusPrime (0.14 ± 0.18 and 0.06 ± 0.21, respectively) and Highlander (0.49 ± 0.27 and 0.40 ± 0.42, respectively); however, they tended to be negative in Texel (−0.25 ± 0.49 and −0.36 ± 0.33, respectively), but linked to high standard errors. Genetic correlations of Stemp with the weight traits had no clear pattern of association and were linked to high standard errors; therefore no clear result was obtained. Phenotypic correlations of

Table 4. Genetic (rG) and phenotypic (rP) correlations (±SE) of skin thickness at 11-mo of age (ST11) and skin temperature (Stemp), with production traits; subcutaneous FD, loin-eye muscle depth (EMD) and loin-eye muscle width (EMW), weaning weight (WWT), live weight at FD, EMD, and EMW scanning (LWS), live weight at 12-mo of age (LW12), fleece weight at 12-mo of age (FW12) in FocusPrime and Texel sheep

	FocusPrime				Texel			
	rG		rP		rG		rP	
	ST11	Stemp	ST11	Stemp	ST11	Stemp	ST11	Stemp
Stemp	−0.40 ± 0.20		−0.24 ± 0.03		−0.72 ± 0.26		−0.28 ± 0.05	
FD	0.25 ± 0.23	−0.25 ± 0.19	0.04 ± 0.04	−0.05 ± 0.04	−0.10 ± 0.34	−0.63 ± 0.28	0.02 ± 0.07	−0.08 ± 0.07
EMD	0.02 ± 0.22	0.14 ± 0.18	−0.07 ± 0.05	−0.02 ± 0.05	0.42 ± 0.43	−0.25 ± 0.49	0.06 ± 0.07	0.04 ± 0.07
EMW	0.02 ± 0.24	0.06 ± 0.21	−0.09 ± 0.04	−0.01 ± 0.05	0.72 ± 0.41	−0.36 ± 0.33	−0.12 ± 0.07	0.08 ± 0.07
WWT	0.02 ± 0.18	−0.19 ± 0.15	0.04 ± 0.03	−0.08 ± 0.04	0.14 ± 0.34	0.04 ± 0.41	0.04 ± 0.05	−0.09 ± 0.05
LWS	−0.03 ± 0.18	−0.19 ± 0.14	0.02 ± 0.04	−0.14 ± 0.05	−0.05 ± 0.42	0.18 ± 0.54	0.10 ± 0.07	−0.10 ± 0.07
LW12	−0.13 ± 0.22	0.12 ± 0.20	0.10 ± 0.03	−0.04 ± 0.04	0.69 ± 0.26	−0.33 ± 0.34	0.09 ± 0.05	−0.13 ± 0.05
FW12	.	.	.	.	.	.	.	.

A dot is displayed where no records were available to provide an analysis.

Table 5. Genetic (**rG**) and phenotypic (**rP)** correlations (±SE) of skin thickness at 11-mo of age (ST11) and skin temperature (Stemp), with production traits; subcutaneous FD, loin-eye muscle depth (EMD) and loin-eye muscle width (EMW), weaning weight (WWT), live weight at FD, EMD, and EMW scanning (LWS), live weight at 12-mo of age (LW12), fleece weight at 12-mo of age (FW12) in Romney and Highlander sheep

	Romney				Highlander			
	rG		rP		rG		Rp	
	ST11	Stemp	ST11	Stemp	ST11	Stemp	ST11	Stemp
Stemp	−0.53 ± 0.81		−0.05 ± 0.04		−0.38 ± 0.27		−0.08 ± 0.03	
FD	0.32 ± 0.26	−0.28 ± 1.45	0.07 ± 0.04	−0.12 ± 0.05	0.30 ± 0.32	−0.39 ± 0.35	0.13 ± 0.05	0.00 ± 0.05
EMD	0.44 ± 0.22	.	0.09 ± 0.04	.	−0.55 ± 0.21	0.49 ± 0.27	0.05 ± 0.05	−0.06 ± 0.05
EMW	0.07 ± 0.31	.	0.06 ± 0.04	.	−0.47 ± 0.33	0.40 ± 0.42	0.06 ± 0.05	−0.07 ± 0.05
WWT	0.04 ± 0.28	−0.57 ± 1.18	0.01 ± 0.04	−0.04 ± 0.04	0.29 ± 0.22	0.15 ± 0.26	0.07 ± 0.03	−0.04 ± 0.03
LWS	0.09 ± 0.25	.	0.00 ± 0.04	.	0.26 ± 0.22	−0.13 ± 0.25	0.07 ± 0.04	−0.13 ± 0.04
LW12	0.10 ± 0.24	−0.57 ± 1.15	0.13 ± 0.04	−0.09 ± 0.04	0.39 ± 0.21	0.33 ± 0.25	0.02 ± 0.03	−0.14 ± 0.03
FW12	0.20 ± 0.22	.	0.21 ± 0.04	.	0.55 ± 0.19	−0.09 ± 0.23	−0.03 ± 0.03	−0.08 ± 0.03

A dot is displayed where no records were available to provide an analysis.

Stemp with EMD, EMW, WWT, LWS, and LW12 were generally negative and low. No correlation was found for Stemp with FW12 in Highlander due to high standard errors.

Discussion

Skin thickness at around 11 mo of age had moderate h^2 estimates in all breeds, while ST5 h^2 estimates were moderate in FocusPrime, but low in Texel and Highlander. These estimates were found to be comparable with those compiled by Gregory (1982a), Slee et al. (1991), Janssens and Vandepitte (2004), Tait et al. (2015) and Soltani-Ghombavani et al. (2017). Furthermore, regarding Stemp, a high heritability estimate was found in FocusPrime, whereas low estimates were found in the other breeds. However, estimates in Texel and Romney were linked to high standard errors. No previous published reports were found for the h^2 of Stemp in lambs of 11 mo of age. Nevertheless, the heritabilities obtained here for most breeds were similar to the estimates for rectal temperature in Merino lambs within 18 h of birth (Brien et al., 2010). Moreover, high heritability estimates were found in rectal temperature in Merino weaners and hoggets (Rose and Pepper, 2001), which were similar to the ones found in FocusPrime.

Ewe lambs of FocusPrime and Texel breeds in the present study showed thinner skin than ram lambs at 11 mo, whereas the opposite was observed in Highlander. Data collected by Cloete et al. (2004) and Van Der Merwe et al. (2021) somewhat supports the observations in FocusPrime and Texel, where skin thickness appeared to be affected by the sex of the individual, with rams having heavier skin weights or producing thicker leathers, compared to ewes. On the other hand, Soltani-Ghombavani et al. (2017) observed that ewe lambs of approximately 8 mo of age had thicker skin when compared to ram lambs, which would be in agreement with the results in the current study regarding the Highlander breed. Meanwhile, Jopson et al. (2000) found no difference between sexes. Furthermore, the sex of an individual also had an effect on Stemp, where ewe lambs of FocusPrime and Texel breeds had higher recordings of Stemp than the ram lambs. As the ewe lambs within these breeds also showed a thinner skin than their ram peers, it may appear that having thinner skin creates less insulation and therefore more heat from the body escapes to the surface. In support of these effects, Soltani-Ghombavani (2021) observed that during an induced cold stress period, thick-skinned, new-born, Romney lambs had lower Stemp than thin-skinned lambs. Consequently, it was proposed that having a thicker skin could positively affect thermoregulation in lambs by minimizing heat loss through the skin surface while reducing the heat production required to maintain body temperature.

All genetic correlations of ST11 with Stemp tended to be negative in all breeds. A lower skin temperature would indicate that more endogenous heat would remain within the body with less loss into the environment, thereby maintaining homeothermy in cold conditions (Dwyer and Lawrence, 2005). Selection to increase cold tolerance in lambs is known to be genetically positively associated with traits such as skin thickness and total body insulation (Stott and Slee, 1987). Therefore, animals that have thicker skin or possess better insulation such as a larger body weight, deeper wool coat, or a great amount of fat reserves would be more suitable to endure cold conditions, and therefore have greater chances of survival under adverse conditions. Further, this negative association between skin thickness and skin temperature corroborates the observed relationship between these 2 variables in new-born Romney lambs subjected to cold stress Soltani-Ghombavani (2021), where thick-skinned lambs had significantly lower skin temperature, compared to thin-skinned counterparts. It was also found in that study, presumably due to being more heat dissipated through the skin, the thin-skinned lambs were found to generate significantly more heat in order to maintain their core body temperature.

Within the present study, genetic and phenotypic correlations of ST11 with FD tended to be low positive, but were linked to high standard errors. These results agree with Jopson et al. (2000), where sheep selected for increased backfat were observed to have thicker skin. This impact on FD when selecting for skin thickness might be regarded as unfavorable for the meat market (Soltani-Ghombavani et al., 2017). Nevertheless, in the case of extensively managed animals that live in colder environments, such as hill sheep, more layers of insulation would increase survival (Dwyer and Lawrence, 2005) and increase the numbers available for sale. For this reason, it might be more desirable to have a somewhat fatter lamb despite the market needs (Greeff et al., 2008; Mortimer et al., 2017). Besides, the FD measurements observed within the dataset analyzed, which varied between 3.17 to 3.83 mm on average, are associated with being within the "low fat content" fat class by the New Zealand Meat Classification Authority (2004), therefore, a modest increase in FD is unlikely to incur a market penalty. Furthermore, negative genetic and phenotypic associations were generally found between Stemp and FD, adding to the above statements that a greater FD would mean more insulation, therefore less heat would be lost through the skin.

In addition to fat being an important insulation trait, the conjoined effects of a larger body weight could exert a positive effect on cold tolerance (Plush et al., 2016). In the current study, all body weight traits tended to be positive with ST11 in Highlander, also, LWS and LW12 tended to be positive in Romney, as well as WWT in Texel. Similarly, Soltani-Ghombavani (2021) reported a positive genetic correlation between the skin thickness of Romney lambs of around 9 mo of age with LWS and LW12. Overall, these observations may be in accordance with previous reports, where skin growth was positively associated with the increase in body weight (Passman and Sumner, 1987), therefore heavier lambs would have heavier skins (Van der Merwe et al., 2021). Consequently, it would be likely to observe heavier body weights linked to a thicker skin in lambs after selecting for skin thickness, enhancing further body insulation and therefore potential lamb survival in adverse weather conditions during lambing. Due to large standard errors in these correlations, further studies are required to confirm this. Moreover, correlations of Stemp with weight traits had no clear pattern of association, making it difficult to provide a clear result for each breed.

Genetic and phenotypic correlations of FW12 tended to be positive with ST11 measurements at scanning in Romney and Highlander. These results were in agreement with previous reports, where thicker skin was associated with greater fleece weight at around 8 mo (Soltani-Ghombavani et al., 2017) and 15 mo (Gregory, 1982b). Given a deeper coat provides greater insulation (Stott and Slee, 1987; Slee et al., 1991; Plush et al., 2016), this partnership with thicker skin would become essential for survival in cold environments. Accordingly, sheep breeders have highlighted the importance of considering skin thickness in making selection decisions towards wool improvement (Gifford et al., 1995).

Additionally, skin thickness at 11 mo and the muscle traits at scanning showed a great variety of results, from a tendency to zero in FocusPrime, to positive values in Texel and Romney and negative values in Highlander. Previously, a weak unfavorable genetic correlation was observed between skin thickness and EMD in Romney lambs (Soltani-Ghombavani et al., 2017). That study included ewe lamb data and utilized a much bigger dataset exclusively from Romney lambs, as opposed to the relatively smaller sample size and only ram data of the current study. This considered, and given there is limited literature exploring the relationship between skin thickness and muscle traits, further research into how muscle traits are associated with skin thickness is required. Furthermore, the correlations of Stemp with the muscle traits tended to be positive in FocusPrime and Highlander and negative in Texel. Hence, it seems that selecting for Stemp might impact the muscle traits in different directions according to the breed.

Conclusions

Skin thickness was observed to be moderately heritable, particularly when measured at 11 mo of age. Within the breeds, this trait has been shown to be positively correlated with fleece weight and FD, though estimates are associated with relatively large standard errors. Also, an overall favorable negative correlation was found between skin thickness and infrared-measured skin temperature, which is an indicator of the heat loses to the environment. However, considering the inconsistency in heritability and correlations across the 3 breeds, coupled with high standard errors, further research employing a larger dataset is warranted. Also, the genetic association of skin thickness and skin temperature with lamb survival in these 3 breeds should be explored. If a positive association of these 2 traits with lamb survival is evinced in those studies, there is scope for skin thickness and skin temperature to be potentially included in breeding programs aimed at improving lamb survival.

Supplementary Data

Supplementary data are available at *Journal of Animal Science* online.

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Author contributions

Andrea Graña-Baumgartner (Data curation, Formal analysis, Writing—original draft, Writing—review & editing), Venkata Dukkipati (Conceptualization, Funding acquisition, Supervision, Writing—review & editing), Patrick Biggs (Software, Supervision, Writing—review & editing), Paul Kenyon (Conceptualization, Funding acquisition, Supervision, Writing—review & editing), Hugh Blair (Conceptualization, Funding acquisition, Supervision, Writing—review & editing), Natalie Pickering (Resources, Writing—review & editing), Danitsja Van der Linden (Resources, Writing—review & editing), and Nicolas Lopez-Villalobos (Software, Supervision, Writing—review & editing)

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