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Genetic parameters and response to selection for weight, muscle depth, fat depth and EUROP carcass classification in Icelandic sheep

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ABSTRACT

The breeding goals of the Icelandic sheep breed have focused on fast growth, muscularity and low proportion of fat in lambs at slaughter, and selection has focused on these traits for the past decades. However, the weights of adult sheep and birth weights are also important traits to consider, because of feed and space requirements, and may be affected by selection on growth and body composition. We used data collected at the Hestur research flock from 1999 to 2022 to estimate heritability, genetic correlations and genetic trends for standard reference weight of ewes (SRW), birth weight (BW), and traits related to weight, fat and muscularity of slaughter lambs. The heritability of SRW was 0.65, direct heritability of BW was 0.15, and maternal heritability of BW was 0.30. Genetic correlations and genetic trends indicate that selection for higher weaning weight can lead to increased SRW and BW, while selection for more muscularity at fixed weight has the opposite effect.

Keywords: Adult weight, birth weight, genetic correlation, lamb, response to selection

YFIRLIT

Erfðastuðlar og úrvalssvörun fyrir þunga, vöðvadýpt, fitudýpt og kjötmat í íslensku fé

Ræktunarmarkmið fyrir íslenskt fé hafa síðustu áratugi lagt áherslu á hraðan vöxt lamba og hátt vöðvahlutfall við slátrun og mjög ákveðið val hefur verið fyrir þessum þáttum. Þyngd fullorðins fjár og þyngd lamba við fæðingu eru þó einnig mikilvægir eiginleikar vegna fóðurþarfa og umhirðu fjárins og geta orðið fyrir áhrifum óbeins úrvals vegna erfðafylgni við afurðaeiginleika. Við notuðum gögn sem hefur verið safnað á tilraunabúinu á Hesti frá árunum 1999 til 2022 til að meta arfgengi, erfðafylgni og úrvalssvörun fyrir staðalþunga áa, fæðingarþunga lamba og eiginleika sem tengjast þunga, vöðva og fituhlutfalli í sláturlömbum. Arfgengi staðalþunga reyndist hátt, 0,65. Arfgengi beinna áhrifa á fæðingarþunga var 0,15 og arfgengi mæðraáhrifa var 0,30. Erfðafylgni og úrvalssvörun í hjörðinni bendir til þess að val fyrir auknum haustþunga geti leitt til hækkandi staðalþunga og fæðingarþunga en val fyrir vöðvaþykkt og gerð við fastan þunga geti haft öfug áhrif.

INTRODUCTION

The main production from Icelandic sheep are lambs that are slaughtered at three to six months of age for meat production. Consequently, the weight and tissue proportions at that age are important for their production value. Lambs that are heavy early in the season and have a high proportion of muscle tissue are the most valuable. However, the weight of sheep at other stages of their development is also important for feeding and management of the flock. Therefore, studying the weight of sheep from birth until adult weight is reached is valuable.

Indoor winter feeding of ewes is a major cost for Icelandic sheep farms. Maintenance nutrition requirements are proportional to animal metabolic live weight (e.g., NRC 2007) and space requirements are also proportional to adult size. Sveinbjörnsson & Örnólfsson (2024) estimated the standard reference weight (SRW) of Icelandic sheep at body condition score 3.0 to be 70.4 ± 3.4 kg. The SRW indicates the inherent weight of fully mature sheep, corrected for body condition score and production stage. However, the heritability of adult weight, or SRW, and genetic correlations to other traits have not been estimated for the Icelandic sheep breed.

Birth is another timepoint in the life of sheep where their weight is important. The birth weight (BW) of lambs is related to lamb survival according to studies in other breeds, with heavier lambs (Riggio et al. 2008) or lambs with intermediate weights (Everett-Hincks & Dodds 2008) having more chance of survival in harsh conditions. Icelandic research suggests that ewes having heavier lambs are more likely to need assistance for lambing (Pálsdóttir 2018). Furthermore, lamb BW affects the nutrition requirements of ewes around lambing. However, the heritability of BW and genetic correlations to other traits are unknown for Icelandic sheep.

The Icelandic sheep population has been selected intensively for more muscularity and less fat on carcass (Thorsteinsson 2002, Eiríksson & Sigurdsson 2017), along with selection for number of lambs born and for faster growing lambs (Árnason & Jónmundsson 2008). The research flock in Hestur farm pioneered progeny testing for the selection for muscular and lean lambs, aiming for genotypes with short and thick legs, which correlated with high lean percentage (Thorsteinsson & Björnsson 1982, Thorsteinsson 2002). The use of ultrasound measures of eye muscle depth (UMD) and fat depth over eye muscle (UFD) over the 3rd lumbar vertebra in live lambs post weaning and the EUROP carcass grading system for carcass conformation (CC) and carcass fat (CF) boosted the progress in these traits, both in the research flock (Thorsteinsson 2002) and the national flock (Eiríksson & Sigurdsson 2017). Both the EUROP carcass grading system and the ultrasound measurements have proven useful for predicting lean and fat percentage in carcass (Thorsteinsson et al. 1994, Einarsson et al. 2014). The percentages of muscle, fat, and bones in growing sheep are dependent on the proportion of adult weight that growing animals have reached, with bones and muscles growing proportionally faster with a low degree of maturity, while the growth rate of fat tissue increases as animals approach adult weight (Thorgeirsson and Thorsteinsson, 1989; CSIRO, 1990; Friggens et al. 1997). Therefore, selection for muscle or fat percentage at fixed weight might be selection for proportion of SRW that the lamb has reached, and thus is related to the inherited SRW of the animals.

Therefore, the aims of this study were (1) to estimate the heritability of SRW and BW in Icelandic sheep, (2) to estimate genetic correlations of UMD, UMF, and carcass score with weaning weight (WW), SRW, and BW, and (3) to estimate genetic trends in the Hestur research flock, both for directly selected traits and for the possible correlated response of BW and SRW.

MATERIALS AND METHODS

Data

The data for this study have been routinely collected at the Agricultural University of Iceland Hestur research sheep flock, based in Borgarfjörður, Southwest-Iceland. The production system and management of the farm are typical for Icelandic sheep farms, with lambing in April and May and slaughter in September and October after grazing on summer pasture. The flock management is described in more detail by Sveinbjörnsson et al. (2021). The breeding goals within the flock from 2001 to 2010 were to increase muscle growth, reduce carcass fat, increase carcass weight and reduce the number of ewes having singles. After 2010, the goal was to maintain moderate carcass fat rather than to reduce the fatness, but otherwise the goals were the same as 2001 to 2010. The main selection steps were the selection of breeding rams among the lambs, selection of elite rams to use for artificial insemination (AI) in the flock, and selection of ewe lambs as replacement ewes. The selection of lambs (ram and ewe) for muscularity and fatness were based on UMD, UFD, scoring of eye muscle width, and *in vivo* scoring of muscularity in the leg and shoulder after weaning. The selection for weight was based on WW, weight at approx. 6 weeks, and ewe production index of the dam (based on CW of offspring). After 2007, the animal model estimated breeding values (EBV) based on pedigree (i.e. parent average for lambs) for the ewe production index (Árnason & Jónmundsson, 2008) were also included in the selection for weight. The selection of AI rams for use in the flock was primarily based on EBV for CC, CF, ewe production index, and number of lambs born. Around 20-25% of the dams were artificially inseminated with semen from elite AI-sires each year. All rams in the flock were progeny tested on their first year, but the best rams from the progeny testing were sold to national AI stations.

Data on 20,937 lambs born in the years 2001 to 2022 were used for this study, including the BW, WW, UMD, UFD, carcass weights, and carcass classification. The SRW of 2,618 ewes born in from 1999 to 2017 was estimated as body weight of ewes on their 5th year of age and at body condition score 3. That was done with random individual effects according to Table 4 (1266 ewes) and Equation 1 (1352 ewes) in Sveinbjörnsson & Örnólfsson (2024), as described in more detail in that paper. Additionally, we had access to the pedigree recordings of the Icelandic sheep population from the Farmers Association of Iceland.

The data were filtered such that only records on animals with known dam and sire were included. For lamb records to be included, information on litter (singles, twins, triplets, or quadruplets) and how they were raised (as singles, twins, or triplets) had to be available. Progeny of dams recorded with more than 49% of leadersheep ancestry was excluded. Leadersheep are a specific line or breed within the Icelandic population that have been selected for behaviour rather than production. The EUROP carcass classification was converted to a linear scale as in multiple other studies with EUROP carcass classification (e.g. Eiríksson and Sigurdsson 2017, Einarsson et al. 2015, Maxa et al. 2007), such that for CC classes the values were E=14, U=11, R=8, O=5 and P=2. For CF, the values were 1=2, 2=5, 3-=7, 3=8, 3+=9, 4=11 and 5=14. The number of records for each trait, the means and standard deviations are presented in Table 1. The distribution of the traits is presented in Figure 1.

Table 1. Number of records, means, and standard deviation for the analysed traits, along with age at weaning and carcass weight.

Trait	N	Mean	Standard deviation
SRW	2 501	70.8 kg	5.9 kg
BW	20 314	3.8 kg	0.7 kg
Age at weaning	17 541	139.3 days	8.3 days
WW	17 541	38.3 kg	5.3 kg
UMD	17 541	27.7 mm	3.25 mm
UFD	17 541	2.74 mm	0.87 mm
Carcass weight	15 559	16.0 kg	2.2 kg
CC	15 559	9.59	1.95
CF	15 559	5.98	1.72

SRW: Standard reference weight, BW: Birth weight, WW: Weaning weight, UMD: Ultrasound measure of eye muscle depth, UFD: ultrasound measured fat over eye muscle, CC: Carcass conformation score, CF: Carcass fat score.

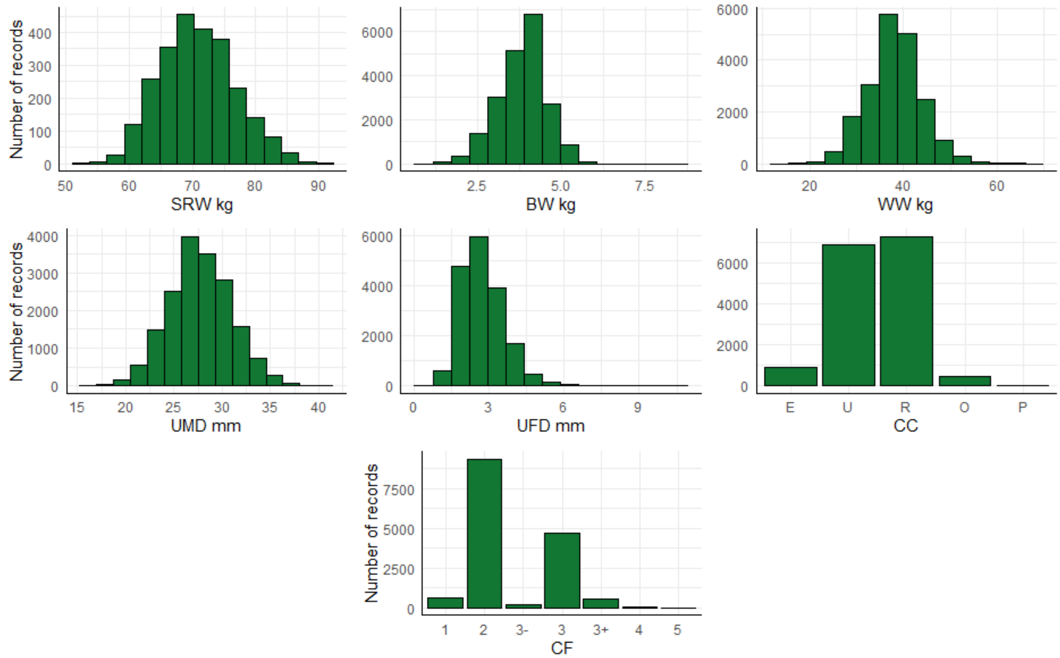

Figure 1. Distribution of standard reference weight (SRW), birth weight (BW), weaning weight (WW), ultrasound measured eye muscle depth (UMD), ultrasound measured fat thickness over eye muscle (UFD), carcass conformation score (CC) and carcass fat score (CF). Note that the 3- fat class was only used in two years (2008 and 2011).

For correcting systematic effect of age of (foster) dam, groups were formed for every year of age, except that six-year-old ewes and older formed a single group. For the correction of systematic effects of number in birth on BW, five groups were constructed: singles from one year old dams, twins from one year old dams, singles from two years and older dams, twins from two years and older dams, and triplets or quadruplets from two years and older dams. For WW, 11 groups were formed based on the combination of number in the litter, number of lambs raised together by the same dam, and age of dam and foster dam (one year old or older). The groups were 1) raised as singles by one-year old dams, born either by one-year old dams single or by older dam, 2) born and raised as twin by one-year old dam, 3) born as twin by one-year old dam, raised as single by one-year old dam, 4) born by a one-year old dam but raised as a twin by older foster-dam, 5) born and raised as single by older dam, 6) born single but raised as twin by older dam, 7) born twin but raised as single by older dam, 8) born and raised as twin by older dam, 9) born triplet or quadruplet but raised as single by older dam, 10) born as triplet or quadruplet but raised as twin by older dam, 11) raised as triplet.

The pedigree for estimation of genetic parameters and prediction of breeding values was traced from sheep with records back to animals born in 1990. In total, the pedigree included 29,306 sheep.

Estimation of genetic parameters

We estimated genetic parameters for SRW, BW, WW, UMD, UMD, CC, and CF using the data from Hestur research flock. The models used for SRW was relatively simple since the SRW was already corrected for most systematic factors. The model was

$$y_{ij} = year_j + a_i + e_i$$

where y_{ij} is the SRW of ewe i born in year j, $year_j$ is the fixed effect of birth year j, a_i is additive genetic effects of the individual, and e_i is independent, normally distributed residual. The model for BW included both direct and maternal effects and correction for systematic effects:

$$y_{ijklmn} = year_j + sex_k + dage_l + LS_n + s_{mk} + v_m + u_m + a_i + e_i$$

where y_{ijklmn} is BW of lamb i born to dam m, sex_k, is the fixed effect of sex k of the lamb (male or female), $dage_l$ is the fixed effect of dam age group l, LS_n is the fixed effect of litter size group n, s_{mk} is the random effect of common litter of dam m, in the year k, v_m is the random effect of permanent environment of the dam, u_m is the random maternal additive genetic effect. For WW, the model was like for BW except that maternal effects were connected to the foster dam in cases of cross-fostering and regression on the age at weaning was added. Thus, the model for the genetic parameter estimation for WW was

$$y_{ijkfop} = \beta_1 d + year_j + sex_k + f\,dage_o + LFS_p + s_{fk} + v_f + u_f + a_i + e_i$$

where y_{ijkfop} is WW of animal i, d is the age at weighing in days, is the regression coefficient on age at weaning, $fdage_o$ is the fixed effect of age of foster dam o, LFS_p is the fixed effect of litter size and type of rearing group p, s_{fk} is the random effect of common litter effect of (foster)dam f in year k, v_f is the random effect of permanent environment of the (foster)dam, and u_f is the random maternal additive genetic effect of the (foster)dam. For weight corrected UMD and UMF, systematic effects relating to the dam did not improve fit in preliminary testing. The model for genetic parameter estimation of UMD and UFD was

$$y_{ijk} = \beta_1 d + \beta_2 r + \beta_3 r^2 + year_k + sex_j + a_i + e_i$$

where y_{ijk} is the UMD or UMF measurements, r is the weight of the lamb at the time of measurement (WW), and β_2 and β_3 are regression coefficients. For carcass traits the model for genetic parameter estimation was

$$y_{ijk} = \beta_1 d + \beta_2 w + \beta_3 w^2 + year_k + sex_j + a_i + e_i$$

where y_{ijk} is the CC or CF grading on the linear scale, and w is the carcass weight.

The additive genetic effects (a_i) for all traits were assumed to follow a multivariate normal distribution with variance σ_a^2 and relationships modelled with the numerator relationship matrix based on registered pedigree. The relationship matrix accounted for inbreeding but did not include unknown parent groups, because the pedigree records were mostly complete in the years where we had phenotypic data. Genetic correlations between traits were included in the model. The maternal additive genetic effects (u_m and u_f) were assumed to follow multivariate normal distribution with maternal additive genetic variance σ_u^2 and relationships among (foster) dams based on the numerator relationship matrix. Direct and maternal genetic effects were assumed to be correlated within and between traits. The common litter (or rearing) effects ($s_{m,k}$ and $s_{f,k}$) were assumed to be independent among dams and years and to follow normal distribution with variance σ_s^2. The common litter effects for BW and WW were assumed to be independent. The permanent environment effects of dam (or foster dam) (v_m and v_f) were assumed to be independent among dams and normally distributed with variance σ_v^2. The permanent environment of dam effects on BW and permanent environment of (foster) dam effects on WW were assumed to be correlated. The residuals were assumed to be independent and normally distributed with variance σ_e^2 and correlated between traits within animal.

The genetic parameters were estimated with the AI-REML algorithm, as implemented in the DMUAI module of the DMU package (Madsen & Jenssen 2023). Because of convergence issues when all traits were included in the same run, the genetic parameters were estimated with three separate multi-trait estimations. Estimation I included SRW, BW, WW, UMD, and UFD, estimation II included SRW, BW, CC, and CF, and estimation III included WW, UMD, UFD, CC, and CF. In that way, all modelled correlations were estimated in at least one estimation. The presented results on variance components and genetic correlations are from estimation I for traits included in estimation I, from estimation II for traits included in estimation II but not in estimation I, and estimation III for the remaining.

Genetic trends

For estimating genetic trends, we estimated the breeding values for all traits in a multi-trait model using the DMU5 module of the DMU package (Madsen & Jenssen 2023). The genetic parameters were combined from estimations I, II, and III, such that for (co)variance components included in multiple estimations the average was used. The resulting covariance matrix was positive definite. The genetic trends for direct effects on BW, direct effect on WW, UMD, and UFD were estimated as the mean EBV of sheep born in the flock each year from 2001 to 2022. For maternal effects on BW and WW, we used sheep born from 2001 to 2020, and for SRW, sheep born from 2001 to 2017. Annual rate of genetic trend was estimated as the regression coefficient of mean EBV for each year of birth on year of birth.

RESULTS

The estimated genetic parameters are presented in Table 2. The heritability estimates were accurate, with standard error 0.03 for SRW and lower for other traits. The SRW had the highest heritability, 0.65±0.03 (±standard error), while the heritabilities of UMD, UFD and CC were also above 0.4. Maternal heritability was higher than direct heritability for BW, 0.30±0.02 compared with 0.15±0.02. However, for WW, the maternal genetic effect was less important with maternal heritability of 0.11±0.01. Common litter effects explained 2% of the phenotypic variance of BW but 25% of the WW variation. Permanent environmental effects of the dam explained 5% and 8% of the variation of BW and WW, respectively.

The estimated genetic correlations between traits are presented in Table 3. The genetic correlations between SRW and other weight traits were positive, the highest being 0.68±0.07 for direct effect on WW but 0.26±0.07 and 0.26±0.04 for direct and maternal effects on BW, respectively. Both UMD and CC had negative genetic correlations with SRW. Increased fat was related with lower SRW with a genetic correlation between UFD and SRW of

Table 2. Additive genetic variance of direct (σ_a^2), and maternal (σ_u^2) effects, variance component of common environment of litters (σ_s^2), variance component of permanent environment of dams (σ_v^2), residual variance (σ_e^2), direct heritability (h_b^2), and maternal heritability (h_m^2). For SRW, BW, WW, UMD, and UFD the results are from estimation I. The CC and CF parameters are from estimation II. Standard errors of the estimates are in subscripts.

	σ_a^2	σ_u^2	σ_s^2	σ_v^2	σ_e^2	h_b^2	h_m^2
SRW	$24.9_{1.8}$				$13.4_{1.1}$	$0.65_{0.03}$	
BW	$0.05_{0.05}$	$0.10_{0.08}$	$0.006_{0.002}$	$0.017_{0.004}$	$0.157_{0.004}$	$0.15_{0.02}$	$0.30_{0.02}$
WW	$3.3_{0.3}$	$2.6_{0.4}$	$6.0_{0.2}$	$1.9_{0.3}$	$10.0_{0.2}$	$0.14_{0.01}$	$0.11_{0.01}$
UMD	$2.8_{0.1}$				$3.48_{0.08}$	$0.44_{0.02}$	
UFD	$0.24_{0.01}$				$0.33_{0.08}$	$0.42_{0.02}$	
CC	$1.7_{0.1}$				$1.40_{0.06}$	$0.55_{0.02}$	
CF	$0.53_{0.04}$				$1.24_{0.03}$	$0.30_{0.02}$	

SRW: Standard reference weight, BW: Birth weight, WW: Weaning weight, UMD: Ultrasound measure of eye muscle depth, UFD: Ultrasound measure of fat over eye muscle, CC: Carcass conformation score, CF: Carcass fat score.

Table 3. Genetic correlations between the studied traits. Standard errors of the estimates are in subscripts. The correlations were based on estimation I for the correlations between traits included in estimation I, based on estimation II for the correlations included in estimation II but not in I, and from estimation III for the remaining.

Trait	SRW	BW dir.	BW mat.	WW dir.	WW mat.	UMD	UFD
BW dir.	$0.26_{0.07}$						
BW mat.	$0.26_{0.04}$	$-0.05_{0.06}$					
WW dir.	$0.68_{0.05}$	$0.36_{0.07}$	$0.36_{0.06}$				
WW mat.	$0.29_{0.06}$	$-0.07_{0.09}$	$0.36_{0.07}$	$-0.01_{0.08}$			
UMD	$-0.54_{0.03}$	$-0.09_{0.06}$	$-0.17_{0.04}$	$-0.56_{0.04}$	$-0.17_{0.05}$		
UFD	$-0.22_{0.04}$	$-0.12_{0.06}$	$-0.28_{0.04}$	$-0.17_{0.05}$	$-0.15_{0.05}$	$0.10_{0.03}$	
CC	$-0.29_{0.04}$	$-0.06_{0.06}$	$-0.41_{0.04}$	$-0.38_{0.06}$	$-0.45_{0.05}$	$0.48_{0.03}$	$0.10_{0.04}$
CF	$-0.08_{0.05}$	$-0.10_{0.07}$	$-0.34_{0.05}$	$-0.05_{0.07}$	$-0.42_{0.06}$	$-0.01_{0.04}$	$0.64_{0.03}$

SRW: Standard reference weight, BWD: Birth weight, WW: Weaning weight, UMD: Ultrasound measure of eye muscle depth, UFD: ultrasound fat over eye muscle, CC: Carcass conformation score, CF: Carcass fat score, dir.: Direct effects, mat.: Maternal effects.

-0.22±0.04, but the genetic correlation between CF and SRW was weak. Direct genetic effect on BW was correlated to direct effect on WW with a genetic correlation of 0.36±0.05, but genetic correlations with maternal effects, UMD, UMF, CC, and CF were low. The maternal effect on BW was positively genetically correlated with direct and maternal effects on WW but negatively correlated with UMD, UMF, CC, and CF. The genetic correlation between CC an CF was 0.32±0.04.

Table 4 shows the annual genetic trends for the studied traits. There were significant genetic trends in all traits except SRW. In genetic standard deviations per year ($\sigma_a y^{-1}$) of each trait, the most gain was in UMD, 0.074±0.008 $\sigma_a y^{-1}$, which equals 0.11±0.01 mmy^{-1}. The genetic trend in UFD and CF was towards less fat. For BW (direct and maternal), WW (direct and maternal), UMD, UFD, CC, and CF the trend was within 0.02 to 0.04 $\sigma_a y^{-1}$.

Figure 2 shows the mean EBV for year of birth for SRW, BW, and WW, based on the results of estimation I. From 2000 to 2010, the trends in SRW and the direct effects on BW and WW seem downwards, but after 2010 the trend was towards higher weights. The trends in maternal effects were more stable. Figure 3

Table 4. Annual genetic trends from 2001 in lambs born in the Hestur research flock.

Trait	In unit	In gen. std.	Significance
SRW	0.03 kg $_{0.03}$	$0.006_{0.006}$	NS
BW direct effects	0.0048 kg $_{0.0005}$	$0.024_{0.002}$	***
BW maternal effects	0.007 kg $_{0.002}$	$0.025_{0.006}$	**
WW direct effects	0.04 kg $_{0.01}$	$0.023_{0.006}$	**
WW maternal effects	0.034 kg $_{0.004}$	$0.020_{0.002}$	***
UMD	0.11 mm $_{0.01}$	$0.074_{0.008}$	***
UFD	-0.016 mm $_{0.002}$	$-0.033_{0.005}$	***
CC	$0.031_{0.006}$	$0.024_{0.005}$	***
CF	$-0.028_{0.003}$	$-0.038_{0.004}$	***

NS: not significant, * : p<0.05, ** : p< 0.01, *** : p<0.001
SRW: Standard reference weight, BW: Birth weight, WW: Weaning weight, UMD: Ultrasound measure of eye muscle depth, UFD: ultrasound fat over eye muscle, CC: Carcass conformation score, CF: Carcass fat score.

shows the genetic trends for UMD, UFD, CC, and CF. For all four traits, the genetic trends were clearer in 2001 to 2010 than they were in the later period.

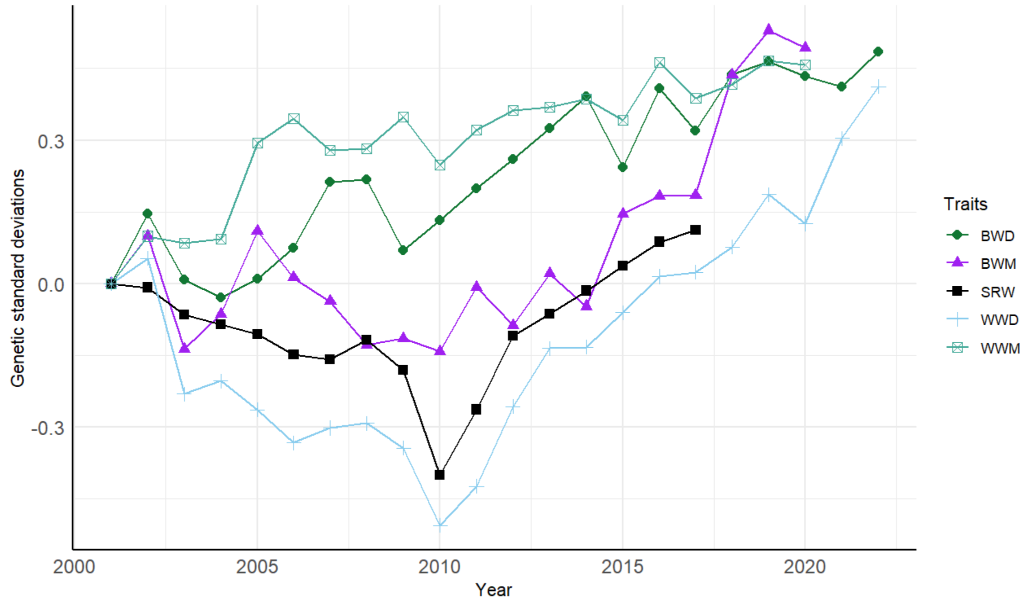

Figure 2. Mean estimated breeding values by birth year for standard reference weight (SRW), direct effect on birth weight (BWD), maternal effect on birth weight (BWM), direct effect on weaning weight (WWD), and maternal effect on weaning weight (WWM) for lambs born at the Hestur research flock.

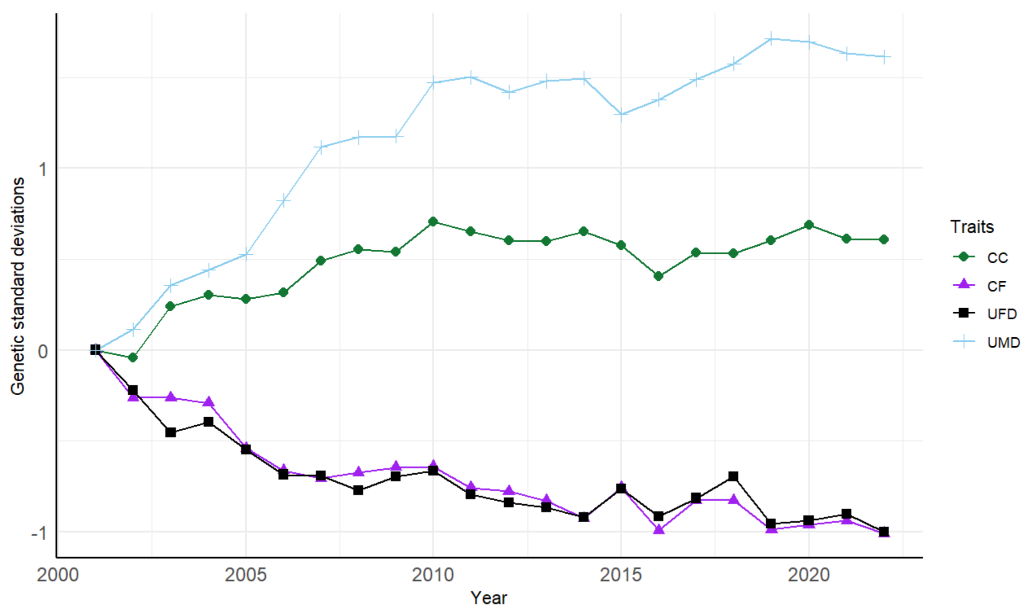

Figure 3. Mean estimated breeding values by birth year for ultrasound eye muscle depth (UMD), ultrasound fat depth over eye muscle (UFD), carcass conformation score (CC), and carcass fat score (CF) in lambs born at the Hestur research flock.

DISCUSSION

We found that SRW was highly heritable and with a genetic correlation with traits that are part of the breeding goal. We have also confirmed heritability of birth weights for Icelandic sheep, where maternal genetic effects account for twice as much as direct effects. We found positive genetic correlations between weight traits at different ages of sheep. Genetic gain was confirmed in the Hestur research flock from 2001 to 2021 for WW, muscularity and lower carcass fat. Correlated response in BW was confirmed, but for SRW the genetic trend was not statistically significant across the studied period.

The high heritability of SRW (Table 2) was not surprising since the trait was based on multiple weighing of the ewes and corrected for multiple systematic effects (Sveinbjörnsson & Örnólfsson 2024). Adult weights of sheep from meat breeds had considerably lower heritability of 0.29, according to the meta-analysis of Safari et al. (2005), but those are not fully comparable because of the corrections involved in estimating SRW. For Australian Merino sheep, Walkom and Brown (2016) found heritability up to 0.73 of adult weights at specific points in the production cycle, higher than our estimate for SRW, but lower when using data from multiple points in the production cycle. Using SRW rather than less standardized adult weights minimizes effects of factors other than inherited adult size on the weight, such as effect of the degree of maturity, body reserves and pregnancy.

The heritability of BW was similar to the estimates for meat breeds from Safari et al. (2005), with the same numerical value (0.15) for the direct effects but slightly higher (0.30 compared to 0.24) for maternal effects in our study. More recent meta-analysis found similar heritability for the direct effects, of 0.165 (Medrado et al. 2021). The direction and benefit of selection for BW are not obvious. In the Icelandic production system, lambs and ewes are on pasture for most of the lamb growing period, while feeding of ewes in pregnancy and around lambing is the more expensive indoor feeding (Sveinbjörnsson et al. 2021). Therefore, having the lambs reaching high WW by growing faster rather than with high BW may be more economically beneficial. However, the connection between BW, survival and ease of lambing also needs consideration, for which data on the Icelandic breeds are limited.

The heritability of WW or slaughter weight has been reported from multiple studies, both for the Icelandic breed (Eythórsdóttir 2012) and internationally (Safari et al. 2005, Medrodo et al. 2021). Our results are largely in line with those studies. The estimated correlations between direct and maternal genetic effects on WW are variable in the literature (Safari et al. 2005, Eythórsdóttir 2012), but the structure of the data may affect those estimates. Our results showed no, or low, negative genetic correlations between direct and maternal effects, both for BW and WW. The data included multiple generations, and dams were in most instances with their own records which supports accurate estimates of these correlations. However, the standard errors of these correlation estimates were relatively high, 0.06 for BW and 0.08 for WW.

The genetic correlations between maternal and direct effects on BW and WW were positive but not between maternal effects on WW and direct effects on BW. Still, the values of these correlations were lower than reported for other breeds (Safari et al. 2005, Medrado et al. 2021). The genetic parameters and correlations between BW, WW, and daily gain in different periods would be a valuable addition to understand the underlying genetics for the correlations, or lack thereof, between BW and WW. The effect of factors other than genetics on weight and growth has been examined extensively for the study flock (Sveinbjörnsson at al. 2021), but further analyses of the genetics of growth in different periods for Icelandic lambs would be valuable.

The genetic parameters of UMD, UMF, CC, and CF fall mostly within previous estimates on fixed weight basis from the Icelandic sheep breed (Eythórsdóttir 2012, Einarsson et al. 2015, Eiríksson & Sigurdsson 2017), with the exception of higher heritability (0.55±0.02) for CC in our results. All these traits are highly heritable and showed a large response to selection in the

Icelandic sheep breed (Eiríksson & Sigurdsson 2017). Our results showed a continued genetic trend towards more muscularity and less fat, as reported for the same flock in the decades before this study (Thorsteinsson 2002). However, the annual gain in UMD and decrease in UMF were lower in our results than reported for the wider population by Eiríksson and Sigurdsson (2017). The lower emphasis on selection for less fat after 2010 can be seen in the flattening of the trend in UFD and CF in the later years (Figure 3). The lower response in CC and UMD in the last years was more surprising. However, at the same time, weight traits show more upward trends, indicating selection emphasis has shifted towards higher WW and faster growth. One reason could be that the main selection step in the flock was the selection of replacement rams and ewes. This was largely based on phenotypic UMD and additional *in vivo* scoring of muscularity, particularly muscularity of the leg, without systematic correction for weight. Like UMD, the *in vivo* scoring was affected by weight (Einarsson et al. 2015), such that heavier animals may be preferred. For the selection for less fat, the opposite connection with weight may favour lighter lambs if weight correction was not included. Thus, the selection of replacement lambs without correction for weight might have contributed to the increased gain in WW, while gain in weight-corrected UMD and CC was reduced between 2010 and 2021. Before 2010, the selection for less fat may have counteracted this. Another contributing factor could be the introduction of animal model EBV for the ewe production index (Arnason & Jonmundsson 2008) in 2007, which includes both direct and maternal effects on CW and could have made selection for weight more impactful in the latter half of the studied period.

It is generally accepted as a basis for diet formulation that the pattern of fat and protein deposition in sheep is similar across sexes and genotypes when scaled as proportion of mature size, with fat tissue growing faster as animals approach their mature weight, i.e., with increasing maturity (CSIRO 1990, Oddy & Sainz 2002). If the fatness of growing sheep was mainly determined by the degree of maturity, measured as the proportion of SRW the sheep has reached, strong negative genetic correlations between fat traits at fixed weight and SRW were expected. Although negative correlations were observed, they were not strong (Table 3). Furthermore, the genetic trend in SRW was not significant, despite trends towards less fat at fixed weights. This suggests that genetic differences in UFD or CF at fixed weights were not mainly because of differences in SRW, and therefore in the proportion of SRW the lambs have reached, but rather in other factors. At weaning and ultrasound measurements, the lambs were around half of their SRW. According to the general growth functions (CSIRO, 1990), fat content of each kilogram of gain is approximately 9% greater at 55% compared to 50% at maturity. This is a considerable difference, but the observed differences in fat measurements (UFD and CF) do not necessarily fully reflect differences in total body fat content, as there are also differences in distribution of fat in the body that can be related both to degree of maturity and genetic selection (Thorgeirsson & Thorsteinsson, 1989). Different connections might thus be present for different genotypes and stages of maturity. Previous research on the Hestur sheep flock demonstrated considerable differences between two selection lines, where a line selected for good conformation had higher total fat at fixed weight and higher ratio of subcutaneous fat to intermuscular fat at fixed weight at a young age. For both lines, this ratio increased with degree of maturity (Thorgeirsson & Thorsteinsson, 1989). Since those studies were conducted, more than 40 years ago, the selection in the Hestur research flock has focused on increased lean yield and lower fat simultaneously (Árnason & Thorsteinsson 1982, Thorsteinsson et al. 2002). This selection could have favoured genotypes that affect muscularity and fat independently, rather than through difference in SRW. Árnason & Thorsteinsson (1982) reported the finding of such genotypes in the flock at Hestur. Furthermore, Eiríksson & Sigurdsson (2017) reported genetic correlation between CC and CF for data from three periods in a population with strong genetic trends towards more muscularity and less body fat. They found a decreasing genetic correlation, from 0.41 in 2001 to 2003, to 0.26 in 2011 to 2013. One explanation could be the selection for genotypes that combine low fat and high muscularity.

It is of practical relevance for the breeding program to know the indirect response of selection on WW, UMD, UMF and of carcass traits on SRW and BW. The positive genetic correlation between WW and SRW, and between WW and BW, suggest that an indirect response towards higher BW and SRW could be expected. The similarity in genetic trends between the body weight traits (Figure 2) suggests an indirect response has taken place. However, the negative genetic correlation of weight corrected UMD and CC to body weight traits may counteract the indirect selection towards higher SRW. Therefore, balanced selection of muscularity and body weight may result in desirable gains in these traits without resulting in a large indirect response in SRW. Based on the genetic correlations presented here, selection for less carcass fat is not likely to affect SRW as much as the selection for muscularity. Furthermore, despite negative genetic correlations of fat traits with weight traits (Table 3), the genetic trend in direct effects on WW and on SRW seems negative from 2001 to 2010 (Figure 3), when successful selection for lower fat was done.

CONCLUSIONS

Selection on increased weight of lambs at weaning or slaughter, which are important breeding goal traits for Icelandic sheep, can lead to indirect responses towards more adult weight of ewes. The increase in adult weights can increase feed requirements and thus increase cost, reducing the economic advantage of heavier or faster growing lambs. However, selection for thicker muscles at fixed weight might reduce adult weight and counteract the effect of selection for body weight. Selection for fatness of carcass in the current population is not expected to have a large effect on adult weight. Genetic correlations between breeding goal traits and BW and an indirect response to selection on BW were also present, but more studies on lambing difficulties and lamb survival are needed to determine the most beneficial direction of response in BW. The research flock at Hestur has continued to show genetic trends towards more muscularity and less fat, but since around 2010 the trends in these traits were lower than previously, while genetic trends towards increased weights were more evident after 2010.

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