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Heritability of longevity in the Icelandic sheep breed and the reproduction factors affecting it

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Acknowledgements

Abstract

In recent years higher focus has been put on increasing welfare and decreasing negative environmental effects of animal production. One way to access this is increasing and understanding the factors affecting the animal's longevity. Longevity is a complicated trait that can normally only be recorded after the animal's death and creates a biased data for younger animals in the heard (Iversen et al., 2020). A new way of estimating the trait with a linear model when animals are assigned 0 for years where they live another year and 1 for their last year has been created and has given good results for heritability estimations at an early age.

This study estimated the heritability of longevity in the Icelandic sheep system based on the 1-0 model run as a simple sire model, sire model with the environmental effect of the dam and sire-dam model. Longevity was recorded a heritable trait giving heritability between h^2 0.019-0,031 for annual basis record and h^2 0.86-0.14 when estimated for average lifetime records of 5.28 years. The sire-dam model gave the strongest heritability when the sire and dam were given equal values but otherwise gave a low heritability for sires and high for dams. The simple sire model gave the lowest explanation out of the models.

Longevity increases with higher age at first lambing and if the ewe had any years without lambs during her lifetime. Ewe effect of EWE_REARED, EWE_BORN and DAM_AGE had low effect on longevity while litter effect L_REARED and L_BORN and HAD_MIN had higher effect on the trait.

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Introduction

In the beginning of the 20-century animal breeding took a turn with structured breeding program being introduced. Later in the century a new change appeared with the appearance of biotechnology which opened the door for new breeding options such as artificial insemination (AI) embryo transfer and gene transfer. With these changes animal breeding became an organized format with structured breeding goals aiming for higher production and yield. At first there was little knowledge about the effects human selection could have on health and life quality of animals. Now it has been shown that high intentional selection can cause disruption to an animal' breed's homeostatic balance; the genetic correlations between production traits and health traits have been shown to be negative in many cases (Sandøe et al., 2009). Strong selection and breeding goals only focussing on production traits such as faster growth and higher yield, many livestock have started to develop negative trajectories. In health, physiological, immunological and behavioural traits (Rauw et al., 1998).Genomic selection today opens the door for even higher selection intensity and precision than before. Therefore, the importance of understanding the effects of selection is higher than ever. Breeding programs need to find a balance between increasing production traits while maintaining and protecting heath traits (Sandøe et al., 2009).

One way to attain this balance is to consider both production and longevity in the selection program. The genetic correlation between high production and decreased lifetime has been studied and shown to be negative in multiple studies across many species (Essl, 1998; Hoffman & Valencak, 2020; Rauw et al., 1998; Strapák et al., 2005). Moreover, longevity has been shown to be a heritable trait but estimates vary between species and breeds (Ricklefs & Cadena, 2008). How longevity is defined can also vary, one way to estimate it being one being production longevity measured e.g., as number of days between first lambing and culling. Another definition is that of (Ducrocq & Sölkner, 1998) in which longevity is adjusted for production and as the whole lifetime of an animal. Studying production animals' longevity is complicated by the human effect. (Hoffman & Valencak, 2020) found that the average life length of large-bodied livestock mammals ranged from 7-31 % of the species' maximum. On of the main push for the fast Turnover of animals in livestock production is the desire for higher economic gain through higher production of younger genetically superior animals. This increases the replacement cost (Essl, 1998) which (Komlósi et al., 2010) has shown to be the second most economic important trait in dairy cattle farming second to milk yield. Showing that the quick rotation of animals has quite high negative economic effect in

milk sheep the economic weight of longevity did not appear high while fertility had high effect (legarra et al, 2007). A Czech study on non-dairy breeds agreed with fertility rate being the most economically important, but it showed longevity to also be highly economically important along with lamb survival (wolfova et al., 2009). (Fuerst-Waltl & Baumung, 2009) also estimated a negative economic value for longevity in milking sheep likely due to decreasing milk yield in older ewes.

The Icelandic sheep breeding system.

The Icelandic sheep breed is the largest breed out of the Northern European short tail sheep breeds with about 500 000 animals in total. The breed is the only breed found in Iceland and is not crossbred with other breeds (Dýrmundsson & Niżnikowski, 2010). The Icelandic sheep breed has an especially high fertility success rate of around 98% for adult ewes and 60-80% for mated ewe lambs. the mean born per ewe average being around 1,82 in the last 10 years (Einarsson et al., 2020) The breed matures early (Einarsson et al., 2020) and the new animals are normally included in the reproduction system at 7-8 months of age (Dýrmundsson & Thorgeirsson, 1989). The Icelandic sheep breed has a good genetic diversity (0.71) and low inbreeding rate (0.09) (Hanrahan, 1989; Tapio et al., 2005). The Icelandic sheep production has a well-structured breeding program, and the use of AI there is one of the strongest in the Europe. about 30.000 ewes, (around 5-7%), are artificially inseminated with semen from 50 rams from the AI stations each year (Dýrmundsson, 2004), with a history back to 1931 (Dýrmundsson et al., 2007; Gíslasson, 1945).

In early 2000's a national breeding goal was introduced, with 96-97% of all sheep in the country currently being recorded in the system (Jónmundsson & Eyþórsdóttir, 2013)The main focus of the breeding program has been to increase growth rate and improve carcass conformation, but today more focus is also put on sustainability and diversity The current goal set up by *fagráð sauðfjárræktar* is to preserve the uniqueness of the breed while breeding for a better sustainable and economically suitable breed, i.e. to improve the main production traits, fertility, productivity, meat, and wool quality as well as all traits that could be used in breeding or to maintain their uniqueness. The program puts a special weight on the health and longevity of animals ("Ræktunarmarkmið ", 2019).

Some effects on longevity in the Icelandic breed have been studied but the heritability of the trait has not been estimated before. Objective of this study is to estimate the heritability of longevity in the Icelandic sheep breed, as well as estimate the effects the ewes litter environment, reproduction and litter sizes had on their longevity. Heritability will be

estimated using lineal 1-0 model. Longevity it hypothesised to be a heritable trait but to be also highly affected by reproduction an litter effects. Heritability will be run as three different models, simple sire-model, sire-PEdam model and Sire-dam model. The models loglik results will be compared to estimate the strongest heritability model. It's hypothesized that the numbers of successful lambing's will have the highest effect on the longevity of the ewe followed by the effect of reproduction traits are expected to have high effect on the trait while early life effect are expected to have lower effect on longevity. Litters Born and Litters Reared. Other traits are expected to have lower effect.

Material & methods

To study longevity, data was gathered from 15 sheep farms spread equally over the north-west, north-east, east, south and west of Iceland (picture 1)
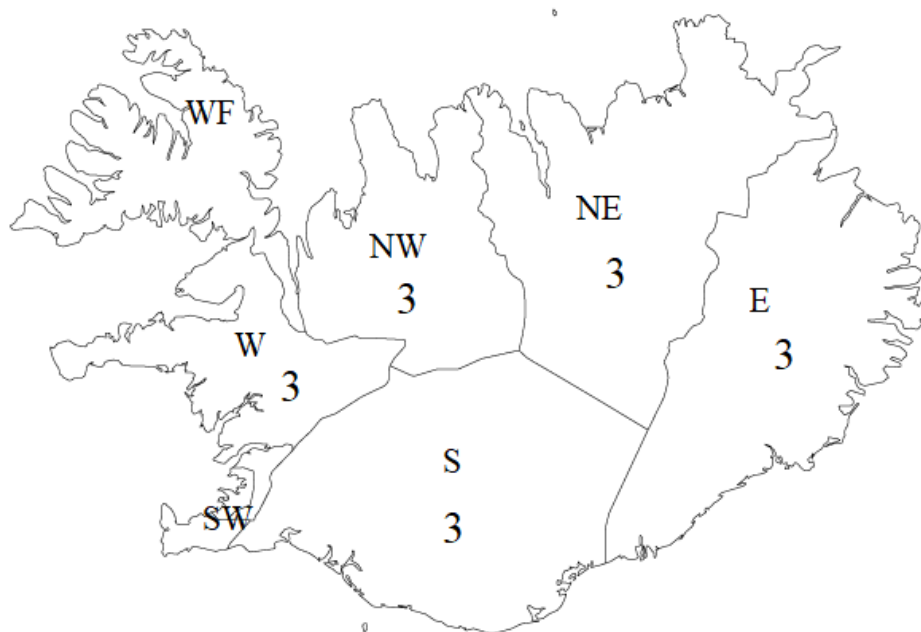
Picture 1 Spread of sheep farms included in the dataset split by regions.

 The information was obtained from the Icelandic sheep recording system Fjárvís (fjarvis.is). The data was obtained in three different parts. The first was the vorbók ('Spring book: SB); a dataset with 71750 records based on the identities of breeding stock ewes and their litters, spawning over the years 2008-2022. The second dataset was the haustbók ('Fall book: FB) with 145627 records over the years 2007-2022, with individual lambs' and their records. The

last dataset was the pedigree data, containing unique identities of sire and dam for all individual lambs recorded in the Icelandic breeding program, with records starting for individuals even born before 1950.

The SB and FB contain a lot of the same information but are based on two different periods of the yearly prod cycle: The SB contains information on the dams and their litters from the lambing season in the spring, and the FB on the weaning and slaughter information of the individual lambs in the litters in the fall. The SB contained information of Dam and Sire of the lambs (Dam_ID), (SIRE_ID), as well as the lamb identity (LAMB_ID), the dams birth year (DAM_BY) and death year (DAM_DY) and herd identity (Herd). Contained were also the litters' birthdate, number of lambs born (L_BORN) and information on reared / weaned (L_REARED) per ewe each year, and sex of the lambs. The SB also contained information on ewes for years in which they did not produce lambs due to young age, fetal loss, health, or other reasons (HAD_LAMBS).

The FB contained information on the lamb id (LAMB_ID), the Dam and Sire id's (Dam_ID and SIRE_ID, respectively as well as farm identity (Herd), lambs' birth date, sex of the lamb (Sex), number of siblings in litter the lamb is born to (L_BORN) and reared with (L_REARED).

Data selection and management

Data management was done in SAS 9.4 and analyses in R studio 4.2, ASREML-R, and SAS 9.4.

Information from the SB and FB was first merged into one dataset using LAMB_ID as the combining factor. A total of 1016 lambs with missing sire information were removed from the merged dataset. In the resulting merged data, few ewes had more than 3 lambs in one lambing: 143 records were of ewes having 4 lambs, 3 records of ewes having 5 lambs and 1 record of a ewe having 6 lambs. These lambs were therefore assigned as 4+ lambs born per year. Female (LAMB_ID) were merged with the DAM_ID to form a new variable named (OUR_EWE). For these ewes, new variables were made based on the dam and lamb data; variable for their birth year (EWE_BY), death year (EWE_DY), and their running age (EWE_AGE). Moreover, number of siblings the ewe grew up with (EWE_REARED), how many siblings it was born with (EWE_BORN) and the age of her mother at her birth (DAM_AGE) were added. Age of first lambing variable was created and combined with the (HAD_LAMBS). Ewes that had their first lamb in their second or third year were marked as (F2) and (F3). Sheep's that had years without lambs after their first lambing year had that

year marked as 0. All years with lambs were marked as (1) and were these four variables combined into the variable (HAD_MIN). Finally, a heard-year class (HY) was created. The longevity variable (LONG) was based on the 1-0 model defined as follows: ewes were given the score 0 for each year they survived and the score 1 for their final year. Ewes still alive in the last year of the dataset (2022) have their longevity censored though including EWE_AGE in the fixed effect.

The final ewe dataset contained 43060 observations from 10957 ewes born between 2008 and 2022. These ewes made up a total of 43060 records (Table 1).

Table 1 Number of records of ewes per production year.

Year	Number of animals	%
2009	49	0.11
2010	210	0.49
2011	568	1.32
2012	1078	2.50
2013	1686	3.91
2014	2444	5.66
2015	3250	7.53
2016	3889	9.01
2017	4433	10.27
2018	4757	11.02
2019	4906	11.37
2020	5138	11.90
2021	5330	12.35
2021	5322	12.56

The pedigree file was reduced to contain only data relevant to our ewes and was traced back 7 generations.

Statistics

To estimate fixed effects and variance components for longevity the data was analysed by the following univariate models (model 1-5)

$$Y = Xb + e \qquad \qquad \text{Model 1}$$

$$Y = Xb + Z_s sire + Vhy + e \qquad\qquad \text{model 2}$$

$$Y = Xb + Z_s sire + Z_m mom + Vhy + e \qquad \text{model 3}$$

$$Y = Xb + Z_s sire + Z_d dam + Vhy + e \qquad \text{model 4}$$

where **Y** is a vector of observations of longevity (1-0 variable) **X, Z$_s$, Z$_m$, Z$_d$** and **V** are known incidence matrices, **b** is a vector of fixed effects. **sire** and **dam** are vectors of random additive genetic effects of the parents with either sire/dam ~ N(0, **A** $\sigma_{sire/dam}^2$) where $\sigma_{sire/dam}^2$ is the additive genetic variance, and A is the relationship matrix. Moreover, mom is the vector of permanent environmental effect of the ewe with ~ N(0, I σ_{PEmom}^2), where σ_{PEmom}^2 denotes the permanent environmental variance of ewes. Then, HY is a vector of HY effects with HY ~ N(0, **I** σ_{HY}^2) where σ_{HY}^2 is the variance of HY effect. Finally, **e** is a vector of residuals with e ~ N(0, **I** σ_e^2) where σ_e^2 is the residual variance. The joint additive genetic effects of the sire and dam $\sigma2_{SD}$) were also calculated in a version of Model 4. The model as sire-dam model with the environmental effect of the dam included was also run, but it did not converge, pointing to too little information in the data to estimate these many variances.

To exemplify the covariance structures assumed, it is shown below for the most complex model; Model 4:

$$var \begin{bmatrix} sire \\ dam \\ HY \\ e \end{bmatrix} = \begin{bmatrix} \sigma_{sire}^2 & 0 & 0 & 0 \\ 0 & \sigma_{dam}^2 & 0 & 0 \\ 0 & 0 & \sigma_{HY}^2 & 0 \\ 0 & 0 & 0 & \sigma_e^2 \end{bmatrix}$$

and correspondingly for the other models.

The first model run was a simple fixed effect model (model 1) to estimate effects affecting longevity. The effect included were EWE_AGE, DAM_AGE, EWE_BORN, EWE_REARED, L_REARED, L_BORN, LB_Y, HAD_MIN.

Table 2 Effects included in the fixed effects model

Effects

EWE_AGE	Age of the ewe at each recorded year (1-10)
EWE_REARED	Number of lambs in the litter the ewe was reared in (1-3)
EWE_BORN	Number of lambs in the litter the ewe was born in (1-4+)
DAM_AGE	Age of the ewe´s dam at her birth year (1-9)
HAD_MIN	Records on years the ewe had lambs (1) and did not have lambs (0) and the ewe's that did had their first lambs in second or third year. (F2) (F3)
L_REARED	Yearly litter size the ewe reared over the summer (0-3)
L_BORN	Yearly litter size the ewe birthed (0-4+)

In this model, significance of the fixed effects was assessed with a conditional Wald F-test by the incremental form (F.con). F.con tries to estimate conditional wald statistics for each term in the fixed effects. In the heritability equations (models 2-6) trait EWE_REARED and HAD_MIN were included as fixed effects. Other traits were excluded from the heritability equation, DAM_AGE was removed due to its low effect on the trait, L_BORN and EWE_BORN and L_REARED were removed to exclude effects from heritability of fertility traits. Fertility traits have a rather high heritability in the Icelandic sheep breed $h^2 = 0,10$-0.17 (Sveinbjörnsson et al.) and could therefore reduce the heritability of longevity.

In model 2- 5 various additional effects to the error were included in the equation. The variance components significance of the random effects is estimated by the Z-ratio which is calculated by dividing the variance components with the standard error (SE). Z-ratio above 2 is estimated to indicate significant effect.

$$Z.\text{ratio} = Variance\ componetns\ /\ SE$$

On an animal level, longevity is a repeatable trait where permanent environmental effects are normally included. However, due to the data structure of the longevity model with only one potential outcome being repeatable for dying (1), the permanent environmental effect cannot be estimated in an animal model (Iversen et al., 2020). Due to this, a sire model/sire-dam model was chosen as a basis for the study. Then the permanent environmental effect of the animal is removed but the permanent environmental effect of the dam can be estimated.

The formulas used for estimation of heritability were the following for annual basis records (SR) and average lifetime records (AR) heritability of both dam and sire was calculated from model 4 and Equation 5.2 was used when one joint estimate was calculated for the genetic variance of sires and dams (SD).

$$h^2_{sire,model\ 2} = \frac{\sigma^2_{sire}}{(\sigma^2_{sire} + \sigma^2_{HY} + \sigma^2_e)} \qquad \text{2.1. model 2 SR}$$

$$h^2_{sire,model\ 2} = \frac{\sigma^2_{sire}}{(\sigma^2_{sire} + \sigma^2_{HY} + \sigma^2_e * 1/5.28)} \qquad \text{2.2 model 2 AR}$$

$$h^2_{sire,model\ 3} = \frac{\sigma^2_{sire}}{(\sigma^2_{sire} + \sigma^2_{PEmom} + \sigma^2_{HY} + \sigma^2_e)} \qquad \text{3.1. Model 3, SR}$$

$$h^2_{sire,model\ 3} = \frac{\sigma^2_{sire}}{(\sigma^2_{sire} + \sigma^2_{PEmom} + \sigma^2_{HY} + \sigma^2_e 1 * 1/5.28)} \qquad \text{3.2. Model 3 AR}$$

$$h^2_{sire,model\ 4} = \frac{\sigma^2_{sire}}{(\sigma^2_{sire} + \sigma^2_{dam} + \sigma^2_{HY} + \sigma^2_e)} \qquad \text{4.1. Model 4 SR}$$

$$h^2_{sire,model\ 4} = \frac{\sigma^2_{sire}}{(\sigma^2_{sire} + \sigma^2_{dam} + \sigma^2_{HY} + \sigma^2_e 1 * 1/5.28)} \qquad \text{4.2. Model 4 AR}$$

$$h^2_{dam,model\ 4} = \frac{\sigma^2_{dam}}{(\sigma^2_{sire} + \sigma^2_{dam} + \sigma^2_{HY} + \sigma^2_e)} \qquad \text{4.3. Model 4 SR}$$

$$h^2_{dam,model\ 4} = \frac{\sigma^2_{dam}}{(\sigma^2_{sire} + \sigma^2_{dam} + \sigma^2_{HY} + \sigma^2_e 1 * 1/5.28)} \qquad \text{4.4. model 4 AR}$$

$$h^2_{SD,model\ 4} = \frac{\sigma^2_{SD}}{(\sigma^2_{SD} + \sigma^2_{HY} + \sigma^2_e)} \qquad \text{5.1. model 4 SR}$$

$$h^2_{SD,model\ 4} = \frac{\sigma^2_{SD}}{(\sigma^2_{SD} + \sigma^2_{HY} + \sigma^2_e 1 * 1/5.28)} \qquad \text{5.2. model 4 AR}$$

The significant difference between the models was determined by use of the likelihood-ratio testing (LRT). A test where the maximum likelihood estimates of a more complex nested

model is compared with that of a simpler model to estimate whether to include the extra parameter.

$$LRT = 2 * (InLcomplex - InSimpler)$$

The LRTis chi- square distributed with number of degrees of freedom equal to number of additional variance components (parameters) estimated.

Results
HY
Figure 1 shows large variance in number of records per HY class, varying from a few animals up to 800 animals. The smallest numbers were mostly due to A) different farm size with the farms ranging from around 100 up to 1000 animals. B) as well as few animals in the first years of data, since Ewes born before this year were excluded. Therefore the first year in the dataset only has 1 year old ewe´s from 2008. The size of the year groups then grew until year 2019 when the number stabilises (Table 1). Due to the small subclasses for HY in the first year(s), HY was included as a random effect in the models.
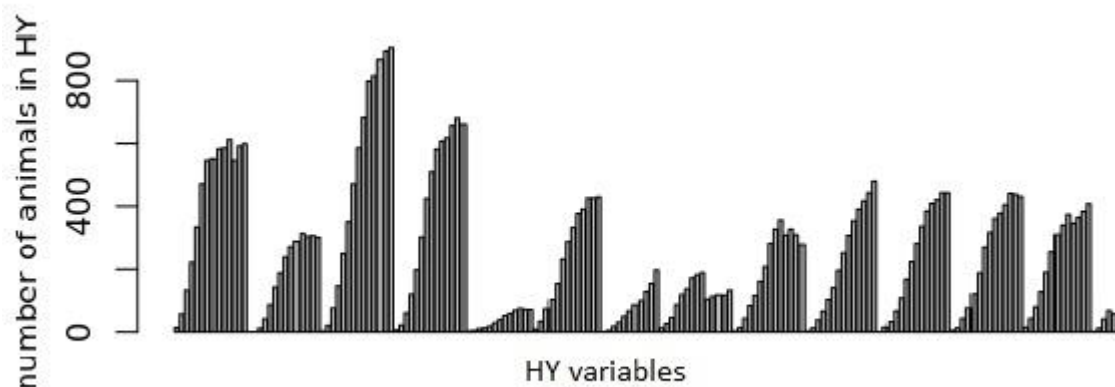
Figure 1 spread of HY over the dataset.

Figure 2 and 3 show the spread of L_BORN and L_REARED, in both cases the twin lambs were the most common variable. And >2 lambs the rearest.
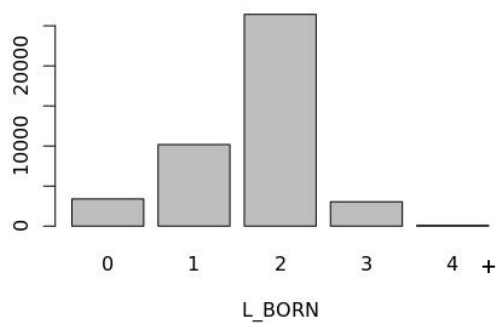
Figure 2 Average number of lambs born (L_BORN) Average number of lambs born (L_BORN) by ewes in the dataset.
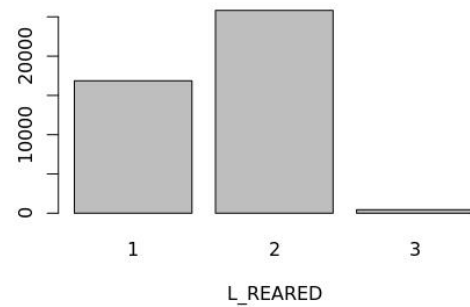
Figure 3 Average number of lambs reared (L_REARED) by ewes in the dataset.

Table 3 variables included in HAD_MIN effect. Age at first lambing and HAD_LAMBS, frequency and %

Age at fist lambing	Frequency	%
1	35501	83.08
2	7107	16.63
3	124	0,29
Had lambs		
0	3389	7,86
1	39740	92.14

Survival curve of the Icelandic breed

Table 4. presents the deathrate of animals born between the years 2008 and 2012. These animals have all had full opportunity time to die since the dataset spawns a minimum of 10 years, which was the highest life length of ewes. In Table 4 the average weighted death age of the ewe's was 5.28 years.

Table 4 Frequency of ewes dying at various ages and the corresponding cumulative frequencies; for ewes born 2008-2012, with full opportunity time to die.

Death_age	Frequency	Cumulative %
1	104	5,63
2	174	15.04
3	202	25.97
4	198	36.69
5	231	49.19
6	293	65.04
7	297	81.11
8	253	94.81
9	70	98.59
10	26	100

Figure 4 shows the survival curve for the ewes included in Table 4. The survival was high in the first two years, but then dropped at an equal rate until about the age of 6 when the survival started decreasing faster until 9-year age when it flattens out again until all ewes were dead at the age of 10.

Fixed effects
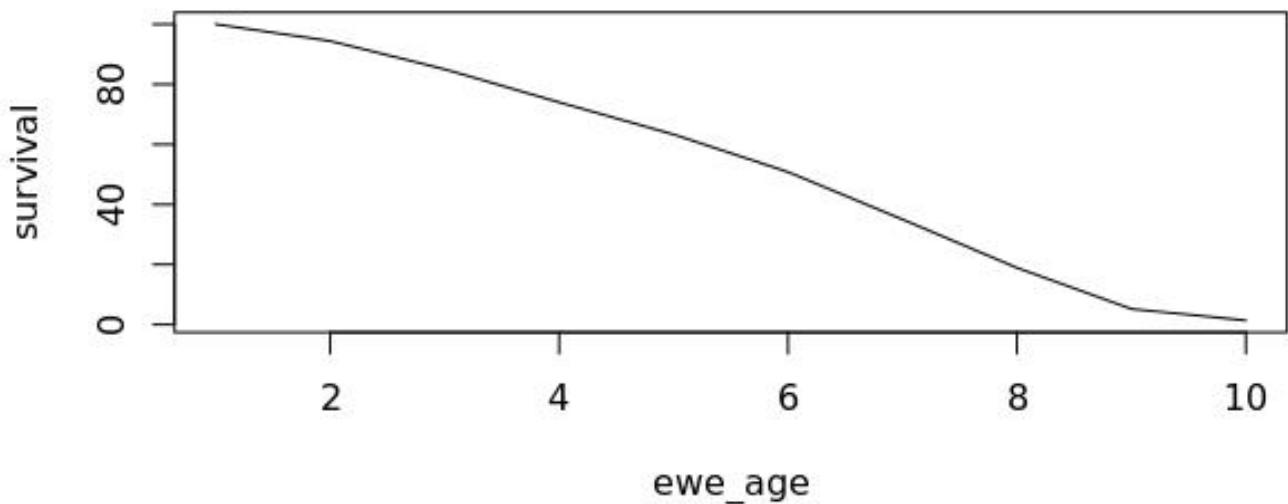
Figure 4 Survival curve for sheep with full opportunity time to die 2008-2012

Fixed effects

Figure 5 presents the effect the fixed effects have one ewe's longevity with 1 representing full risk of death and -1 zero risk of death. Table 5 represents the significance of the fixed effects on the longevity of the ewes. EWE_AGE had the highest effect (F.con =640.6). EWE_BORN had low effect = (F.con = 1.4) and was the only trait with non-significant effect (P value = 0.24) with a trend for ewe´ quadruple and single born ewe's having the shortest longevity. EWE_REARED had higher effect (F.con =4.0) with longevity being highest for single reared ewe's and lowest for twin reared ewe´s. DAM_AGE had low effect on longevity (F.con =2.0) but significant (P value = 0.04) with longevity increasing with higher age of dam until the last age group when it decreased again. HAD_MIN had the highest effect out of the regular fixed effect (F.con = 327.8) the ewe not producing lambs at some point in her life (0) decreased her longevity. Having the first lamb in the second year (F2) gave lower longevity than having the first lamb in the third year (3). L_BORN had some effect on longevity (F.con = 23.5) with single born litters having the highest longevity and lowest for ewes with twin born litters. L_REARED had high effect (F.con = 536.8) out of the fixed effects with the twin reared litter giving the longest longevity and single reared litters causing the lowest longevity. Little difference was recorded between twin and triplet reared litters.
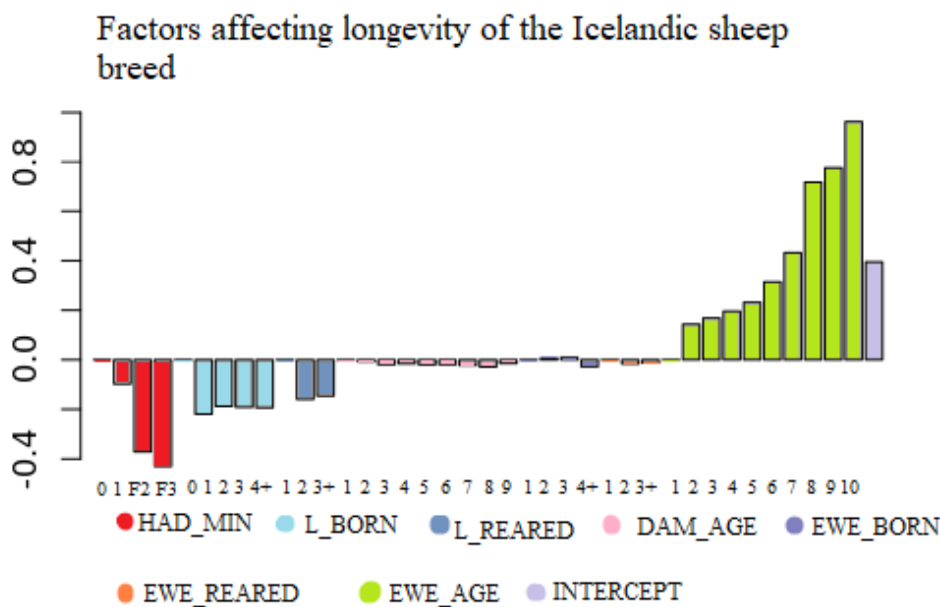
Figure 5 Effects of fixed effects on longevity in the Icelandic sheep breed. Increasing numbers representing higher death risk.

Table 5 Results from Wald Chi-Squared Test on significance explanatory variables on longevity.

Trait	DF	F.con	Probability
Intercept	1	9387.0	0.000
EWE_AGE	9	655.1	0.000
EWE_BORN	3	1.4	0.245
EWE_REARED	2	4.0	0,017
DAM_AGE	8	2.0	0.042
HAD_MIN	3	327.8	0.000
L_BORN	4	23.5	0.00
L_REARED	2	536.8	0.00

Heritability

Tables 6.-9 presents the variance components of the random effects in the heritability models (model 2-4). All components had a Z.ratio above 2 indicating a significant effect on the trait expect sire effect in the sire-dam model (model 3). The variance components of the genetic effect of the sire and dam gave different results. Dams HY had a rather high effect on the trait in all models. The Z.ratio for all traits was above 2. Indicating a significant effect except the sire effect in model 3 (table 7). Out of the genetic effects the equal weight of the sire and dam (SD) genetic effect gave the highest Z.ratio (table 9).

Table 6 Variance components model 2

Effect	Component	SE	Z-ratio
HY	0.0025	0.0003	7.094
Sire	0.0005	0.0001	4.072
Error	0.1053	0.0007	145.298

Table 7 Variance components Model 3

	Components	SE	Z.ratio
HY	0.0003	0,0004	7.089
Sire	0.0006	0,0001	1.784
PEdam	0.0004	0,0002	3.875
Error	0.1045	00008	139.706

Table 8 Variance components Model 4

	Components	SE	Z.ratio
HY	0.0023	0.0003	6.882
Sire	0.0051	0.0001	3.360
Dam	0.0008	0.0002	3.938
Error	0.1046	0.0007	141.995

Table 9 Variance components Model 4, sire and dam given equal weight (SD)

	Components	SE	Z.ratio
HY	0.0023	0.0004	6.911
Sire	0,0006	0.0001	5.478
Dam	0,0006	0.0001	5.478
Error	0.1047	0.0007	142.73

Table 10 presents the heritability for longevity based on the different models. Heritability of longevity for yearly records was rather low in all models swinging between h^2 0.019-0,031. Correspondingly, for the average lifetime records, when dividing the error variance by 5.28 (years, the average life length) the heritability rose to h^2 0.86-0.14. Moreover, the heritability over an average lifetime had a lower standard error (SE) than yearly records, but all were significant. The genetic effect of the dam was recorded stronger than the genetic effect of the sire with dam having 20% higher heritability than the sire in model 4. To estimate the same genetic effect of both parents sire and dam were given equal weight in heritability model 5.1 and 2. This gave sire and dam the same genetic weight of h^2 0.032 for annual records and h^2 0.107 for average records.

Table 10 Heritability of longevity estimated by models 2-4. based on annual records and repeated records of average lifetime (5.28 years)

Estimated variance components (model)	h^2	SE	H2 – average records	SE
Sire + HY (model 2)	0.022	0.005	0.102	0.025
Sire + PEmom + HY (model 3)	0.021	0.005	0.096	0.024
Sire + Dam + HY (model 4) sire effect	0.019	0.005	0.087	0.025
Sire + Dam + HY (model 4) dam effect	0.031	0.008	0.142	0.033
Sire + Dam + HY (model 4) SD effect	0.034	0.008	0.107	0.019

The significance of adding new random effects was tested by comparing the max log likelihood of the more complex models 3-4 to the simpler model 2. Including the genetic effect of the dam gave significantly better results than the regular sire model (model 2). Including the environmental effect of the dam (PEdam) to the sire model (model 3) did have a significant effect better loglike results than the sire but lower than model 4.

Table 11 log likelihood, 2 ln log likelihood difference of models 3, 4 and 5 relatives to model 2, and corresponding significance level (P-value)

Estimated variance components	Ln log likelihood	2 log likelihood differenceA of models	P-value
Sire + HY (model 2)	26671.58		
Sire PEmom (model 3)	26673.22	1.641	0.070
Sire dam model (model 4)	26682.94	10.360	5.314357e-06
Sire:dam model (model 4)	26681.26	9.677	6.094378e-05

Discussion

The factors affecting longevity varies much between environments and species. Figure 6 from (Kirkwood & Holliday, 1979) shows the different survival curves that different animal can have. Curve *a* shows a population with a consistent mortality at all ages. Curve *b* represents a common life curve of wild animals while curve *c* represents the curve of slowly reproducing mammals in a natural environment. Curve *d* represents the protected populations, for species that follow this curve the longevity is mostly affected by high age.
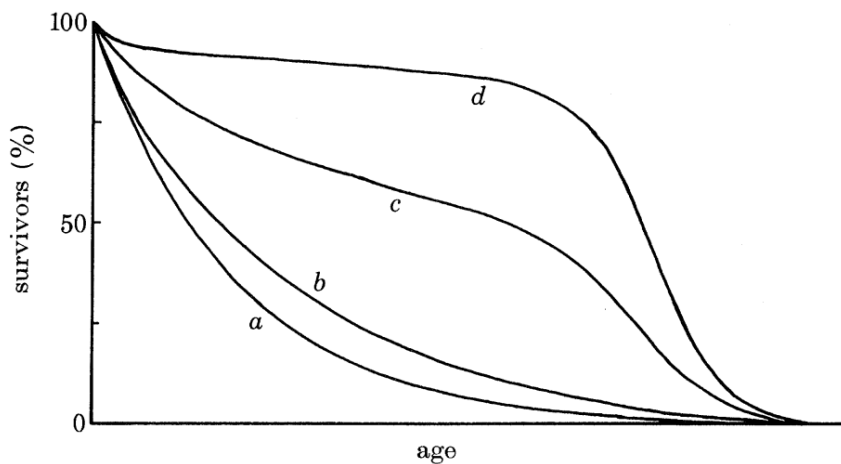

Figure 6 Survival curve. From paper (Kirkwood & Holliday, 1979)

For animals following the *d* curve it can be suspected that the heritability can appear higher since it is affected by fewer traits. In zoo animals that lived in a protected environment and estimated to largely follow the d curve, the heritability of death age fluctuated between species but had the mean estimate of h^2 at 0.53 across species (Ricklefs & Cadena, 2008). There are multiple factors that affect aging and age-related death. Accumulation of genetic damage, mutations in genes, chromosomes, damage by reactive oxygen; loss of immune function and autoimmunity; decline in muscle strength; inflammatory damage to tissues, decline in homeostasis and hormone imbalance, being among them (Holliday, 2006). When looking at the other survival curves in Figure 6 the factors affecting longevity start to become more complicated. Instead of the longevity being controlled by the animal's ability to age well and its resistance to the age-related deaths, its ability to survive through different life stages becomes more important. With production animals the human factor also starts to play a big role in the longevity of the animals but increased control by the farmers reduces the effect of age-related survivability and increases the effect of production-based survival (Milerski et al., 2018). In natural environment those high production traits would likely

decrease the animals longevity though the trade-offs between production and health trait (Sandøe et al., 2009; Strapák et al., 2005). Production animals in agriculture tend to live around 20-30% of their maximum life-length, reaching down to 7% for pigs and up to 31% for sheep (Hoffman & Valencak, 2020). The longevity of sheep is highly affected by breed and production system (Annett et al., 2011; Bosdan et al., 2019). Survival curve for the Icelandic sheep was presented in figure 4 and the calculated average life length of sheep in this data was 5,28 years. The oldest sheep recorded in this dataset was a dam that reach the age of 13 years. The average lifespan of the Icelandic sheep is 40% of the maximum lifespan, 10% higher than the average sheep longevity recorded by (Hoffman & Valencak, 2020).

Heritability

As presented in Table 10 longevity is a heritable trait that increases with age, demonstrated by being higher for an average life than for one single year. Yearly records gave a low heritability around $h^2 = 0,019$-$0,031$ depending on the model and whether it was calculated for the genetic components for dams or sires. For the average lifetime of 5.28 years the heritability increased to $h^2 = 0.086$-0.142. The increased heritability recorded with repeated records is caused by the isolation of the genetic factor effects with multiple records. Similar study on Merino sheep where the phenotypic variation for longevity was 0.00 for two-year-old ewes and 0.11 for 5-year olds. (Hatcher et al., 2009). The same changes have been recorded in cattle's and stated that survival was genetically not the same trait over the whole life span due to the changing heritability over time (Van Pelt et al., 2015). This fits with study by (Mekkawy et al., 2009) where the culling reason of ewes were shown to differ between age groups: Udder conditions and mastitis was high culling reason for the younger ewe´s while in older ewe´s teed and mouth conditions became important.

Model design

Longevity traits are collected late in life or after the animals are dead. For the younger animals or the animals that are still alive to express the phenotype, the observations are censored and creates a bias whether they are included or excluded from the model. If the animals are excluded, it erases information of animals with long longevity in the later years. If the animals are included, they cause underestimation of the phenotype of the animals that are still alive. Due to the censored data, longevity traits can´t be calculated with regular linear models and has instead generally been studied with Survival Kit (Iversen et al., 2020). The Survival Kit is a program running a univariate proportional hazard model with a single

response time, the model runs well with smaller research samples, but the model is complex and therefore badly suited for large datasets. It is also not possible to run the hazard model in a multi-trait model with other linear traits that are generally used in breeding value estimations (Iversen et al., 2020).

When comparing a hazard model with a linear model the hazard model gave higher heritability, due to it being unable to estimate the common environmental effect it was likely overestimated. While the models give different heritability based on their different trait definitions they both appear to predict survival well (Ødegård et al., 2006).The correlation between estimated breeding value (EBV) and true breeding value (TBV) is higher in the hazard model and remains the same over all timepoints while it increases in the linear model with more years though reduced error variance (Jamrozik et al., 2008). Based on this, the hazard model might still be preferred in smaller scale studies while the linear model can rather be used in large scale studies and in breeding value estimation. With the new recording of survival with the linear model at each parity with the 1-0 model it is possible to estimate longevity and take account of the problem with censored data. The 1-0 model also makes it possible to include the heard-year effect which makes it possible to take model a farm's between-years variation in environmental conditions. Comparison of pig longevity records based on the 1-0 model with a single record longevity phenotype, with production of a sow within a period from first farrowing, showed a stronger prediction accuracy for young animals in the 1-0 model as well as giving information earlier. (Iversen et al., 2020). Unlike in the single record longevity model the 1-0 model defines the end of life time.(Iversen et al., 2020) sows were included in the 1-0 data after their first farrowing and marked with a phenotype of 1 when they didn´t reproduce a litter the next year. Here, the ewe´s got the marking of 1 in the year they died. Moreover, the ewes had an opportunity to not produce lambs at some point during their lifetime as well as in the last year or have lived some years without producing lambs. The definition was changed in this study due to the relatively high likelihood of ewe´s not producing lambs in one year but still being kept in the system and given the opportunity to produce the next year. Ewers that did not have lambs in their last year were included in the data as well since if the ewe´s were not culled the year before they had been chosen to stay in the production for another year, removing them would therefore give a skewed view of the culling decision of the farmers the year before. The effects of different of the different lambing was accounted for in the fixed effect model as HAD_MIN variable.

Animal model vs. Sire model

The basic model in this study was a sire model instead of an animal model to remove the permanent environmental effect of the ewes. In the animal model the breeding value is fitted for the animal itself and we get the permanent environmental effect of the animal itself though the repeated records In the sire model only the effect of the sire is fitted on records of the progeny (van der Werf, 2012). The permanent environmental effects are normally included in a repeatability animal model but due to the structure of the phenotype with only 0's being repeated, the permanent environmental variance is not estimable. Because of this the sire model is advantageous in estimation of genetic variances since it does not model the permanent environmental effect. The first model run was a pure sire model (model 2). The sire model EBV can be slightly less accurate and potentially biased due to there not being any correction for differences between dams, and all dams are assumed to be form the same homogeneous population with the same expected mean (van der Werf, 2012). To increase the reliability of the sire model the effect of the dam was added. Maternal effects are strictly environmental for the offspring but can have genetic and environmental components., It is usually assumed that maternal effects are genetic although part of it might also be permanent environmental (van der Werf, 2012). Thus, the additive genetic effect of the dam (model 4) and the environmental effect of the dam (model 3) were both run, giving the highest preference to the sire-dam models (table 11) and the sire-PEdam (model 3) above the sire model (model 2) (Table 11).

In estimation of breeding values, however, the animal model, without the permanent environmental effect of dam, should likely have preference to having only the genetic of environmental effect of the dam, over the sire dam model, but this remains to be validated in a progeny testing scheme relevant for Iceland.

Model Improvements and developments

In this study HY effect was included as a random effect due to not being able to run as a fixed effect due to small size of some HY records. As seen in the variance components results (table 6.-9) HY had a high significant effect on longevity. A test of removing the HY effect from the heritability equations increased the heritability about 1% for the single year records and 10-17% for the repeated records. Based on this a larger dataset with more HY records would give a higher heritability than estimated in this study.

As mentioned previously longevity is a trait that has multiple definition. The model can be run on other longevity definitions to estimate if they have higher heritability than total

longevity. One option would be to run the model as a production lifetime model where only the production years of the ewes are included. This could alter the heritability but unlikely much since the genetic and phenotypic correlation between the longevity and lifetime production has been shown to be positive and strong (Paixão et al., 2019). Heritability of specific death traits could also be estimated with good documentation of culling reason. Another option is to use variations of the model to look at individual genes that affect longevity, but Insulin and/or Insulin-like growth factor and the allele IGD_1R C have been associated with longevity in sheep (Barbieri et al., 2003; Richardson et al., 2004) as well as the frequency of the IGF1R and FOXO3 gene and length of telomere (Byun, 2012). The survival trait recording pattern fits well for maternal traits though more research is needed to investigate the correlation between survival and the maternal traits. If the correlation it strong it is possible to use the longevity and maternal traits to select for each other based on the one that has stronger genetic gain. This does require further studying and recording of the maternal traits and the genetic correlation between those traits and longevity.

Culling reasons

Data collection of culling reason in the Icelandic sheep breeding population is limited despite a good format to document the culling reasons on Fjárvís. Farmers tend to document ewes cause of death or culling as *slaughtered* without giving the reason for why the ewe was slaughtered. Therefore, the main culling reasons in the population are not clear. In (Annett et al., 2011) study on Scottish blackface, and their crossbreeds with Swaledale, North County Cherviot, Lleyn and Texel, the most common reason for culling across breed was barrenness and the second most important was udder problems. Poor teeth conditions, vaginal prolapse, poor body composition score, feet problems, abortions, poor maternal instinct, and lambing difficulties were also mentioned as less common, but documented reasons for culling. In (Bosdan et al., 2019), study on the same subject the main culling reason was aging and dental problems followed by udder problems, diseases, low milk yield, predator attacks birth problems and low fertility. While some of those traits are traits that would likely affect the ewe's longevity in a wild environment (poor teeth condition, poor body composition score, feet problems) other traits would not (poor maternal instinct, low milk yield, low fertility) and in some cases likely have a positive effect on their longevity, like fertility and low milk yield through the negative corelation between longevity and production traits (Sandøe et al., 2009; Strapák et al., 2005)**.**

As presented in figure 5 EWE_AGE had an increasing death risk with higher age until it reaches a full death risk at age 10. Table 4 and figure 4. presents the survival curve of the ewe´s. In the studies of (Abdelqader et al., 2012; Kern et al., 2010) the risk of being culled was highest after the first year of lambing and then decreased until the age of 5-7 years. In this study the results were the opposite for the first year of lambing where the risk of culling was the lowest for one- and two-year-old ewes (5.6%) based on the ewes that had full opportunity to die (table 4). The risk then increased up until 7-year age where the culling risk was the highest for ewes with full opportunity time to die (16.07%). The reason for the high culling rate at 7 can be due to ewes starting to decrease their production efficiency around this age. The fertility of the Icelandic sheep increases until 5-year age when it starts to slowly decrease. The odds of sheep being barren also appeared to increase after they reached six-year age. (Sveinbjörnsson et al., 2018a), and the growth rate of the lambs is highest for 3 and 4 year old ewes (Sveinbjörnsson et al.)so at the age of 7 the ewes have started to show decline in these three main production traits. This gives the farmer less reason to keep them.

Reproduction effect on longevity

When looking at the effect of reproduction rate (HAD_MIN), not having lambs after the first lambing decreased longevity (0). This fits with previous findings of higher production traits decreasing longevity (Essl, 1998; Hoffman & Valencak, 2020; Rauw et al., 1998; Strapák et al., 2005). Missing lambing year can also decrease longevity though increasing the risk of culling. Farmers can be more likely to remove sheep from the system if she does not lamb in one year instead of risking another empty year. Missing years of lambing decreased longevity but later first lambing increased it. Ewes that had their first lamb at 3-years of age (F3) had higher longevity than ewe´s that had lambs in their second year (F2), and both gave stronger positive effect on longevity than lambing records (1) indicating a positive effect of not lambing in the first year. The effect of age at first lambing on longevity has been studied in multiple research projects and many research have found a negative effect of lower age at first lambing on longevity (Abdelqader et al., 2012; Kern et al., 2010; McLaren et al., 2020; Thomson et al., 2021). Previous study on the Icelandic breed has though shown the oldest ewes recorded to be more likely to have had lambs in their first year than not (Níelsdóttir, 2014). This study did not estimate the difference between survival of ewe´s at all life stages based on if they had lambs in the first year. While not lambing in the first year appears to give higher longevity ewes that have lambs in their first year appear to have higher fertility than the ones that did not, through most of their adult life. Lambing in the first year did also

show a trend towards higher growth rate of lambs for adult ewes (Níelsdóttir, 2014) as well as significantly increased birth weight of lambs has been observed until the dams reached 6 year of age (Karlsdóttir, 2018). These traits have also been shown to have negative effect on longevity due to the trade- off between the investment in metabolic resources in reproduction and longevity. But have a positive effect on culling rate since farmers might be more willing to keep ewes that have more lambs per year over a longer time through higher likelihood of a higher number of lambs.

Litter effect on longevity

(L_REARED) had the strongest effect on longevity out of the fixed effect with rearing 2 lambs giving the longest longevity. Rearing 1 lamb had gave the lowest longevity. While rearing one lamb should have positive effect on the ewe´s longevity in natural environment though lower intensity of milk production and physical stress (Snowder & Glimp, 1991) the ewe's production value decreases though fewer lambs return per year. Rearing only one lamb cans also point to the ewe not being considered health enough in the spring to rear more lamb giving the farmers another reason to not keep it the next year.L_REARED had a lot higher effect on longevity than L_BORN, (Table 5), though it should be kept in mind that the traits interact in many cases. The traits could possibly be combined into one trait that estimates the effect of L_BORN and L_REARED. Twin rearing ewes having the highest longevity points towards a competition between longevity and production, resulting in the average producing sheep having the longest longevity. Number of lambs born (L_BORN) had medium effect on longevity (Table 5) and was the highest for ewe's with single born lambs in accordance with (Pineda-Quiroga & Ugarte, 2022) though the difference between the trait was not significant. An estimated negative Pearson correlation between litter size and longevity traits has been recorded (Byun et al., 2012) There is through a possibility that ewe´s carrying the *þokugen* a single gene that causes increased fertility in the sheep's increasing their mean lambing rate up to 3-5 lambs per year does not appear to have a reduced their longevity (Dýrmundsson & Ólafsson, 1989). This study does not have enough data to give results on this, but L_BORN 4+ gave a little better longevity than L_BORN 3.

Early life effects on longevity.

Out of the early life effects EWE_REARED had the had the highest effect (F.inc = . with longevity being highest for single reared ewe's and lowest for twin reared ewes.
EWE_BORN had low effect on longevity but showed a trend for being highest for

quadruplets born ewes and lowest for triple born ewes. Age of the dam of the ewe had low effect on longevity (table 5) and increased with higher age until the oldest age group (9) (figure 5). Part of the higher effect of EWE_REARED could be caused by the effects of competition on the pre-weaning growth of the young ewe. The way the ewes are reared as lambs affects their early life growth curve. Single born lambs have the highest growth rate during the whole summer and their growth rate is more closely associated with milk production than for multiple born lambs (Snowder & Glimp, 1991; Sveinbjörnsson et al.). In the early summer the lamb's main source of nutrition comes from the ewe's milk. The summer pasture becomes their main source of nutrients. The triplet lamb's high competition for the milk in the early spring decreasing their growth potential which increases in the mid-summer when the pasture becomes their main source of nutrients of the lambs (Karlsdóttir, 2018; Sveinbjörnsson et al., 2018b). This would also fit with the low effect of EWE_BORN since it does not affect their growth rate (Sveinbjörnsson et al., 2018b).

Conclusion

Longevity is a heritable trait in the Icelandic sheep with heritability of h^2 0.019-0,031 for annual records and h^2 0.86-0.14 for average lifetime records and it best estimated by the sir-dam model. The current breeding goal in sheep breeding in Iceland focuses on increasing longevity of the sheep. With implementing the heritability estimation with the 1-0 model it is possible to directly breed for longevity and possible to include it a multi-trait model with other linear traits used in the breeding value estimations (Iversen et al., 2020). The trait is not possible to estimate by the preferred animal model, but the sire-dam model was the model that gave the best heritability explanation out of the sire models run in this study. By breeding for longevity farmers can breed against multiple factors that increase the risk of death with one breeding goal instead of only being able to avoid environments that decrease it longevity. The effect of the litter environment the ewe grew up has little effect on longevity, but the effect of her litters is stronger. Ewe´s that did not have lambs at 1 year age have higher longevity than ewe´s that do but after their first lambing a year without lambs increases the risk of culling.

This thesis has shown that longevity is heritable. While there are still many factors unknown about the heritability and more studies are needed before it can be included in breeding value estimations, the door for breeding of longevity in the Icelandic sheep breed has been opened.

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