THESIS

GENETIC RELATIONSHIP BETWEEN EWE LONGEVITY AND STRUCTURAL FOOT AND LEG TRAITS IN SHEEP

Submitted by

Hilal Yazar Gunes

Department of Animal Sciences

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2022

Master's Committee:

Advisor: R. Mark Enns
Co-Advisor: Scott E. Speidel

Milton G. Thomas
Timothy Holt

ABSTRACT

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Longevity is a desirable trait in sheep production systems as it increases profitability by decreasing the culling rates and female replacement costs while increasing the number of marketable lambs. Unfortunately, due to the limited data on culling reasons and exit dates from the flocks submitted to sheep breed associations, historically ewe longevity has not been widely evaluated. Moreover, the limited studies of longevity of ewes report a low heritability which makes the genetic improvement of ewe longevity very hard to achieve through phenotypic selection. Furthermore, due to the necessity of waiting for the animal or its relatives to leave their respective flocks for obtaining the observation of longevity, the time lag makes it challenging to improve this trait. Conversely, as one of the main culling reasons in sheep operations, structural foot and leg traits can be recorded relatively early in life and are known as more highly heritable than longevity, which makes using them as an early predictor for ewe longevity more efficient. Conversely, the heritabilities and repeatabilities of structural foot and leg traits in sheep, and the knowledge of genetic relationships between structural foot and leg scores and longevity is not available in the literature. Therefore, proper identification of both ewe longevity and structural foot and leg traits in sheep is essential. To fill in the gaps in the literature about the heritabilities and repeatabilities of structural foot and leg traits in sheep, and to identify the genetic relationship between ewe longevity and structural foot and leg traits in sheep, this thesis project was conducted. Data utilized

in this investigation was extracted from Sheep Improvement Limited (SIL)'s database and was provided by Focus Genetics. In general, this thesis was divided into three separate studies to make it easier to understand.

The first study involved a repeated measures animal model to estimate the heritability and repeatability of structural foot and leg scores in sheep. For these estimations, data were provided by Focus Genetics and performance information on 309,509 sheep with pedigree data collected between 2000 and 2020 from seedstock and commercial ewes and rams. The data were sifted based on observations for the structural foot and leg traits with those without those scores removed from the data set before analysis. For the analysis, repeated records of structural foot and leg traits including overall foot scores, back and front feet pastern angle scores, back and front feet claw, and hoof shape scores were used. Those records included 31,615 overall foot scores (OFS), 31,578 back pastern angles (BPAS), 31,612 front pastern angles (FPAS), 31,610 back feet claw and hoof shape scores, (BCHS) and 31,612 front feet claw and hoof shape scores (FCHS). In the raw data set, although there was a total of 412 ewes that lived more than 7 years (8-, 9-, 10-, and 11-years old animals) and have structural trait observations, these observations were assigned as unknown in the data set due to having a small number of animals for each age that caused biased representation for these ages. Culling due to age in New Zealand is 6 to 7 years according to technical notes of SIL. A total of 283 ram structural foot and leg observations were also assigned as unknown in the data set due to not representing the group of ages and having a small number of animals. (3 years old - 234 animals), 4 years old - 44 animals), 5 years old - 5 animals). Males commonly had a single observation typically collected at 1 year of age, while females were typically scored more than once. According to the results, while the heritability estimations for each structural foot and leg trait were low, some of the repeatability estimations were derived as moderate. Heritability (h^2) and repeatability (r) estimates were as follows: OFS ($h^2 = 0.11 \pm 0.01$, $r = 0.30 \pm 0.01$), BPAS ($h^2 = 0.11 \pm 0.01$, $r = 0.21 \pm 0.01$), FPAS ($h^2 = 0.17 \pm 0.01$, $r = 0.31 \pm 0.01$), BCHS ($h^2 = 0.09 \pm 0.01$, $r = 0.19 \pm 0.01$), FCHS ($h^2 = 0.07 \pm 0.01$, $r = 0.14 \pm 0.01$). These estimates imply that, direct selection of these traits will result in slow genetic improvement but within the realm of improvement when used through genetic prediction technologies. Furthermore, by building more robust structural foot and leg traits databases for sheep flocks, it will be possible to differentiate the animals which maintain their favorable structure over time from the others that begin to regress. If we select our next generations according to these outputs, this will allow us to have a chance to decrease culling rates due to foot and leg problems, which could result in increased profitability and longevity.

The second study focused on the estimation of ewe longevity heritability using a single-trait animal model. Structural foot and leg and pregnancy scores (number of embryos) recording ages were used to conduct the study and they were collected between 2000 and 2020 from 77,837 ewes (progeny of 2,466 sires and 41,260 dams). Due to the culling date and reason sparsely recorded in the SIL's database we used the approach suggested by McLaren et al. (2020) to determine longevity. In this approach, the ewe's last production record (last lambing) can be used as a proxy for the culling age. In the case where structural foot and leg score recording age was present but pregnancy age was not recorded despite the animal being retained in the flock, a separate column was created to assign last recording age for structural foot and leg score to pregnancy age as a recording age for both traits. From the repeated records to form a final data set which has one unique observation for each animal, longevity observations were assigned to ewes according to the difference (in years) between their first lambing (at 2 years old) to last lambing records. Heritability was found for ewe longevity as 0.14 ± 0.01. This result suggested that ewe longevity is a lowly heritable trait in sheep, which was coincidence with previously reported results, implying that direct selection on ewe longevity will result in slow genetic improvement. Even though, genomic selection can be an option to improve the traits difficult to measure like ewe longevity.

Finally, the third study had as objectives as 1) to fill the gaps of knowledge about the genetic relationships between structural foot and leg scores and ewe longevity in the literature 2) to estimate the genetic and phenotypic correlations between ewe longevity and structural foot and leg traits in sheep 3) as to determine if structural foot and leg scores can or cannot be potential early predictors for ewe longevity. To achieve these objectives, pregnancy, performance, and structural foot and leg traits performance data were extracted from SSIL's database that was collected between 2000 and 2020 and included information from 77,836 ewes (progeny of 2,466 sires and 41,260 dams). Longevity observations were assigned to ewes according to the difference (in years) between their first lambing (at 2 years old) and their last lambing record. Multi-trait analyses were run separately for each recording age (2 through 7) to estimate the correlations between ewe longevity and structural foot and leg traits for identifying the ideal recording time for these traits. Additionally, to determine which of the structural foot and leg scores could be best used as an early-life predictor for the ewe longevity, correlated responses were calculated and compared. Based on the results of correlations from multi-trait analyses and the correlated response analyses, we conclude that structural foot and leg scores recorded at early ages in sheep can be used as early life predictors for the ewe longevity. According to the correlated response analyses outputs (we expect a negative response due to score 1 standing for the best one and 5 being the worst one), the best and earliest age should be 3 years old for using the structural foot and leg scores as an early life predictor for ewe longevity. Moreover, the best scores that can be used were found as OFS and BPAS. Breeders may choose one of them, probably, being as an overall evaluation OFS, would be the best and easiest choice for the breeders.

ACKNOWLEDGMENTS

I would like to express my deep gratitude to my advisor Dr. R. Mark Enns for his guidance, patience, making all the connections with the New Zealand Research group, and continuous support during my master's degree journey. Without his help, this project and my journey at CSU would be impossible. I will always be grateful to you, Dr. Enns.

I also want to express my gratitude to my co-advisor Dr. Scott Speidel and valuable professor Dr. Milton G. Thomas; their doors were always open to me when I have questions or confusion.

I would also like to thank Dr. Tim Holt for serving as my committee member and providing extremely valuable feedback that has significantly enhanced the quality of this research effort.

I would like to express my special gratitude to the Focus Genetics - New Zealand Research Group, especially Dr. Natalie Pickering for providing us with the data set and the guidance.

My deepest gratitude to my beautiful home country, TURKEY, and Republic of Turkey Ministry of National Education for giving me this unique opportunity and the financial and emotional support required for my master's degree period. This project was made with the support of the Republic of Turkey.

Lastly, I would like to acknowledge my bestie – Roderick Alexander Gonzalez Murray- within the Animal Sciences Department at CSU for his support, friendship, and encouragement to keep going despite any adversity.

DEDICATION

This thesis is dedicated to my beautiful country, REPUBLIC OF TURKEY, and the Turkish Ministry of National Education that have made it possible this unique opportunity. Your supports enabled me to always move forward and work hard to overcome any challenge during this journey.

I also dedicated this thesis to my family for encouraging me to always pursue my goals no matter how difficult they seem to be and for the unconditional support that you have provided to me during all these years that I have been away from home studying.

Lastly, this thesis is also dedicated to everyone who loves sheep and science!

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CHAPTER 1 – INTRODUCTION

The ideal ewe is the one that is both productive and long-lived. Hence, ewe longevity which is defined as how long ewes remain in the flock as productive animals (Borg et al., 2009) is an important trait for sheep operations due to being capable of directly affecting the profitability and efficiency of the sheep production systems. While decreased ewe longevity in a flock may seriously decrease the profitability due to dealing with a persistently high replacement cost, increased ewe longevity enables decreased culling rates in turn reducing female replacement cost. Accordingly, breeders may apply more selection pressure when choosing replacement females and this could result in higher age-related performance. Cruickshank et al. (2009) who modeled a breeding flock reported that if the age at which ewes were culled increased from 5 to 6 years of age, 13% fewer replacement ewes were needed each year, therefore culling pressure on other traits could be increased. Most importantly, increased ewe longevity results in more market lambs to sell at the end of the day. Even with this importance, ewe wastage (Flay et al., 2021), losing the ewe before they hit their potential lifespan, is a common problem worldwide. Interestingly, in the breeding schemes, ewe longevity is often underemphasized but strongly suggested that it should be considered as one of the selection criteria because keeping the ewes that have potentially low longevity rates cost time and money. On the other hand, many countries have started to include some measure of longevity in their national breeding objectives (Van Raden, 2002) but before attempting to move to a genetic solution for increasing ewe longevity across countries, it is important to understand what the main causes of ewe mortality or culling (voluntary or involuntary) within systems are. Based on these results, we can identify early-life predictors for ewe longevity.

One of the main culling reasons for sheep is the lameness caused by foot and leg issues. Although lameness occurs not only due to structural problems at foot and legs, structural defects on foot and legs are famous for preparing foundation for lameness. As sheep age and gain weight, accordingly, foot and leg structure changes. Often foot and leg issues develop with age and may not be apparent at younger ages. Hahn et al. (1984) reported that in cattle, with an increased age, hoof angles decreased, particularly in the back hooves. Same authors also indicated that, they observed increased hoof length on older Holstein cows with an increased weight on larger surface area. Similarly, Giess et al. (2017) reported that with an increasing age, foot size tends to increase and back leg set tends to grow more curved in Angus cattle. According to the study that was done by Kaler et al. (2010), with increased age, in addition to the changes in foot and leg structure, some reduction occurs in resistance to footrot in ewes. Additionally, Vittis and Kaler (2020) reported that lambs younger than 1 year old had 25% lower lameness than the ones that were 1 year and older. Especially at older ages, these structural changes in foot and leg may negatively affect health and ultimately reduce longevity, particularly in ewes. Additionally, Martini et. al., (2001) reported that, although the sheep reach sexual maturity at approximately 7-12 months of age, depending on breed, the closure of the physeal plates of the long bones may still occur as late as 36 months. Thus, for a proper structural evaluation it is important to score foot and legs at different ages. Moreover, over time, the variation in foot scores will increase as some sheep maintain their favorable structure, while others begin to regress. Therefore, breed associations suggest scoring adult sheep multiple times over their life in the flock which adds useful information beyond their first score. Unlike the data available from research flocks, which may record cull/death dates and reasons, data collected from commercially recorded flocks seldom provide sufficient detail to assess different causes of ewes leaving the flock (McLaren et.al, 2020) and the contribution of structural changes to the culling rate. This makes it difficult to identify the average longevity in flocks and specific causes for leaving the flock. However, McLaren et al. (2020) suggested that using the age of the ewe at her last recorded lambing event is a longevity trait that could potentially be investigated across research and commercial data sets from different sources to better understand commonalities across populations.

Improved foot and leg traits enhance animal welfare and likely increase longevity while reducing the cost of treatment and animal replacement. Some Sheep Breed Associations have started to build foot and leg score databases and suggest their members record these traits to improve the accuracy of selection and reduce culling losses. More observations will enable higher production of higher accuracy EBVs for structural foot and leg traits. The same goes for recording the culling reasons which can help to identify the specific reasons for culling and ultimately inform selection decisions. Nevertheless, according to a recent report by McLaren (2020), breeding values for ewe longevity are not yet widely available in most countries and breeding associations. There are just a few international examples of longevity traits included in national breeding indices, or as breeding values, using commercially recorded data available from performance recording schemes (Ireland and New Zealand: Santos et al., 2015; UK: McLaren et al., 2017).

Considering the importance of both ewe longevity and ideal foot and leg structure, we proposed a project examining the genetic and phenotypic correlations between ewe longevity and structural foot and leg traits in sheep with the goal of providing results to industry to aid selection processes and ultimately improve the financial viability to sheep production through increased longevity.

Given the relatively limited published research in sheep, other species provide guidance for structural evaluation. In the literature, cattle's body conformation traits are considered in breeding schemes as indicators of longevity because of moderate favorable correlations between these traits. Sewalem et al. (2004) used Holstein cattle to understand which type traits could be used to increase longevity and reported that one of the most important type traits affecting longevity are foot and leg structure traits. Type traits especially those describing feet and leg conformation have been reported to show favorable correlations with longevity by different authors (Vukasinovic et al. 1995; Caraviello et al. 2004). Based on that, we hypothesized that if the foot and leg traits are genetically influenced in sheep and correlated to ewe longevity, we might use structural foot and leg traits recorded in young animals as an early-life predictor of ewe longevity. This could be especially useful as longevity observations are recorded when the ewe leaves the flock and are therefore challenging from a time-to-observation perspective we thought that a potential relationship could help us to select both for increased longevity and idealized foot and leg scores. The general objective of this project is to identify the relationship between ewe longevity and foot and leg structural traits in sheep using historical foot and leg scores and longevity measures. There is a dearth of scientific literature reporting genetic parameters for both longevity and structural foot/leg traits in sheep, and therefore this study was designed to add to the base of knowledge. The general objective of this thesis was to assess the genetic relationship between ewe longevity and structural foot/leg traits in sheep.

Specific objectives are as follows:

1) Estimate the heritability and repeatability for each structural foot and leg trait (overall foot and leg scores, back and front feet pastern angle scores, and back and front feet claw and hoof shape scores) in sheep,

2) Estimate heritability for the ewe longevity,

3) Estimate the genetic and phenotypic correlations between ewe longevity and assess whether foot and leg scores could be a potential early predictor for ewe longevity.

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CHAPTER 2 – LITERATURE REVIEW

2.1 Structural foot and leg traits in sheep

2.1.1 The importance of structural foot and leg traits in sheep

Having structurally sound feet and legs is vitally important for sheep because the legs and feet provide a unique springing system and act as shock absorbers that give the ability for the body to have a smooth ride, very much like the shock absorber systems in our vehicles. Usually, feet and legs are considered separately but they should be also seen as one entity because, if the legs have faults, this will cause problems with the feet, even with the other structures in the body. Kim and Breur (2008) reported that more body weight was loaded on the front legs than on the back legs in sheep, at 59% and 41% of body weight, respectively. Similarly, other studies reported by different authors also indicated that the front hooves of cattle (Pastell et al., 2006), horses (Hood et al., 2001), and pigs (Pluym et al., 2013) support more weight than the back hooves, and the center of the gravity was found closer to the front legs than the back legs, while weight was evenly distributed between the left and right side of the body. Moreover, several researchers (Baumgarter, 1988; Baumgarter and Distl, 1990; Vermunt, 1990) reported that significant differences were observed in dimensions of claws that exist between front and back claws in cattle. Russell et al. (1982) reported that the inner and outer claws of the back legs often were in different shapes, but the authors could not be able to explain whether this was a cause or an effect. Interestingly, although approximately 40% of the animal's weight is carried by the back legs (Atkins, 2009), Blowey (1998) reported that 86% of all lameness cases in cattle were involved the back feet and 85% of these cases were involved the outside of claw. In contrast to what Blowey (1998) reported, Van Amstel and Shearer (2008) reported that 46% of the lameness cases on front legs involved the inside of the claw while 32% involved the outside of the claw and 22% on the foot skin. Erlewein et al. (2002) and Lambertz et al. (2014), also indicated that the front and back legs were found structurally different in sheep and reported that the claws of the front leg in sheep are longer and greater in dorsal angle than the claws of the back leg. In addition to this, Leopold and Prietz (1980) reported that the water content of the horn in back claws was higher than in front claws in sheep and suggested that it may be related to being exposed to more intense wetting of rear legs than front legs. Besides all this, it is considered that the weight of the milk in the udders affects the distribution of the weight on the legs of dairy animals. This idea was supported by the findings of the study which reported that in dairy cows 89% of the milk weight was carried on the back legs conducted by Chapinal et al. (2009). In consequence, Neveux et al. (2006) indicated that dairy animals had difficulty shifting weight from back legs to front legs. In addition to this, several researchers (Leach et al. 1998; Livesey et al. 1998; Webster, 2001) reported that most lameness cases appear during peak lactation when the udders are heaviest and full of milk every day. From all these findings, we can forecast that front and back legs have different structural characteristics, and physiological processes such as milking or gaining weight can change the weight distribution on all legs. Interestingly, Best et al. (2021) reported that they observed higher overgrown hoof shapes in ewes that have higher body condition scores (BCS) (>3.0), compared to the fit ewes (BCS=3.0). They associated this result with the one unit increase in BCS which equals approximately 17% increase in weight. Scoring both front and back foot, and legs may be beneficial to accurately characterize the conformation of the foot and legs. Lastly, any reason that breaks the balance of the weight distribution, can be considered to affect all structures in the sheep body.

In livestock animals, the legs from shoulder and hip to the feet develop with a number of angles each of which is extremely important. The angle at the hock is known as the most vital because, in addition to being a shock absorber, it provides forward thrust allowing the animal to run and jump (Anonymous, 2015). The ideal hock on sheep is known as about 20 degrees of the set to provide maximum flexibility and power (Anonymous, n.d.). If the hocks are too straight the animal loses the "spring" and the power of motion and it will have great difficulty walking up hills. A ram with the same fault may have a problem with mounting the ewes. The other structure which needs some angle to provide springing is the pasterns. According to Penn State University's ram selection principles guidelines (Anonymous, 2020), the ideal pastern angle for sheep is approximately 50 to 55 degrees. If the pastern angle becomes greater than this, support can become an issue as the animal gains weight. If the sheep lack enough angle, they will experience more lameness issues, and decreased longevity in the flock when compared to the sheep with too much angle (Anonymous, 2015). Additionally, a shallow pastern is likely to result in a long hoof due to uneven wearing and may increase the likelihood of lameness, especially in males during the breeding season. When the angle of the pasterns is not as ideal, this situation forces animals to walk on the side of the foot, overlapping the toes. This is something similar that is seen in about 7% of people and is called overlapping toes syndrome (Dufour et al. 2017). When the toes are too close, the moisture and the friction between the toes are preparing a perfect place for the contagious bacteria growing that causes the foot rot and foot scald. Both are the major diseases in sheep production and cause lameness, excessive pain, and losses in production (Nieuwhof and Bishop, 2005; Kaler and Green, 2008). Moreover, for evaluating the structural soundness in sheep, to see how stifle, hock and pastern align in a solid step may be helpful. Ideally, these three joints will align at an angle between 140 and 145 degrees in a structurally sound sheep (Daniel Jr and Kriese-

Anderson, 2018). The illustration that compounds the ideal foot and leg joint angles for sheep can be found in Figure 2.1.

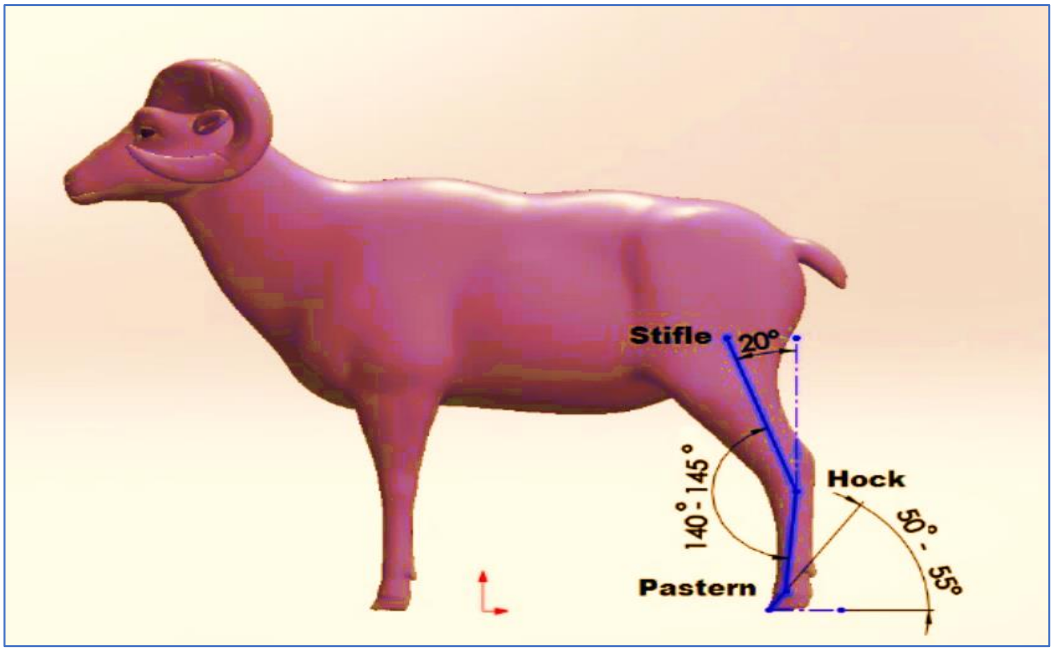

Figure 2.1 Ideal foot and leg joint angles for sheep

According to a report by Blowey (1998), while 88% of lameness cases in cattle involved the feet, only 12% involved legs. Moreover, Shearer (1997) also reported that they found out that 90% of the lameness incidents were caused by claw and hoof disorders in cattle. Therefore, considering the similar duty of the claw and hoof in both cattle and sheep, due to being highly related to lameness that accompanying pain and anxiety, breed associations suggest frequently checking, and scoring the claw and hoof shapes in sheep. Besides, several researchers (Rogers et al. 1989; Distl et al., 1990) indicated that unfavorable feet and leg measurements affected production traits, and reported that longer claws and lower hoof angles were found associated with lower survival rates. Accordingly, to decrease the incidence rates of foot and leg problems in the flocks, breed associations also suggests that scoring other structural parts of foot and legs and, when the animals that have unacceptable scores are detected, culling those animals.

Structural foot and leg defects cause pains and an animal with a painful foot or leg is less likely to walk or eat which will reduce the weight gain and production compared to that of an animal able to walk easily and consume its daily needs. According to Faull and Clarkson (1990), the loss of production due to discomfort associated by foot and leg problems can be considerable as 0.5 kg per week in fattening lamb. In addition to these, it is reported that chronic pain due to lameness can reduce the work rates of breeding rams during the breeding season (Henderson,1990). Therefore, identifying these types of structural defects in the first place is important to decrease the incidence rates in the flocks. Structural foot and leg defects can be seen immediately after the lambs are born or they can be formed when the lambs are growing due to different reasons. Unfortunately, there are many common and undesired structural foot and leg faults are seen in sheep called such as splay-footed (when a lamb has toes that point outward), pigeon-toed (which is the reverse of splay-footed, when a lamb has toes that point inward), sickle-hocked (when a lamb has too much set or angle at the hock), post-legged (a serious fault- when a lamb has too straight rear legs), bow-legged (also known as O-shaped – the opposite condition of cow-hocked – when a lamb has hocks that are too far from each other), or cow-hocked (also known as X-shaped or knock-kneed – lamb has hocks that are set too close together). All these defects are unwanted and when they are detected, the animals which have the defect should be culled. Both ideal and undesirable foot and leg structure illustrations in sheep are shown in Figure 2.2. In the next section (2.1.2), environmental factors that affects foot and leg structure will be described.

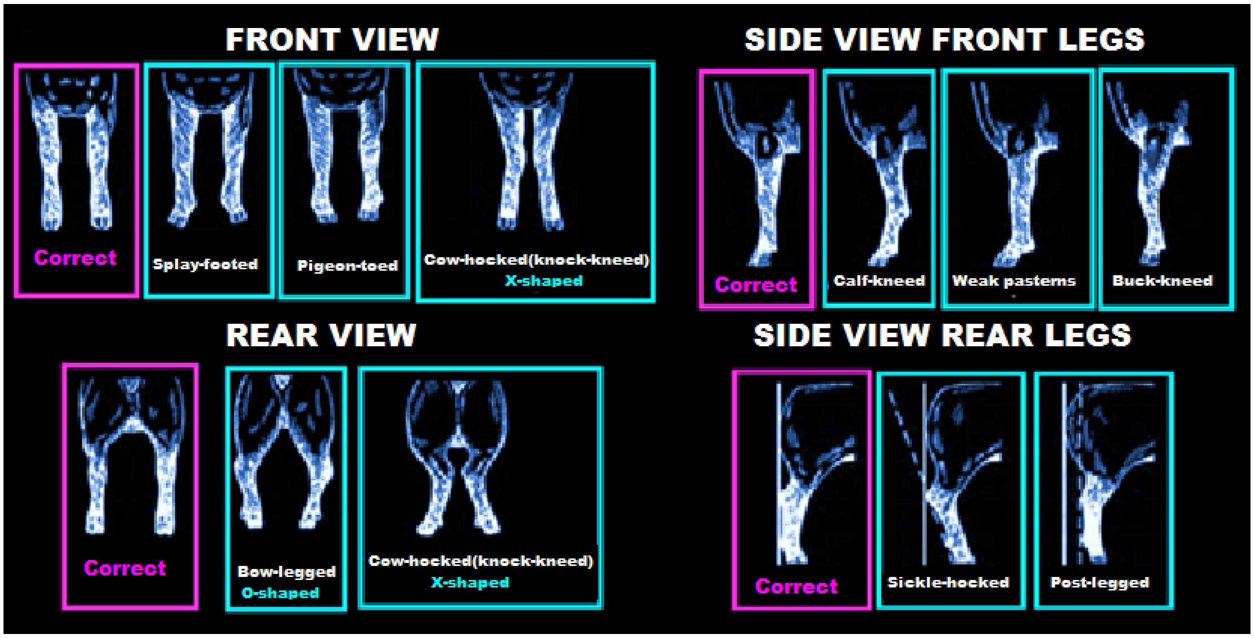

Figure 2.2 Both ideal and undesirable foot and leg structure illustrations in sheep

2.1.2 Environmental and management factors affect the foot and leg structure in sheep

There are many environmental and management factors that affect the foot and leg structure in sheep. Briefly, these factors can be listed as season, nutritional factors, the type of housing, and grazing, management practices, and all are considered as affecting growth rate of claws.

Dekker et al. (2005) determined the growth rate of claws in sheep by measuring the growth rate of the hoof horn and reported that in the lambs as 0.44 mm per day while in the ewes as 0.29 mm per day. On the other hand, Shelton et al. (2012), reported lower hoof growth rate for sheep than the one reported by Dekker et al. (2005), as 0.11 mm per day. Shelton et al. (2012) associated this the difference between the environmental factors that have effect on two studies, and the usage of different measurement methods. In the study of Dekker et al. (2005), sheep were housed on a hard surface while in the study of Shelton et al. (2012) at pasture. This growth rate for the cattle and pigs, were reported in cattle (~0.13 mm per day; Prentice, 1973), and pigs (~0.20 mm per day; Jonhston and Penny, 1989).

The season is known as one of the important factors that especially affects the growth rate of claws (Hahn et al. 1984; Rakes and Clark 1984). Moreover, Hahn et al. (1984), and Rakes and Clark (1984), both reported that claw horn growth is a cyclic process and maximum growth occurs during warmer parts of the year (late spring-early summer). Besides, Wheeler et. al. (1972) reported that hoof growth rates of sheep were reduced lower ambient temperatures and were drastically reduced in the month following shearing but were not affected by changes in day length. Wheeler et al. (1972) hypothesized that reduced hoof growth at lower ambient temperatures may be related to decreased blood supply to the distal leg.

Nutritional factors also have big impacts on the foot and leg structure of livestock. It was reported by many researchers that rations' protein and energy content can change the hardness and growth rate of claws. Manson and Leaver (1988) reported that they observed higher rates of claw horn growth in the animals which were fed with high-protein rations than in cows def low-protein diets. Similarly, Greenhough et al. (1990) reported that the growth of sole horns was increased in the beef calves that were fed high-energy rations. Additionally, in the growing phase of lambs, due to malnutrition the malfunction of the bone metabolism can cause the bent-leg syndrome of lambs (Bagley, 2004).

The type of housing, and grazing are otherr factor that had found as significant effects on foot and leg issues. According to Erlewein (2002), sheep indoor housing usually has softer and longer claws than sheep on pasture. Vittis and Kaler (2019) in the study where they investigated environmental effects on sheep lameness, reported that there was a negative relationship between Selenium concentration of soil and lameness incidances of sheep and for each extra unit of Se in soil, lameness decreased by 84%. The same authors also reported that considering the pasture length, their findings suggested that for medium (6-10 cm) and short (up to 5 cm) length, lameness decreased by 17% and 32%, respectively, in comparison to long (>10 cm) length. They suggested that this result may be related to the longer length pasture's retaining more moisture ability. Similarly, Dendani-Chadi et al. (2020) indicated that grazing can decrease the lameness incidance in cows, and reported that the percentages of lameness rates in non-grazing cows as 35.4%, in partially grazing cows as 16.4% and in the grazing thouhout the year as 1.3%. According to Camara and Gravert (1971) and Spindler (1973), there were significant differences found in the rate of claw horn wear between dry and wet floors where animals are spend their most of the time. Same authors reported that claw horn was wore up to twice as fast on wet floors than on a dry floors. Similarly, Dewes (1978) reported that severe wear of the claw horn was observed commonly, especially during the wet weather.

Management practices are the other factors that can cause significant differences in the structure of foot and leg in sheep. For example, footbaths affect the claw, especially its hardness. Smit et al. (1986) reported that the use of formalin footbath was found as associated with longer claws. It may be associated with formalin's hardening and dehydrating effect which results in lower moisture content in claws and less wear on claw horns (Vermunt and Greenough, 1995; Arkins et al. 1986). Even, routine foot trimming which is an application for preventing foot and leg problems can cause a higher prevalence of lameness because of the trimmers who are not experienced enough to be careful not to trim the sensitive tissue (Wassink et al. 2003; Kaler and Green, 2009; Winter et al. 2015). It is reported that 30% of lameness in sheep flocks is caused by the trimmers who harmed the sensitive tissue while trimming (Grant et al., 2018). A recent report by Best et al. (2021) that had consensus with the one written previously by Green and Clifton (2018) suggested that trimming is a counterproductive application for sheep, unlike cattle. According to both reports, trimming in sheep increases the risk of permanently misshapen and damaged hooves, it can also accelerate the horn growth rate by 4% (Wheeler et al., 1990).

Flock size is another factor that found related to foot and leg structure, hence linked to lameness incidences in sheep. According to report Vittis and Kaler (2020), flock sizes that had 51-100, 101-200 and 201-400 sheep, had decreased levels of lameness in comparison to the flock size up to 50 sheep by 25%, 36%, and 51%, respectively. The authors of this study suggested that this may be related to that larger flocks are managed with more effective and commercially oriented production strategies and biosecurity measures may be more precisized and standardized. Winter et. al. (2015) also reported results that were in accordance with Vittis and Kaler (2020) that indicated increased flock size was found linked to decreased lameness.

2.1.3 Scoring the structural foot and leg traits in sheep, and detection systems for lameness

Multiple structural scoring systems for structural characteristics in sheep exist. Although scoring foot and leg in sheep are not quite common worldwide, there are some options for scoring foot and leg, and detecting lameness in sheep such as using trained people for visual scoring or using more developed systems: "force-plate systems", “pressure-sensitive walkways” and “accelerometers and gyroscopes”. Each system has its unique pros and cons but nowadays, for scoring sheep's structural characteristics and detecting lameness, the most common method is using trained people. On the other hand, in the systems where for the foot and leg scoring, trained visual scorers are used, due to their subjectivity and differences among scorers, the scores and their reliability are often questioned (Flower and Weary, 2006). Some researchers use different techniques to overcome. For example, Matebesi et al. (2009), in the study where they used a 1-50 scale scoring system for the evaluation of some foot and leg conformation traits for the Tygerhoek Merino resource flock, used at least 3 experienced judges for the allocation of the scores for the individual animals and the scores given by each of the judges were averaged to provide a final score for the trait concerned each animal. On the other hand, due to the difficulty of finding trained visual scorers and the nature of scoring (which takes a long time and labor), this was not always the case in other studies. Janssens et al. (2004) in the study where they aimed to examine the assessor quality of a linear assessment scheme and estimated the repeatability for both assessors and some of the type traits for sheep in Belgium, rated the scorers individually for five criteria such as consistency, conformability, the difference in the median, the difference in proportion and difference in years. The average and differences were computed over all accessors within years and in total there were 12 assessors were evaluated. As a result of this study, the repeatability of the assessors in the scheme was reported as low. The average consistency of assessors, overall, 20 traits (including structural leg traits and other traits), varied from 0.62 to 0.81 indicating that assessors differ in their ability to rank animals consistently. In conclusion, the authors of this study suggested that assessors with low consistency (for some traits) introduce non-systematic errors in the data and this type of error cannot be corrected by statistical techniques continued training of assessors, and accumulation of experience might help to improve the consistency of assessors.

The force-plate system is the second system that can be used for detecting lameness in sheep which had been widely used for cattle along with other species. The force-plate systems, measure the forces of animals for each limb and detect lameness on individual limbs when they are walking over the plates (Rajkondawar et al. (2002a) using the distribution of weight to each of the four hooves. Force-plate systems are found promising for identifying the lameness of animals because a painful and structurally unsound animal will distribute less weight on the problematic legs (Corr et al., 2003). With this system, whereas for milking animals, it is possible to collect foot and leg data on a daily basis and create an overall score for the animal, for the meat animals there is a possibility that to be mounted to the weighing scales and collect their foot and leg data when they step on the scale for being weighed. On the other hand, according to Byrne et al. (2019), these technologies may underperform without certain design features to reduce inaccurate measurements, and Pastell et al. (2008) who worked with dairy cows have reported that they had to discard up to 10% of all the measurements due to these erroneous measurements. In addition to cows, the use of this type of equipment has been well evaluated in other species, such as dogs (Evans et al., 2005), chickens (Corr et al., 2003), dairy (Pastell and Kujala, 2007), and horses (Judy et al., 2001). However, due to the cost of the system, it may not be adopted by sheep farmers easily.

The third system that can be used for detecting the problems on foot and leg in sheep is the pressure-sensitive walkways. This system is using the same logic with force-plate systems but in the force-plates systems animals usually stand not walk, on pressure-sensitive walkways, gait is evaluated. Agostinho et al. (2012), conducted a study on 21 clinically healthy Santa Ines sheep from three different age groups (7 sheep aged 8 to 12 months, 7 sheep aged 2 to 4 years, 7 sheep aged more than 5 years) using pressure-sensitive walkway. Interestingly, opposite to what Pastern et al. 2006 observed for the milking cows, no significant differences were observed for the sheep, in either the front or back legs, between the left and right sides or between the two directions for any of the variables. In another study which was conducted by Kim and Breur (2008) reported that some sheep (e.g., Suffolk females due to their large body masses (69.3 to 103 kg) fight zone and flocking behaviors) breeds may not be suitable for the gait evaluation with pressure-sensitive walkways. On the other hand, in another study, it is reported that, Merino-mix sheep (with a 46 to 90 kg range) were able to be trained for observing the tibial defects on pressure-sensitive walkways (Seebeck et al. 2005).

Except from these systems, alternatively, accelerometers and gyroscopes are commercially available to detect lameness and widely used for tracking the activity both human and dairy cows (Kaler et al. 2020) but for sheep, wearable accelerometers and gyroscopes may not be found economical due to larger flock sizes, and smaller profits per animal when compared to cattle (Byrne et al. 2019). Probably, due to this reason, comparison to cattle, there is limited work in sheep (Alveranga et al. 2016; Barwick et al. 2018; Kaler et al. 2020) and these were focused on only classifying basic activities, such as standing, grazing, and lying, without identifying different features for classification of lameness. Moreover, it is reported that these studies only classify between lame and non-lame sheep as binary and having problem with classification between certain lameness scores (e.g., 0 and 1) (Kaler et al. 2020).

Similar to the variety of the options of the assessor of the scores, there are many scaling options (1 to 5, 1 to 9, 1 to 10, 1 to 50, 1 to 100, etc.) when scoring the foot and legs. While some use a scale from 1 to n with the intermediate value as the optimum and scores toward 1 or n representing deviations from the optimum, other systems score animals from 1 to “n” with 1 representing the best score and “n” the worst one or vice versa.

2.1.4 Identification of an appropriate early scoring age for structural foot and leg traits in sheep

Defining the appropriate early scoring age is necessary to capture the real structural scores regarding foot and leg. To date, different authors suggested different times for recording these traits in cattle but to the best of our knowledge, there is no consensus about ideal scoring age both in cattle and sheep. Considering that, structural foot and leg problems can both be the reason or result of the foot and leg lesions, choosing the right time for scoring is important.

In sheep, for providing a standardized set of visual assessments to the breeders, Australian Wool Innovation (AWI) & Meat and Livestock Australia (MLA) developed “Visual Sheep Scores”

(Visual Sheep Scores, Producer Version 3, 2019) guideline. In this guideline, it is was suggested that feet and leg scoring in sheep, as earliest, should be done on sheep over 4 months old. On the other hand, our dataprovider, Focus Genetics (New Zealand) uses SIL's scoring scoring system and scores the ewes at approximately 2 years old, and rams at 1 years old, not in earlier ages. Even though in the field, these are the ages that are used as the earliest ages for recording foot and leg traits in sheep, when we consider the sheep anatomy, these ages may be too early to see the real potential of the animals. This idea was supported by the findings of Martini et. al. (2001) who reported that, although the sheep reach sexual maturity at approximately 7-12 months of age, depending on breed, the closure of the physeal plates of the long bones may still occur as late as 36 months.

In cattle, some suggestions are available for appropriate early scoring age regarding structural foot and leg traits. American Angus Association (AAA Foot Score Guidelines, 2017) suggested that minimum age for scoring yearling heifers and bulls should be minimum 320 days (~11 months) to 440 (~15 months) days and 320 (~11 months) to 460 days (15.3 months), respectively. In addition to this, they indicated that older scores can also be reported on 18 - months old bulls, females, and mature cows. Moreover, Retallick, (2020) who gave a speech on behalf of Angus Genetics Inc. (AGI), a subsidiary of the American Angus Association, in a webinar (April 2020) named "Facts about foot scoring" indicated that yearling age for cattle (similar to the sheep that is as rising 2 years old, regarding still growing) may not be a good time for foot scoring because of low variation in scores. Scoring them at 2, 3, or 4 years of ages, due to having more variation, or expression in variation on foot and leg structure, could be more beneficial (Retallick, 2020). According to Antari (2018) although cattle reach 90% of their mature height at the age of 12 months (yearlings), their weight corresponds that only 50-60% of their mature weight at that age. Based on this, scoring at this age may not be an indicative for the future structural foot and leg scores because increased weight may change the structure of feet and legs. In addition to this, Stuart (2021), reported that cattle are not considered as fully grown until they are around 3 years old because, although usually cows reach their ideal weight for slaughter around 18-24 months, their skeletal growth continues till approximately 3 years old. Similarly, Summers (2017) reported that skeletal maturity is completed at around 30 months old in cattle. Nevertheless, Peterse (1986) and Smit et al. (1986) both proposed that the ideal time for measuring the claw traits in heifers was prior to the first risk of developing lameness due to the claw lesions, thus before calving, and afterward to identify the cause, and effect. Distl et al. (1984) suggested for the progeny-tested bulls, to measure their claw traits at an age of 12 months because of the increase in the coefficient variation with advancing age.

According to Vermunt (1990), age is one of the effects on claw shape which is one of the important structural foot and leg traits, other than management and environment. Best et al. (2021), reported that ewes aged ≥ 4 years old were more likely to have higher scores which represented higher hoof overgrowth. Similarly, Tadich et al. (2000) reported that they more frequently observed overgrown hooves when the ewes were older than 4.5 years. On the other hand, Angell (2016) reported that they observed more frequent overgrown shapes in hooves in ewes that were older than ≥ 2 years in comparison with yearlings and lambs. Hahn et al. (1984) reported that with an increased age, hoof angles decreased, particularly in rear hooves. The same authors also indicated that, they observed increased hoof length on older Holstein cows with an increased weight on larger surface area. Similarly, Giess, (2017) reported that with increasing age foot size tends to increase and back leg set tends to grow more curved in Angus cattle. According to the report by Johnston and Penny (1989), while there was no difference between front and back leg claw horn growth and wear rates, both rates decreased by age in pigs.

2.1.5 Heritability and repeatability of structural foot and leg traits, and their relationships with other traits in sheep

In the literature, although the heritability estimations for the back and front pastern angle, claw conformation parameters (dorsal angle, dorsal border, diagonal length, heel height, hardness, tubules per unit claw horn area), and some other structural foot and leg traits (hock straightness, etc.) in sheep were available, no published heritability and repeatability estimations for an overall evaluation for feet and leg for sheep could be found. On the other hand, according to the Sheep Improvement Limited, New Zealand's Technical Notes (Natalie Pickering, Focus Genetics, personal communication), the heritability estimations for the structural foot and leg traits in sheep ranges between 6% and 20% and are known as low to moderately heritable in sheep.

These are some studies from the limited literature that reported heritability and repeatability estimates for some of the structural foot and leg traits in sheep:

In the study where Snyman and Olivier (2002) used a dataset, which was collected from the Afrino sheep using a scale from 1 to 50 to evaluate the straightness of the hocks, front, and back pasterns. On this scale, while 1 is representing poor straightness, 25 is used for the average and lastly, 50 is for the ideal straightness. The heritability estimates from this study were reported as 0.36 for straightness of the hocks, 0.21 for straightness of the front pasterns, and lastly 0.08 for the straightness of the back pasterns.

Matebesi et al. (2009) in the study where they used a 1-50 scale scoring system for the evaluation of some foot and leg conformation traits for the Tygerhoek Merino resource flock, reported the direct heritability results for the hocks as 0.32 and for the pastern scores as 0.16. They reported that there was a significant genetic correlation (0.71 ± 0.06) among hocks, and front quarters which was the other subjectively assessed conformation trait in the study.

Fernando de la Fuente (2011) reported the heritability and repeatability estimates for the pastern angle scores which were scored using a nine-point linear scale on the Navajo- Churro breed and they were as follows: for all the lactations heritability estimate: 0.24, repeatability estimate: 0.42, and for the first lactation heritability estimate: 0.07 and the repeatability estimate: 0.28. The same author also reported the genetic and phenotypic correlations between the pastern angle scores (scored with a nine-point scale) and some udder structures and milk production traits (udder depth, udder attachment, teat placement, teat length, udder shape, milk yield, fat content, protein content, Logarithmic somatic cell count), genetic correlations were found all positive between pastern angle scores and the mentioned traits except udder attachment (-0.12) with a range between 0.03 and 0.31. In this study, the highest genetic correlations were obtained between milk yield and pastern angle as 0.29.

Mekkaway et al. (2009) in the study where they estimated genetic relationship between longevity and objectively and subjectively assessed performance traits in sheep using linear censored models, reported that the average heritability for the structural soundness as 0.24. Structural soundness in their study had been scored using a scale from 1 to 10 and indicated that the combination of correctness of limbs (the angle of pasterns) and straightness of legs.

Groenewald and Olivier (1999) in a study where they used Merino breed for a national progeny testing study, reported the heritability estimates for the hock and as 0.26 and 0.12, respectively.

Mortimer et al. (2009), where they identified the genetic parameters for visually assessed front and back leg structures recorded on Australian Merino sheep, indicated the heritability estimations for the front legs as 0.18, and 0.13 for the back legs. They also reported that most genetic correlations between leg structure traits and the wool quality and other conformation traits (face cover, neck wrinkle and body wrinkle) were close to zero. Only, wool character was found positively correlated (low) with front leg structure.

Vermunt and Greenough (1995), described diagonal length and dorsal angle as claw traits which can be measured exactly with high repeatabilities and only slight environmental conditions. Erlewein (2002) who worked on Merinoland and Rhone sheep to compare claw conformation parameters (diagonal length, dorsal angle, dorsal border, heel height, hardness, the area of the horn tubules, and the number of horn tubules) pointed out that one-year-old Merinoland sheep have a longer dorsal length and dorsal border, a higher heel height, and a greater than the dorsal angle of claws of Rhone sheep and reported moderate heritabilities ranging from 0.20 to 0.56 for dorsal angle, dorsal border, diagonal length, and hardness. Besides, same author reported most of the h^2 values for front claws as higher than for back claws. Erlewein (2002) also reported that in Merinoland sheep there were more horn tubules found than in Rhone sheep. Kindler (1990) also identified breed differences in the microstructure of claws comparing German Blackhead Mutton, Merinoland and Merino Mutton, Suffolk, and Gray Heath sheep. According to Kindler (1990) and Vermunt and Greenough (1995), the number of horn tubules per unit claw area determines the water content of the claw and horn quality and large number of horn tubules points out qualified horn in sheep. Dietz and Prietz (1981) also reported that best resistant claw horn is characterized by a high number of horn tubules and fewer tubules result in higher amount of moisture being taken up by the intertubular zone of the claw which can increase the incidence of diseases (Vermunt and Greenough, 1995). Erlewein (2002) reported low to moderate heritabilities for thenumber of horn tubules (0.01 to 0.25) and the area of the horn tubules (0.35 to 0.82) and their repeatabilities were described as high and were ranged between 0.88 and 0.99.

Lambertz et al. (2014) who also worked on claw conformation traits for sheep, like Erlewein (2002), reported that claw conformation parameters showed moderate heritable values for diagonal length and heel height, but claw hardness was not found heritable. The authors of this study associated that due to the influence of environmental effects on the hardness of the claws.

Janssens and Vandepitte (2004), in the study where they estimated the genetic parameters for body measurements and linear type traits in Belgian Bleu du Maine, Suffolk, and Texel sheep, using a 1 to 9 scale for the scoring, scored the forelegs front and side views, and rear legs' rear and side views. In this scale, for the side views, while 1 is used for sickled legs, 9 was representing the buckled legs. For the rearview, 1 was corresponding to X-shaped, 9 was for the O-shaped. The heritability estimations from the multi-trait analysis for the forelegs front view, forelegs side view, rear leg's rearview, and rear legs side view was reported respectively for the three different sheep breed (Belgian Bleu du Maine, Suffolk, and Texel) as follows: Belgian Bleu du Maine (0.07; 0.16; 0.04; 0.31), Suffolk (0.14; 0.15; 0.20; 0.11) and lastly, Texel (0.04; 0.06; 0.08; 0.14). The authors suggested that the low heritability estimates for the leg traits may be related to the inaccuracy of visual scoring as a contributing factor on it.

2.2 Longevity in sheep

2.2.1 Lifespan of sheep

According to the AnAge database (https://genomics.senescence.info/species/index.html), an integrative database describing the aging process in several organisms with maximum lifespan, taxonomic information, etc., the maximum reported age is just below 23 years for the domestic sheep (Ovis aries), which are used in the sheep production systems. As an economically important livestock animal attainment of this maximum age in typical sheep production systems is rare as managers make decisions to select animals to be culled based on their health, productivity, reproductive performance, and other many reasons. In commercial sheep flocks, although the typical culling age for ewes is changing among countries and systems, it was reported by Byun (2012) as six to seven years, which is indicating that we are far from benefiting from their potential lifespan. Hoffman and Valencak (2020), reported that the domestic sheep find only the chance to live about 31% of their potential lifespan (assuming the average culling age is 7 and the maximum expected lifespan is 23). On the other hand, in commercial flocks, culling due to age is a common practice all in the US at five to six years of age (Schoenian, 2019), in Australia at six years of age (Hatcher et al., 2009) and in New Zealand at six to seven years of age (Farrell et al. 2019); however, some farms may choose to keep older ewes for longer or may purchase 'culled for age' ewes from other farms (Griffiths, 2020) as an economic enterprise. However, culling for age is commonplace yet there is little objective data available to support this common practice, or its economic consequences (McGregor 2011; Wishart et al. 2016; Griffiths, 2020). Limitedly available literature written on these subjects suggests different opinions. According to Dickerson and Glimp (1975), the production of ewes tends to peak at around 4 to 6 years of age and to decrease thereafter. In another paper written by Nugent and Jenkins (1993) where they simulated the effects of culling ewes for age and failure to conceive, it was suggested that if ewes were culled at 4 years of age and replaced by genetically superior animals, system efficiency would not suffer greatly. In addition to this, the same authors suggested that there is no reason for keeping ewes to an age > 6 years unless the replacement ewe costs detrimentally large. In another paper written by Blackburn and Taylor (1990) where different culling age practices (culling at 5, 6, or 8 yr of age) were compared by simulation method on a northern Kenya sheep production system, indicated that culling ewes for age at 8 rather than 5 or 6 years was found in more beneficial in terms of flock efficiency.

2.2.2 The features of longevity evaluations and the definition of ewe longevity

Longevity is a trait that is an indicator of overall health of animal (Van Raden and Powell, 2002), and several researchers have explored using a wide range of different statistical methods and models based on different definitions and data properties to improve longevity traits by selection (Hu et al. 2021). However, because it was defined by many researchers as interchangeably and confusedly, the results can be confounded or hard to absorb for the new researchers. Therefore, Hu et al. (2021) suggested standardizing the terms of longevity traits. Some of the terms used for defining longevity until today are as follows: productive life, herd life, functional longevity, true longevity, residual longevity, lifespan, length of productive life, functional productive life even some researchers defined longevity as stayability. All these definitions differentiated at reflecting different periods of animals such as how long an ewe stayed in the flock or how long an ewe stayed productive in the flock, even so, all definition helps us to achieve what we aim for which is the identification of the ewes that can outperform their contemporaries (McLaren et al., 2020). While Connington et al. (2001) defined longevity as the period (days) from birth to culling or death, Rahman et al. (2021), defined it from birth to their last available production record. On the other hand, Mekkaway et al. (2009) defined it, as the time (in years) from 2 year of age (the age at first lambing of most ewes = first production age) to culling or death. In addition to this definition, another group of researchers, McLaren et al. (2020), suggested that when the culling date and reason are not available for the evaluation of the longevity, the ewe's last production record (last lambing) can be used as a proxy for the culling age.

The models to evaluate it is also differing and typically in the evaluation of longevity, linear models, threshold models, random regression models, sire models and survival analysis are often used. Each model has its own advantage and disadvantages and Imbayarwo-Chikosi et al. (2015) indicated that while linear models, threshold models and random regression models can process multiple traits simultaneously which makes it possible the estimation of genetic correlations between longevity and other traits can be obtained relatively fast. In another report which was written by Imbayarwo-Chikosi et al. in 2016, was mentioned that survival analysis can appropriately accommodate the censored data, considering time-dependent environmental impact and manage the skewed distribution of longevity characteristics. On the other hand, it is also mentioned that although the estimated value of the trait from survival analysis is remarkably close to the measured value, calculation speed was relatively slow. In addition, linear, threshold models, and random regression models were reported by many researchers (Ducrocq, 1997; Setati et al., 2004; Jamrozik et al., 2008; Kern et al. 2014) as generally producing lower estimation of heritability of longevity than survival analysis.

Van der Linde & de Jong (2002), in a comprehensive Multiple Across Country Evaluation (MACE) study that they have done for comparing the longevity and parameter definitions of 11 countries (Canada, Denmark, France, Germany, Israel, Italy, New Zealand, the Netherlands, Sweden, Switzerland, the United States), indicated that national, international, and true reliabilities of evaluations still could be consistent, and comparable, even though statistical methods differ. In their study, they aimed to quantify the differences among trait definitions by examining the correlations for longevity with those for yield, somatic cell score (SCS), and conformation within each country. For their aim, they evaluated the longevity using the bulls which were born in different 11 countries between 1985 and 1994. In this study, they identified that different countries used different statistical methods (binomial, and repeated binomial trait analysis using linear models, and survival analysis using non-linear models) and different reporting systems for longevity (true longevity or functional longevity). In conclusion, they reported the correlations of longevity with SCS as uniform across countries. The correlations obtained from this study for the conformation traits were uniform except for New Zealand. Correlations with the birth year (genetic trends) were small but higher for countries in which longevity was favorably correlated with yield. Correlations for yield traits were not uniform. Correlations of functional longevity with milk yield ranged from -0.22 for Italy to 0.26 for France. The US correlations of true longevity with yield were similar to those of France even France removes yield whereas the US does not. New Zealand also does not adjust for yield, and yet the EBV correlation of longevity with milk yield was negative and correlation with protein was near 0. According to VanRaden and Klaaskate (1993), due to low yielding animals are culled phenotypic and genetic correlations often are often found as favorable between yield and longevity.

Nowadays, genomic technology developments and the accumulation of knowledge about animal genomes have introduced an important new dimension into the research of long-lived and at the same time productive animals. These days, scientists are probing into animal DNAs and searching for possible markers for long-lived animals. Interestingly, Byun et al. (2012), in the study they have done in with sheep, have detected that several “aging” genes are associated with longevity in sheep. Similarly, in cattle production, it was reported that there was an association between genetic variation in the bovine calpastatin gene (CAST) and longevity and fertility in dairy cattle (Garcia et al., 2006). Given the genetic similarity between cattle and sheep and the conservation of many metabolic systems across the animal kingdom, it might be possible to identify specific longevity genes in sheep and ultimately use them to improve productivity (Byun, 2012). Moreover, it was reported by different researchers (Benetos et al. 2004; Zhao et al. 2013) who worked with humans and animals that we may have an interesting tool for searching for the key for longevity in DNAs with the help of telomeres. Telomeres are the repetitive sequences of noncoding DNA found at the terminal ends of linear chromosomes and are famous for their important role in maintaining DNA stayability and integrity (Blackburn, 1991; Shay et al. 2019). López-Otín et al. (2013), reported that average telomere length was considered a biomarker of whole-organism health and biological aging, and short telomeres were reported as associated with an increased risk of death. Froy et al. (2021), tested this on wild Soay sheep using blood samples collected over years (19-yr period) and longitudinal data and aimed to identify the causal role of telomeres on sheep longevity. According to their study, there is a genetic correlation between telomere length and sheep longevity, but no association could be found between telomere shortening and sheep mortality risk. Further research is needed for understanding the relationship between telomeres and different sheep breeds' longevity.

Another recent approach the investigation of livestock's' health, longevity, productivity, and environmental adaptation that was reported very recently by Clarke et al. (2021) that using the epigenetic clocks' DNA methylation profiles as a molecular tool because it is well known that environment can influence DNA methylation. Moreover, Hazard et al. (2020), as a result of the study that they conduct with Romane sheep, reported that global DNA methylation rate in sheep was found as moderately heritable ($h^2 = 0.20$) and genetic selection for this trait is possible. These researchers also suggested that in near future, we can incorporate EWAS (epigenome-wide association studies) and GWAS (genome-wide association studies) into animal breeding schemes to search for epigenetic markers and use them for better understanding. This approach is very novel and needs further investigations but seems promising.

2.2.3 The importance of ewe longevity

The ideal ewe is the one that is both productive and long-lived. Hence, ewe longevity which can be considered as an indicator of the resistance to environmental stressors that can significantly affect both lifespan and productivity is important but is often underemphasized. An "efficient ewe" can be defined in many ways such as profit per ewe, the number of lambs per ewe, etc. and is the driver of profitable sheep production. Ewes that stay longer in the flock will produce more lambs than ewes culled at early ages. Even with this importance, ewe wastage (Flay et al., 2021), losing the ewe before they hit their potential lifespan, is a common problem worldwide.

Decreased ewe longevity may decrease your profitability and may bring the end of your operation due to dealing with a persistently high replacement cost. Increased ewe longevity decreases culling rates in turn reducing female replacement costs. More selection pressure applied when choosing replacement females could result in higher age-related performance. Cruickshank et al. (2009) who modelled a breeding flock reported that if the age at which ewes were culled increased from 5 to 6 years of age, 13% fewer replacement ewes were needed each year, and therefore culling pressure on other traits could be increased. Most importantly, increased ewe longevity results in more market lambs to sell at the end of the day.

2.2.4 How to increase ewe longevity

Before attempting to move to a genetic solution for increasing ewe longevity across countries, it is important to understand what the main causes of ewe mortality or culling (voluntary or involuntary) within systems are. Based on these results, we need to identify early-life predictors of culling, for example, identifying the proportion of culling due to foot/leg problems, etc. In this way, we may better understand whether important traits are similar across populations and whether common solutions to extend ewe longevity are possible or appropriate.

Like in the other livestock production systems, to maintain productivity in sheep flocks, a portion of the ewe flock needs to be replaced every year to maintain numbers. While in the US, in a sheep enterprise, it is customary to cull approximately 15% of the flock each year (Schoenian, 2019), generally, replacement rates in New Zealand sheep flocks vary from 20-35% (MacKay et al. 2012, Farrell et al. 2019). Flock policies regarding culling due to age can differ from each other but in the US, according to the National Animal Health Monitoring Systems study, 2011, age is usually the primary reason for culling ewes and almost 70% of the sheep operations cited age as the primary reason for the culling of ewes. In the US, in 2011, 55.6% of ewes culled were culled due to age and the average age of culled ewes was 6.3 years, compared to 5.9 in 2001 (Schoenian, 2019). Focus Genetics, the company that had provided dataset to us, usually cull animals due to age as a flock policy as well as for non-pregnancy. In Australia, which is another country with a significant sheep industry, culling due to age is a common flock policy, too. In Australia, after their first shearing, sheep are typically retained for 6 years (Atkins et al. 2006). On the other hand, Hatcher et al. (2009) suggest that widespread adoption of precision sheep production systems for wool or dual-purpose (wool & meat) in Australia (Rowe and Atkins, 2006) will lead to a change from age-based culling to variable age culling. The same authors claim that as the reason Australia ewe longevity has not been well-examined in the scientific literature.

The important question arises then, how to increase ewe longevity? There are some management approaches that can be considered for beginning to enable selection for increased longevity: 1) keep good data, recording the reasons for leaving the flocks, 2) use data to determine the primary reasons for death and culling in the flock, 3) reduce or eliminate culling animals based on age, 4) select replacements from long-lived parents, 5) use crossbreeding to increase ewe longevity.

2.2.5 Heritability of ewe longevity, and its relationship with other traits

According to Byun (2012), since the phenotype of longevity can be measured, although only after the fact, and given that the trait is heritable, then it should therefore be possible to breed more long-lived sheep. In general, the reported heritability estimates for ewe longevity range between 0.05 to 0.08 with a range of 0 to 0.33 depending on the species, breeds, production system, and trait definition (Conington et al. 2001; El-Saied et al. 2005).

While some results from studies of the genetic control of ewe longevity suggest that ewe productive life is lowly heritable, with heritability estimates ranging from 0.03-0.13 (Borg et al., 2009; Brash et al., 1994; Conington et al., 2001; Lambe et al., 2008; Lee et al., 2015. McLaren et al., 2017; Zishiri et al., 2013). Other researchers, such as Rahman et. al., (2021) who based their study on the definition of the longevity developed by Conington et al. (2001; from birth to last available production record) reported that the heritability for longevity was 0.22±0.01 in Australian Merino ewes.

According to a recent report by Rahman et al. (2021) heritability for ewe longevity (from birth to last production record) of Australian Merino ewes which was reported by using data available in MERINOSELECT database, as 0.22. Authors indicated that the breeders who submitting the data to the database tend to apply selection pressure and maintain highly selected ewe flocks, speculated that this may be the part of the reason of moderate heritability estimation.

Mekkaway et al., (2009) reported the heritability of ewe longevity as moderate at 0.27 (0.22 to 0.33) in crossbred Mule ewes. They suggested their moderate heritability estimate was due to several reasons; 1) the animals used in the project were all kept on experimental farms where the husbandry and other environmental effects were controlled, 2) tightly defined reasons for culling were applied at all the farms 3) the heritability estimate was derived from the crossbred Mule ewes, rather than a purebred population, it may be inflated by a nonadditive variation--the basis for heterosis effect.

Other studies support the low to moderate heritability of ewe longevity across populations. While Fuerst-Waltl et Baumung (2009) estimated the heritability of functional longevity at 0.12, Pelmus et al. (2020), using the survival analysis to evaluate the ewe longevity for the Romanian Teleorman Black Head sheep, reported the heritability estimate for the ewe longevity as 0.10, and the average length of productive life as 673.16 days (~1.84 years). Milerski et al. (2018) in the study where they defined the ewe longevity as functional longevity and using a survival analysis for Suffolk sheep reported the heritability with a high value of 0.44. Borg et al. (2009) only used ewes that had the opportunity to remain in the flock until 6 years of age for the evaluation of productive life (ewe longevity) in Targhee ewes, and the heritability estimation for the ewe longevity was reported as 0.05 for the single trait analyses and as 0.06 for the multi-trait analyses. Lee et al. (2015) investigated ewe longevity for both the seedstock and commercial flocks in New Zealand sheep populations and reported the heritability estimates as 0.10 and 0.13, respectively. Zishiri et al. (2013) reported the heritability of longevity as 0.05 in Dorper sheep in South Africa. In their study, they used the last lambing date for calculating longevity. Using a slightly different approach, Holland (2018) investigated the ewe longevity for different breeds, reported the heritability estimates for ewe longevity as 0.06 for Columbia breed, 0.07 for Polypay breed, 0.09 for Suffolk, 0.13 for Targhee, 0.16 for Rambouillet breed, and lastly 0.16 for across breed. In the same study, Polypay ewes had the lowest longevity compared to other breeds. In addition to this, ewes born as singles were found as having survivor functions characterized by a higher probability of survival to older ages ($P < 0.05$)—an effect that might influence how breeders select for increased longevity.

Available literature focuses on a wide variety of different traits and their relationships with longevity, but these are limitedly available for the structural foot and leg traits in sheep and are mainly based on other livestock species. These are as follows:

According to Nielsen et al. (1999), the genetic correlation between feet and leg diseases and longevity was negatively correlated (-0.42 and -0.43) in dairy cows. Additionally, Le et al. (2005) reported that leg conformation and longevity was found favorably (0.07 - 0.39) correlated in pigs. Same authors suggested that leg conformation traits can be used as an early life predictor for sow longevity.

Tsuruta et al. (2005) investigated correlations between productive life and some of the of the structural foot and leg traits (foot angle, rear legs side view, rear legs rear view) in cattle and concluded that straighter legs and steeper foot angle were found consistently associated with increased longevity.

Westendorp and Kirkwood (1998) offered a theory called as "disposable-soma theory" which states that increased investments in reproduction results in decreased investment of maintenance, which reduces the lifespan of an animal. In the following years, this theory was tested on both humans and animals by different authors. For example, Gagnon et al. (2009) tested this theory using the data collected from three large demographic women groups and reported that their results were indicating that there is a trade-off relationship between fertility and longevity and clearly, a large number of children can be detrimental for woman's survival prospects in older ages. However, they reported that the trade-off is not as important as Westendorp and Kirkwood previously envisioned it and fertility may need to be fairly high for the trade-off to be revealed. They also reported that an interaction effect between parity and age at last birth that indicates a more complicated scenario, and the detrimental effect of high parity is weaker for women who gave birth to their last child at an older age. Hence, having children late may be taken as a sign of robustness or of delayed aging and this signal would be stronger for women who already had many children. At the end of the study, authors suggested that further research is needed and indicated that, fertility might be negatively influenced by potential longevity genes and vice versa. Similar trends have been observed in sheep by McLaren et al. (2015). They worked with Dorset and Lleyn sheep and reported a moderate negative genetic correlation (–0.40) between longevity and litter size. They claimed that a larger litter size in Dorsets could lead to a shorter lifespan while this was not the case for Lleyn sheep. In this study, the heritability of ewe longevity was found to be 7% for Lleyns and 11% for Dorsets and authors reported a high positive genetic correlation (0.80 - especially in Dorsets) between ewe longevity and the age at first lambing, and accordingly, suggested that the lambing of one-year-old ewe lambs may lead a shorter lifespan, and concluded that, more intensive production animals less likely to have a negative impact on longevity.

Hatcher et al. (2009) who studied on both within ages and cumulative the heritability of survival in adult Merino ewes reported that it was negligible at 2 years of age but tended to increase with increasing age.

The other researchers Mekkaway et al. (2009) focused on the relationship between ewe longevity and culling traits and in the study where genetics parameters and genetic relationships were evaluated in crossbred Mule ewes, reported the genetic correlations between ewe longevity and culling traits as high which ranges between 0.51 and 0.87 and suggested that the selection for the ewe longevity will improve other traits associated with teeth, mouth, and udders. On the other hand, in the same study, the genetic correlations between ewe longevity and growth traits were low and not significant.

Holliday (2006) who focused on the relationship between longevity, and reproduction, indicated that the mutations in genes that increase longevity (in so-called gerontogenes) are likely to have deleterious effects on the phenotype, such as loss of fertility. In addition to this, same author suggested that, in animals and humans there may be ways and means of reducing metabolic rate, or reducing temperature, or increasing sleep, all of which could conceivably increase longevity.

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CHAPTER 3 – ESTIMATION OF HERITABILITY AND REPEATABILITY OF STRUCTURAL FOOT AND LEG TRAITS IN SHEEP USING REPEATED RECORDS ANIMAL MODEL ANALYSES

Summary

Foot and leg soundness can contribute to productivity and longevity in sheep flocks. Sheep are subject to a range of foot and leg issues that causes lameness and ultimately culling due to foot and leg problems. The global mean prevalence of lameness in sheep was reported as 10.2% of individual for 2004 (Kaler and Green, 2004), then, with the adopted prevention, treatment, and culling strategies by farmers, it fell to 4.9% in 2013 (Winter et al. 2015 - the most recent reported value globally). It is considered that the scoring systems for the foot and leg (lesion scoring and structural scoring) and culling based on these observations can play a big role in the further reduction. Yet, in the sheep industry, record-keeping and the scoring of foot and leg structure is not very common, and to date, there are just a few studies that have focused on this subject, most with small numbers or non-repeated scoring. However, to enable breeders to select for improved feet and leg issues, just like other phenotypic traits, we must measure and document observations. Additionally, due to the foot and leg structure change as sheep age, it is suggested that scoring adult sheep multiple times over their life in the flock will likely add useful information beyond early life scores. Although there is limited information on this subject, it is documented in the Sheep Improvement Limited (SIL) New Zealand's Technical Notes (not published – Natalie Pickering (Focus Genetics), personal communication) that structural foot and leg traits are lowly to moderately heritable ranging from 6 to 20%. Therefore, our research objectives were to estimate

the heritability and repeatability for structural traits including overall foot and leg scores, front and back pastern angle scores, front and back claw, and hoof shape scores. The data consisted of 31,615 overall foot scores, 31,578 back pastern angles, 31,612 front pastern angles, 31,610 back feet claw, and hoof shape scores, and 31,612 for the front feet claw and hoof shape scores from commercial ewes and rams, as well as pedigree and corresponding performance records. All data was supplied by Focus Genetics, Ltd, New Zealand. We used a repeated record, animal model with fixed effects of recording age, sex, age of dam, birth rank, rearing rank, heterosis (as a covariate), and contemporary group defined as the combination of birth year, birth flock, and recording mob. Random effects included a direct as well permanent environmental effect. Heritability estimates ranged between 7 to 17% for the structural foot and leg traits which coincidences with the heritability estimates calculated by SIL as 6 to 20% (Natalie Pickering (Focus Genetics), personal communication). The repeatability estimations ranged between 14 to 31%. To the best of our knowledge, although few studies reported heritability estimates for the pasterns and claw and hoof conformation traits (not an overall evaluation for claw and hoof shape) in sheep were available, for the overall evaluation of structural traits in sheep, there was not any prior published heritability or repeatability estimation, therefore results herein add to the base of knowledge.

This study demonstrated that with appropriate, more robust structural foot/leg traits databases, for sheep flocks, it will be possible to differentiate the animals which maintain their favorable structure over time from those that begin to regress and that selection using appropriate tools will decrease the culling rates due to foot and leg problems.

3.1 Introduction

Information on the lifespan of sheep and therefore longevity in a flock is critical to the economic outcomes of production. Unfortunately, due to the limited amount of culling and/or or reason data recorded, ewe longevity has not been widely evaluated. According to the small number studies on ewe longevity, it has a low to moderate heritability (Conington et al. 2001; El-Saied et al. 2005). Another challenge for ewe longevity trait is that producers must wait for the animal or its relatives to leave their respective flocks to obtain a direct measurement for it. On the other hand, to boost ewe longevity and to be able to use it in selection practices, the accumulation of the knowledge about ewe longevity, and the estimation of its heritability for different populations are required and, therefore, the objective of this study was to estimate the heritability of ewe longevity for the ewes mainly Romney and other composite breeds raised in New Zealand-Pamu owned flocks.

3.2 Materials and Methods

The present study utilized data obtained from Focus Genetics flocks which is stored in Sheep Improvement Limited New Zealand's (SIL) database; however, animals within the experimental locations were managed according to the AgResearch Animal Ethics Committee guidelines.

3.2.1 Data collection, preparation, and description

The data were provided by Focus Genetics and consisted of performance information on 309,509 sheep with pedigree data collected between 2000 and 2020 from seedstock and commercial ewes and rams. The data were sifted based on observations for the structural foot and leg traits, with those without scores removed from the data before analysis. For the analysis, repeated records of structural foot and leg traits including overall foot scores, back and front feet pastern angle scores, back and front feet claw, and hoof shape scores were used. Those records included 31,615 overall foot scores, 31,578 back pastern angles, 31,612 front pastern angles, 31,610 back feet claw and hoof shape scores, and 31,612 front feet claw and hoof shape scores. In the raw data set, although there were a total of 412 ewes that lived more than 7 years (8, 9, 10, and 11 years old animals) with structural trait observations, these observations were assigned as unknown in the data set due to the small number of animals for each age that causes biased representation for these ages. Culling due to age in NZ is 6 to 7 years according to technical notes of SIL. A total of 283 rams' structural foot and leg observations were also assigned as unknown in the data due to not representing the group of ages and having a small number of animals. (3 years old - 234 animals), 4 years old - 44 animals), 5 years old - 5 animals). Males commonly had a single observation typically taken at 2 years of age, while females were typically scored more than once. The detailed portrayal and visual rubrics for the structural foot and leg scoring criterias used for sheep in New Zealand can be found in following sections.

3.2.1.1 Structural foot and leg scoring criterias used for sheep in New Zealand

The data used for analyses belonged to Focus Genetics, New Zealand, and Focus Genetics uses a scoring system recommended by SIL. In this system, a 1 to 5 scale was used with 1 representing the best score and 5 the worst one. Ewes are typically scored every year with the first observation taken at approximately 2 years of age, although a subset of ram-exposed ewe lambs may be younger at 18 months or even younger (Natalie Pickering, Focus Genetics, personal communication). Additionally, potential sale rams are scored at 1 year of age. In this scoring system, scores range from 1 to 5 with 1 representing the best and 5 the worst conformation score (Figure 3.1 - Natalie Pickering, Focus Genetics, personal communication). Evaluations are performed when the animals are on a hard flat clean of dirt surface and can walk and stand at ease without being pushed by other sheep. At this first scoring, some animals may be removed from the breeding population based on their scores (Figure 3.1 - Natalie Pickering, Focus Genetics, personal communication).

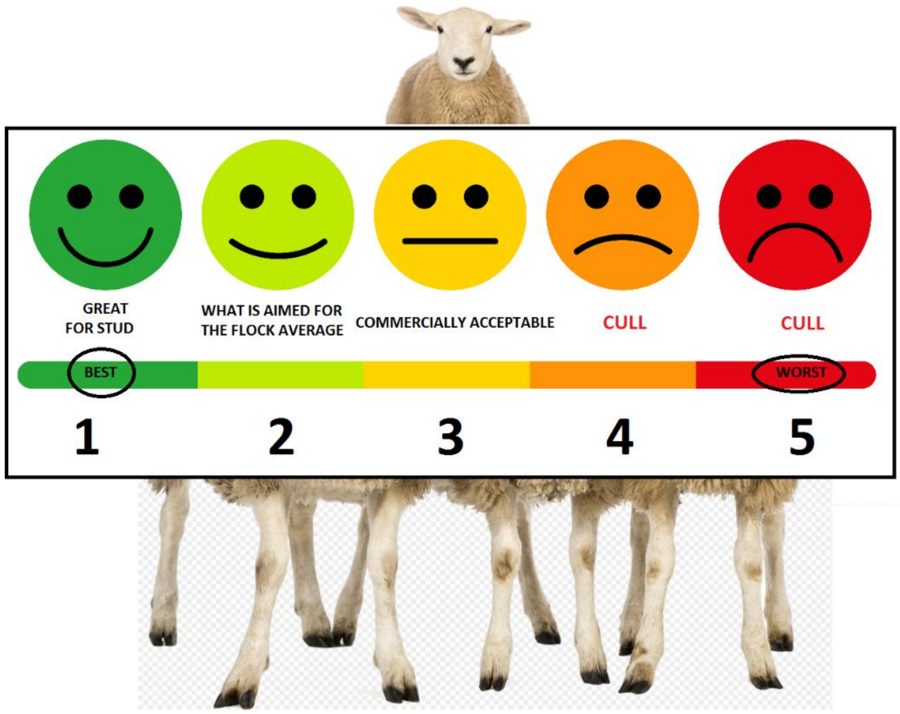

Figure 3.1 Scoring system and culling criteria for structural foot and leg traits in sheep

3.2.1.1.1 Overall foot and leg scores

In overall foot and leg scoring, pasterns, hoof structures, toe placements, and leg rotations were evaluated, and the animal gets an overall score for all. Scoring criteria are illustrated in Figure 3.2 (Natalie Pickering, Focus Genetics, personal communication).

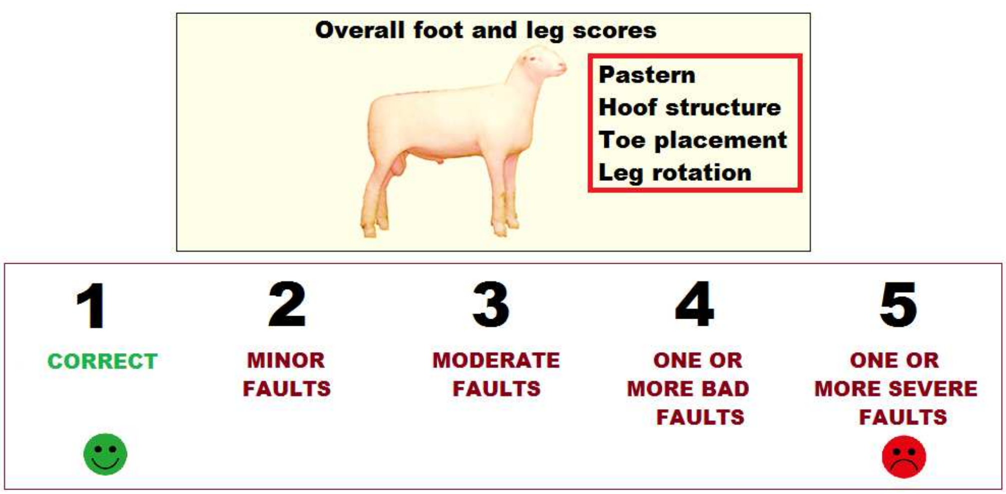

Figure 3.2 Scoring criteria regarding overall foot and leg

3.2.1.1.2 Pastern angle scores

In pastern angle scoring, the angle of the lower joint relative to the leg was scored for both front and back foot, separately. Scoring criteria are illustrated in figure 3.3 (Natalie Pickering, Focus Genetics, personal communication).

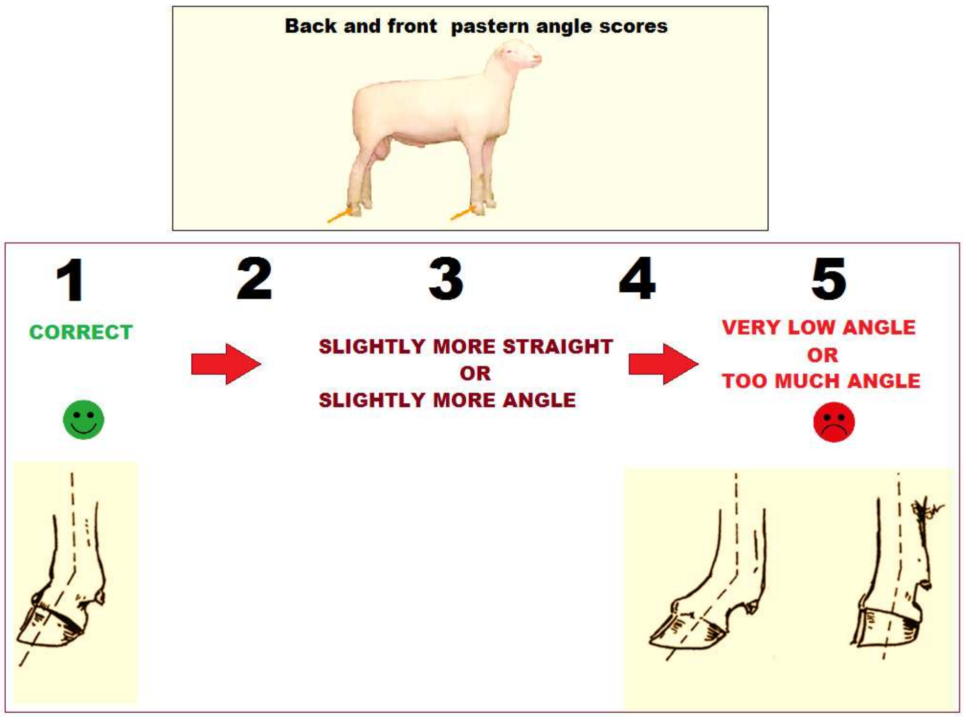

Figure 3.3 Scoring criteria regarding pastern angle

3.2.1.1.3 Claw and hoof shape scores

In claw and hoof shape scoring, the integrity of the front and the back feet considering the side, sole, and individual digit arrangement, are scored by the visual scorer. Scoring criteria are illustrated in figure 3.4 (Natalie Pickering, Focus Genetics, personal communication).

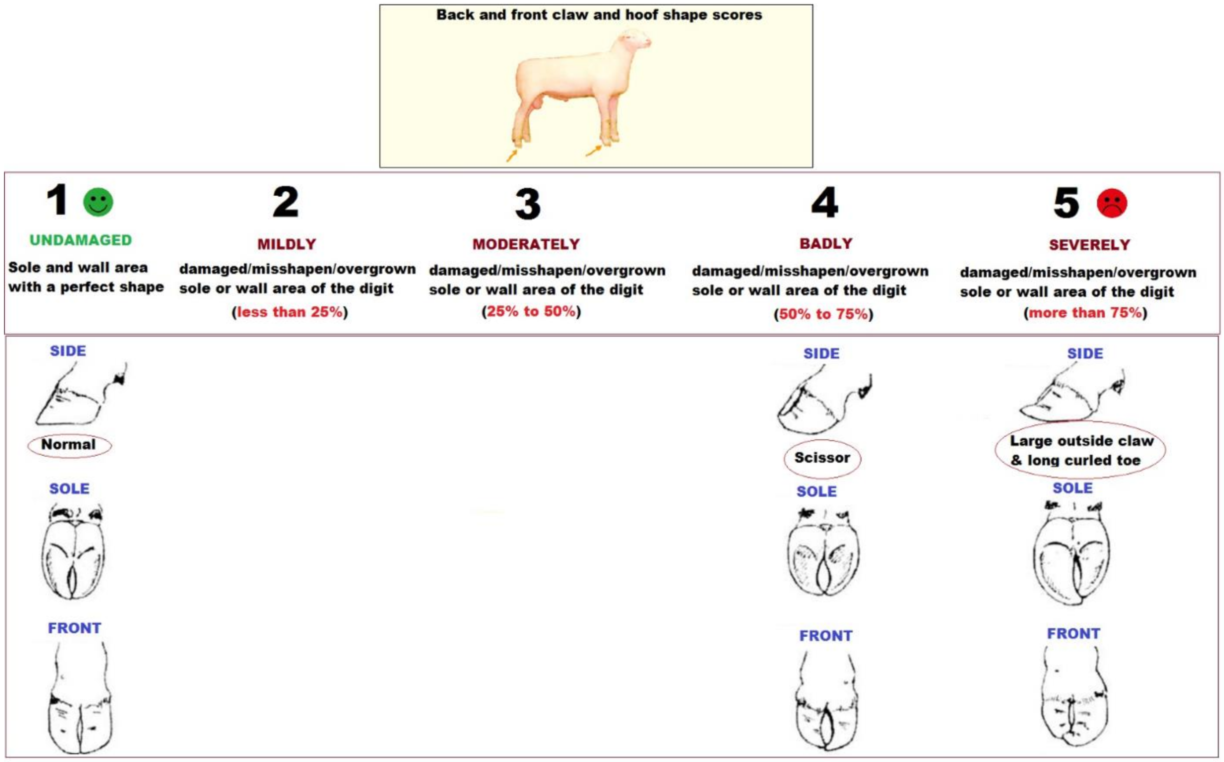

Figure 3.4 Scoring criteria regarding claw and hoof shape

3.2.2 Descriptive statistics of the data sets

The number of observations used for the evaluation of each of the structural foot/leg scores is presented by sex in Table 3.1. The trends in observation numbers for each structural trait for the ewes can be found in Tables 3.4 through 3.8. In Figures 3.5 to 3.9, all structural foot and leg scores tended to increase in ewes as they age.

Table 3.1 The number of observations used for the evaluation for each of the structural foot/leg scores by sex

	OFS[1]	BPAS[2]	FPAS[3]	BCHS[4]	FCHS[5]
EWES	28,282	28,249	28,279	28,278	28,279
RAMS	3,333	3,329	3,333	3,332	3,333
TOTAL	31,615	31,578	31,612	31,610	31,612

[1]OFS = overall foot score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score

Table 3.2 Overall foot and leg scores by ages within sex

Recording Age	Number of observations	Min	Average OFS[1]	Max	SD
EWES					
2 years old	1,369	1	2.60	5	0.91
3 years old	10,753	1	2.69	5	0.69
4 years old	6,942	1	2.73	5	0.73
5 years old	5,024	1	2.87	5	0.76
6 years old	2,948	1	2.92	5	0.81
7 years old	1,246	1	3.01	5	0.86
RAMS					
1 years old	3,333	1	2.65	5	0.81

[1]OFS=overall foot/leg scores

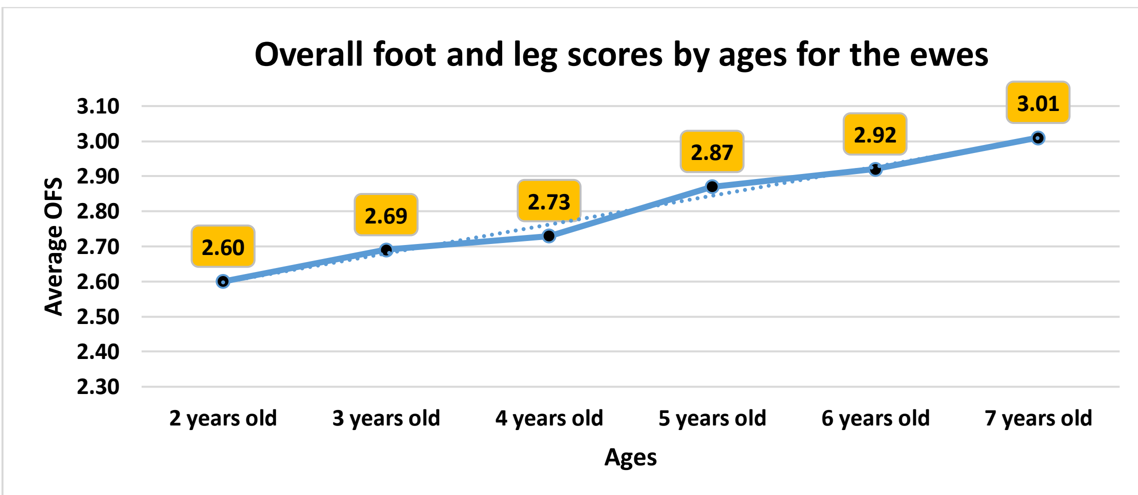

Figure 3.5 Average overall foot and leg scores by ages for the ewes

Table 3.3 Back pastern angle scores by ages within sex

Recording Age	Number of observations	Min	Average BPAS[1]	Max	SD
EWES					
2 years old	1,368	1	1.89	5	0.69
3 years old	10,729	1	2.32	5	0.60
4 years old	6,936	1	2.32	5	0.56
5 years old	5,023	1	2.38	5	0.59
6 years old	2,948	1	2.43	5	0.62
7 years old	1,245	1	2.47	5	0.67
RAMS					
1 years old	3,329	1	2.20	5	0.53

[1]BPAS=back pastern angle scores

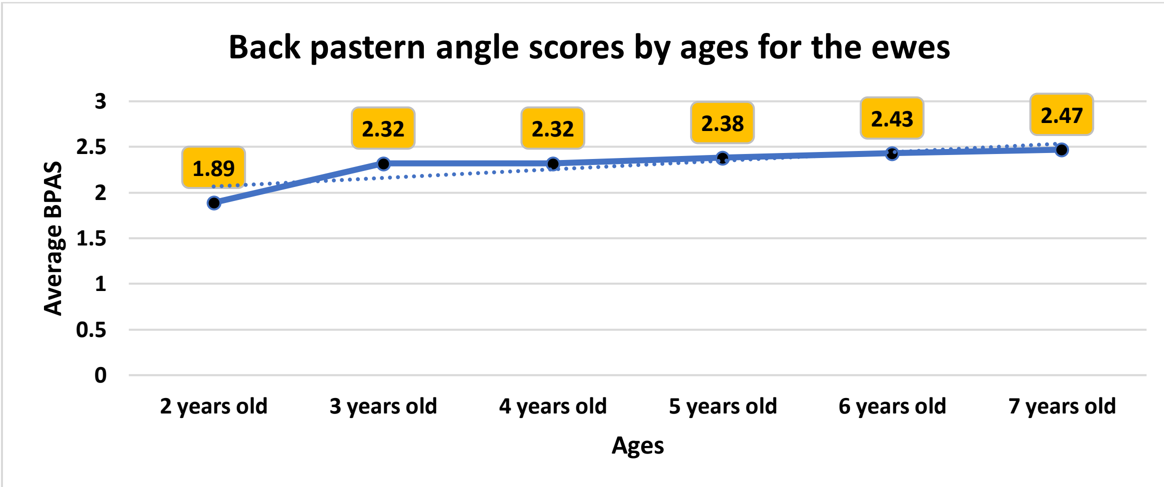

Figure 3.6 Average back pastern angle scores by ages for the ewes

Table 3.4 Front pastern angle scores by ages within sex

Recording Age	Number of observations	Min	Average FPAS[1]	Max	SD
EWES					
2 years old	1,369	1	1.91	5	0.75
3 years old	10,752	1	2.32	5	0.59
4 years old	6,940	1	2.36	5	0.60
5 years old	5,024	1	2.38	5	0.59
6 years old	2,948	1	2.38	5	0.59
7 years old	1,246	1	2.40	5	0.63
RAMS					
1 years old	3,333	1	2.33	5	0.64

[1]FPAS=front pastern angle scores

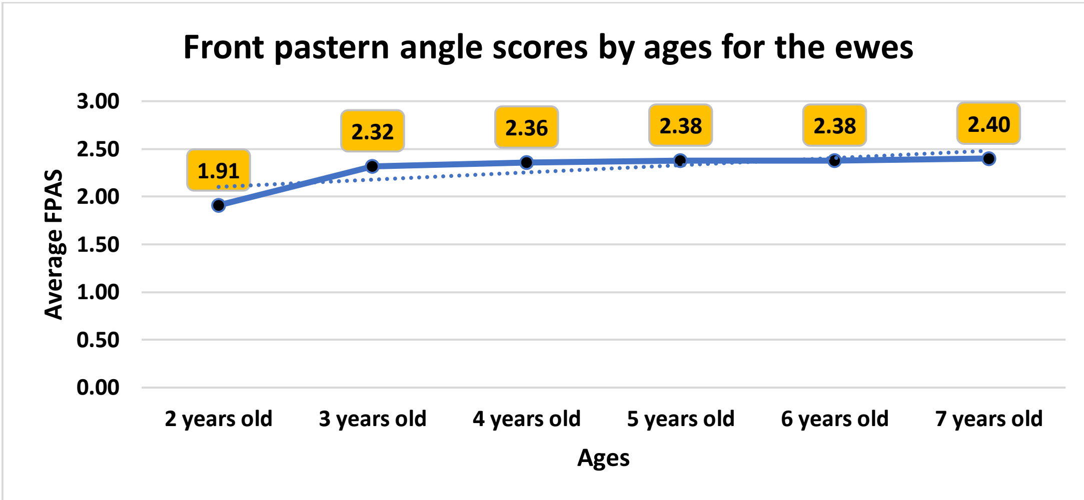

Figure 3.7 Average front pastern angle scores by ages for the ewes

Table 3.5 Back claw and hoof scores by ages within sex

Recording Age	Number of observations	Min	Average BCHS[1]	Max	SD
EWES					
2 years old	1,368	1	2.59	5	0.90
3 years old	10,752	1	2.38	5	0.65
4 years old	6,941	1	2.48	5	0.68
5 years old	5,024	1	2.64	5	0.73
6 years old	2,947	1	2.72	5	0.77
7 years old	1,246	1	2.80	5	0.83
RAMS					
1 years old	3,332	1	2.56	5	0.69

[1]BCHS=back claw and hoof shape scores

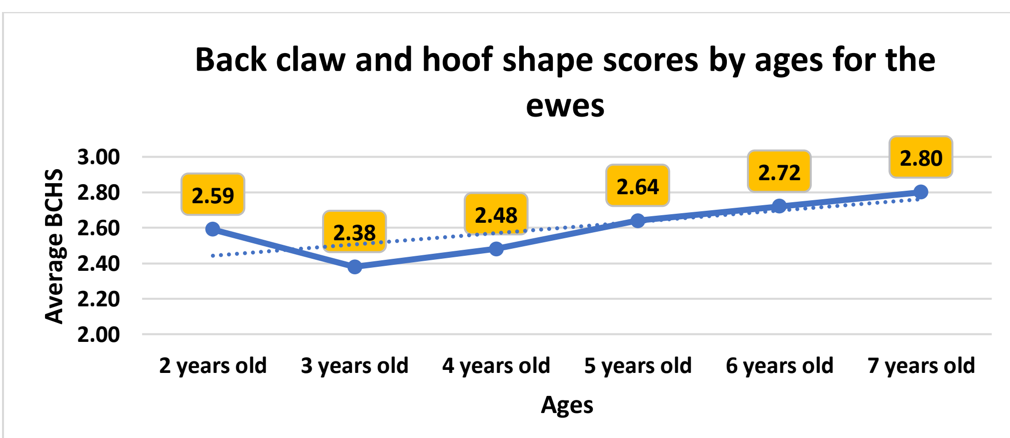

Figure 3.8 Average back claw and hoof shape scores by ages for the ewes

Table 3.6 Front claw and hoof scores by ages within sex

Recording Age	Number of observations	Min	Average FCHS[1]	Max	SD
EWES					
2 years old	1,369	1	2.11	5	0.86
3 years old	10,752	1	2.30	5	0.57
4 years old	6,940	1	2.37	5	0.57
5 years old	5,024	1	2.49	5	0.61
6 years old	2,948	1	2.55	5	0.64
7 years old	1,246	1	2.56	5	0.66
RAMS					
1 years old	3,333	1	2.36	5	0.61

[1]FCHS=front claw and hoof shape scores

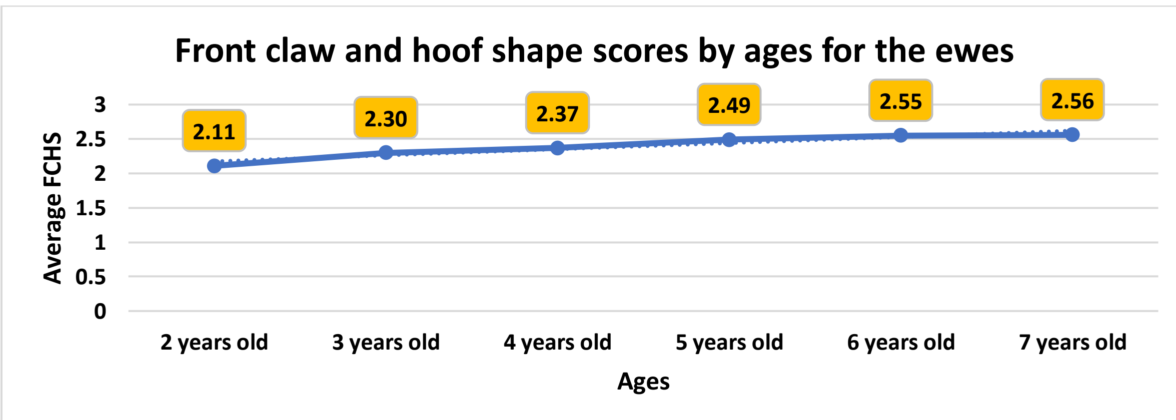

Figure 3.9 Average front claw and hoof shape scores by ages for the ewes

3.2.3 Genetic evaluations for structural foot and leg traits in sheep

Genetic and residual (co)variance parameters were estimated using the statistical software package ASREML 3.0 (Gilmour et al., 2009). Heritability (h^2) was estimated by calculating the ratio of variances, specifically that of additive genetic variance to the phenotypic variance. While repeatability has more than one definition, within this study repeatability (r) was estimated as the ratio of the variance of producing ability to the phenotypic variance.

Structural foot and leg scores was evaluated using a repeated records animal model:

$$\mathbf{y = Xb + Za + Zp + e}$$

(Eq. 3.1)

The mixed model equations for a model with repeated records look like:

$$\begin{pmatrix} X'X & X'Z & X'Z \\ Z'X & Z'Z+\lambda A^{-1} & Z'Z \\ Z'X & Z'Z & Z'Z+\gamma \end{pmatrix}\begin{pmatrix} b \\ a \\ p \end{pmatrix} = \begin{pmatrix} X'y \\ Z'y \\ Z'y \end{pmatrix} \text{ where now } \lambda = \sigma^2_e/\sigma^2_a \text{ and } \gamma = \sigma^2_e/\sigma^2_c$$

where **y** was the vector of observations of structural foot and leg scores, **b** was a vector of fixed effects which included as recording age (years), sex, age of dam, birth rank, rearing rank and heterosis (as a linear covariate) and contemporary group was defined as birth flock, birth year and recording mob], **a** was a vector of additive genetic effects, **p** was a vector of permanent environmental effects, **e** was a vector of residual effects. The matrix **X** was the incidence matrix relating fixed effects to observations in y, **Z** was the incidence matrix for relating random observations to animals (each animal has an additive genetic effect as well as a permanent environmental effect).

The three random effects have the following distribution:

$$\text{var}\begin{pmatrix} a \\ p \\ e \end{pmatrix} = \begin{pmatrix} A\sigma^2_a & 0 & 0 \\ 0 & I\sigma^2_c & 0 \\ 0 & 0 & I\sigma^2_e \end{pmatrix}$$

where $\boldsymbol{\sigma^2_a}$ was the direct additive genetic variance and $\boldsymbol{\sigma^2_c}$ is the variance due to permanent environmental effects. The model shows that those permanent environmental effects for different animals are uncorrelated, and within an animal there was no correlation between its additive and its permanent environmental effect. The total phenotypic variance was the sum of the three variance components.

3.3 Results and discussion

3.3.1 Variance components, heritability, and repeatability of structural foot and leg traits

Heritability and repeatability estimates for structural foot and leg traits in sheep are presented in Table 3.7. The variance components along with the heritability and repeatability of the structural foot and leg scores estimated from the repeated measures animal model are presented in Table 3.8. Except for the back and front pastern angle scores and some of the claw conformation traits (not for the claw and hoof shape), the estimates of heritability and repeatability for the structural foot and leg scores are the first reported values for sheep in our reviewed literature. In general, while all heritability estimates fell within the range previously documented (not published - Natalie Pickering (Focus Genetics), personal communication) values in the SIL Technical Notes, ranging between 7 to 17% for the structural foot and leg traits, the repeatability estimates ranged between 14 to 31%. According to Distl et al. (1984), repeatability can be regarded as the upper limit for the heritability and can be used as an indicator for the suitability of a parameter for selection. Based on our repeatability estimations we can conclude that, genetic improvement of structural foot and leg traits is possible. The heritability estimate (0.11 ± 0.01) for the overall foot and leg scores that represents an overall evaluation for the pasterns, hoof structure, toe placements, and leg rotations was found similar to that reported by Giess et al. (2018) as 0.09 for cattle for a structural foot and leg composite score. As the only previously reported heritability estimations for sheep, the heritability estimates for back (0.11 ± 0.01) and front (0.17± 0.01) pastern angle were not different from the results reported by different authors (0.08 for back pasterns, 0.21 for front pasterns by Snyman and Olivier (2002), 0.12 for both front and back pasterns by Groenwald and Olivier,1999). However, the repeatabilities (0.21-BPAS; 0.31-FPAS) herein were lower than the only value reported for the sheep pastern angles in the literature where repeatability of pastern angle was 0.42 for the Navajo-Churro breed as reported by Fernando de la Fuente (2011). When comparing amongst traits, the front pastern angle had higher heritability (0.17 ± 0.01) and repeatability (0.31) estimates than the other structural foot/leg traits. All the structural foot and leg traits were found lower than anticipated given the typical nature of structure-related traits in other livestock such as hip height in cattle (h^2 = 0.65 - Vargas et al. 1998) or cannon bone circumference (h^2 = 0.44 - Dario et al. 2006) in horses. Conversely, considering their similar anatomy, while the heritability of front (0.09 ± 0.01) claw and hoof shape score was consistent with the reported value (0.08) for cattle claw shape (Giess et al. 2018); the obtained heritability estimate (0.07 ± 0.01) for the back claw and hoof shape score was lower than the estimate (0.15) reported by the same authors for the cattle back claw shape. Regarding the front and back claw and hoof scores, our heritability estimates were not in accordance with the results reported by Erlewein (2002) who reported that the heritability of front claw structure as higher than for back claws in sheep, just the opposite, our results suggested that back claw and hoof scores' heritability was higher than the front one.

Table 3.7 Heritability (h^2 ± SE) and repeatability (r ± SE) estimates for structural foot/leg traits in sheep

Trait	h^2 ± SE	r ± SE
OFS[1]	0.11 ± 0.01	0.30 ± 0.01
BPAS[2]	0.11 ± 0.01	0.21 ± 0.01
FPAS[3]	0.17 ± 0.01	0.31 ± 0.01
BCHS[4]	0.09 ± 0.01	0.19 ± 0.01
FCHS[5]	0.07 ± 0.01	0.14 ± 0.01

[1]OFS = overall foot score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score.

Table 3.8 Variance components, heritability, and repeatability estimates for structural foot and leg scores (±SE)

Effect	OFS[1]	BPAS[2]	FPAS[3]	BCHS[4]	FCHS[5]
Additive genetic effects variance (V_A)	0.05 ± 0.001	0.03 ± 0.001	0.05 ± 0.001	0.04 ± 0.001	0.02 ± 0.001
Permanent Environment Effects variance (V_{PE})	0.10 ± 0.001	0.03 ± 0.001	0.04 ± 0.001	0.04 ± 0.001	0.02 ± 0.001

Between – individual variance ($V_{IND} = V_A + V_{PE}$)	0.15 ± 0.005	0.06 ± 0.003	0.09 ± 0. 003	0.08 ± 0.003	0.04 ± 0.003
Residual variance (V_R)	0.35 ± 0.07	0.25 ± 0.07	0.22 ± 0.07	0.35 ± 0.07	0.29 ± 0.07
Phenotypic variance [(V_P) = (V_A+V_{PE}) + V_R]	0.50 ± 0.004	0.31 ± 0.002	0.31 ± 0.003	0.43 ± 0.004	0.33 ± 0.002
Heritability [(h^2) = (V_A/V_P)]	**0.11 ± 0.01**	**0.11 ± 0.01**	**0.17 ± 0.01**	**0.09 ± 0.01**	**0.07 ± 0.01**
Repeatability [(r) = (V_{IND}/V_P)]	**0.30 ± 0.01**	**0.21 ± 0.01**	**0.31 ± 0.01**	**0.19 ± 0.01**	**0.14 ± 0.01**

[1]OFS = overall foot score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score.

3.4 Conclusion

The heritability estimates obtained for structural foot/leg traits in sheep were low, implying that direct selection on these traits will result in slow genetic improvement but within the realm of improvement when used in conjunction with genetic prediction technologies. Additionally, repeatability estimates were found to be low to moderate suggesting that using the first recorded scores may not be highly predictive of future scores; therefore, culling based on the first recorded structural foot and leg scores may not be a good idea. Even so, by building more robust structural foot and leg traits databases for sheep flocks, it will be possible to differentiate the animals which maintain their favorable structure over time from others that begin to regress. If the next generations are selected according to these outputs, this will potentially decrease the culling rates due to foot and leg problems and could provide higher productivity and longevity rates of ewes.

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CHAPTER 4 – SINGLE TRAIT ANALYSIS FOR HERITABILITY ESTIMATION OF EWE LONGEVITY

Summary

Longevity is desirable in sheep production systems because it directly affects profitability. Increased ewe longevity can lower culling rates and female replacement costs while increasing the number of marketable lambs. Unfortunately, due to the limited data on culling reasons submitted to breed associations, and therefore not available for evaluation of longevity traits, ewe longevity has not been widely evaluated. The limited studies that focus on the longevity of ewes report low heritability which makes the genetic improvement of ewe longevity very hard to achieve through phenotypic selection. Nevertheless, Byun et al. (2012) suggested that given the trait is under genetic control and is heritable, and therefore it should be possible to breed more long-lived sheep. Heritability estimates differ from breed to breed. This study aims to estimate the heritability of ewe longevity using the data set provided by Focus Genetics. The data consisted of the pedigree and performance data of New Zealand Pamu-owned flocks that have mainly had Romney and other composite breeds. Structural foot/leg and pregnancy scores records were used to conduct the study were collected between 2000 and 2020 from 77,837 ewes (progeny of 2,466 sires and 41,260 dams). Due to the culling dates being sparsely recorded in the data, for the calculation of ewe longevity, the approach suggested by McLaren et al. (2020) was used. In this approach, the ewe's last production record (last lambing) was used as a proxy for culling age, and in the cases where structural foot and leg score's recording age was recorded, but for the same age, pregnancy score was not recorded, which means that the animal didn't get any score regarding pregnancy but remained in the flock; the recording age for structural foot and leg score was assigned as the

pregnancy scoring age and created a unique column as recording age for all traits. This column was used later to calculate the actual ewe lifespan and longevity. Longevity observations were assigned to ewes according to the difference (in years) between their first lambing at 2 years old to their last recorded lambing record. All analyses were performed using the statistical software package ASREML 3.0 (Gilmour et al., 2009). Heritability ($h^{2)}$ of ewe longevity estimated to be 0.14 ± 0.01. In conclusion, this result suggested that ewe longevity was lowly heritable which coincides with previously reported results, implying that direct phenotypic selection on ewe longevity will result in slow genetic improvement.

4.1 Introduction

Typically, the domestic sheep's lifespan and ewe longevity are determined by the management decisions based on health, productivity, and reproductive performance. In a commercial sheep operation, the ewe is often six to seven years old before she is replaced (Byun et al., 2012). Culling due to age is a common practice in commercial flocks both in Australia, typically 6 years of age (Hatcher et al., 2009), and in New Zealand at six to seven years of age (Farrell et al. 2019); however, some farms may choose to keep older ewes for longer time periods or may purchase 'culled for age' ewes from other farms (Griffiths, 2020). Although it is common to cull ewes for age, adequate research is not available to support age-dependent culling practice, or to understand its economic consequences (McGregor 2011; Wishart et al. 2016; Griffiths, 2020). Due to these factors, the amount of culling date or reason data recorded, historically ewe longevity has not been widely evaluated. According to the small number of studies which focus on the longevity of ewes, the trait typically has a low heritability which makes the genetic improvement of ewe longevity very hard to achieve, especially based only on phenotypic data. Nevertheless, Byun (2012) argued that given the trait was under genetic control and heritable, it should therefore be possible to breed more long-lived sheep. At the same time, according to the previous studies (Conington et al. 2001; El-Saied et al. 2005), longevity? differs from breed to breed, and it is thought that under the effect of different environmental factors. The objective of this chapter was to estimate the heritability of ewe longevity based on the data set provided by Focus Genetics, which contained the pedigree and performance data of New Zealand's Pamu flocks that are primarily Romney and other New Zealand composite influenced.

4.2 Material and Methods

The present study utilized data obtained from Focus Genetics flocks which is stored in Sheep Improvement Limited New Zealand's (SIL) database; however, animals within the experimental locations were managed according to the AgResearch Animal Ethics Committee guidelines.

4.2.1 Data collection and description

Structural foot/leg and pregnancy scores (number of embryos) recording ages were used to conduct the study and they were collected between 2000 and 2020 on 77,837 ewes (progeny of 2,466 sires and 41,260 dams). Due to the culling date and reasons being sparsely recorded in the Focus Genetic's database, we used the approach described by McLaren et al. (2020) to determine longevity. In this approach, the ewe's last production record (last lambing) can be used as a proxy for culling age. In the cases where structural foot and leg score recording age was present, but pregnancy age was not recorded despite the animal being retained in the flock, a separate column was created to assign last recording age for structural foot and leg score to pregnancy age as a recording age for both traits. From the repeated records to form a final data set which has one unique observation for each animal, longevity observations were assigned to ewes according to the difference (in years) between their first lambing (at 2 years old) to last lambing records.

4.2.2 Statistical Analysis

A single trait animal model was used to estimate variance components for ewe longevity considering the phenotype as a continuous trait. Results from this study were obtained using the statistical software ASREML 3.0 (Gilmour et al., 2009).

The model equation was the following:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

(Eq. 4.1)

where **y** was the vector of observations for the ewe longevity; **b** was the vector of fixed effects, including contemporary group (defined as a combination between birth year and birth flock), age of dam (expressed in the "year" categories as 1 to 10), birth rank, rearing rank, and heterosis was considered as covariate; **u** was the vector of random genetic additive effects; **e** was the vector of random residual effects; **X** and **Z** were incidence matrices relating fixed effects in b and random genetic additive effects in u to observations in y.

4.3 Results and Discussion

The overall mean for ewe longevity as defined in the present study was found as 2 years with minimum and maximum values of 0 and 9 years, respectively. The overall mean for the ewe lifespan was 4.0 years, with minimum 2 and maximum 11 years. As a friendly reminder, in our analyses, while longevity observations were assigned to ewes according to the difference (in years) between their first lambing (at 2 years old) to last lambing records, ewe lifespan was represented as the total life of animal (birth to last available lambing=leaving the flock). Summary statistics for ewe longevity and ewe lifespan are shown in Table 4.1. The number of ewes by age was presented at Figure 4.1. The percentage of ewes by ewe longevity can be found in the Figure 4.2. According to Figure 4.2, the largest portion of the ewes in the data set (28.8 %) lived 3 years (1 year longevity), the second largest portion (19.4%) lived 4 years (2 years longevity), and lastly, the third biggest portion with the 17.5 %, lived 2 years (0 years longevity).

Table 4.1 Summary statistics for ewe longevity and lifespan of ewes

Trait	N	Average	SD	Min	Max
Ewe longevity	77,837	2.00	1.58	0.0	9.0
Lifespan of ewe	77,837	4.00	1.58	2.0	11.0

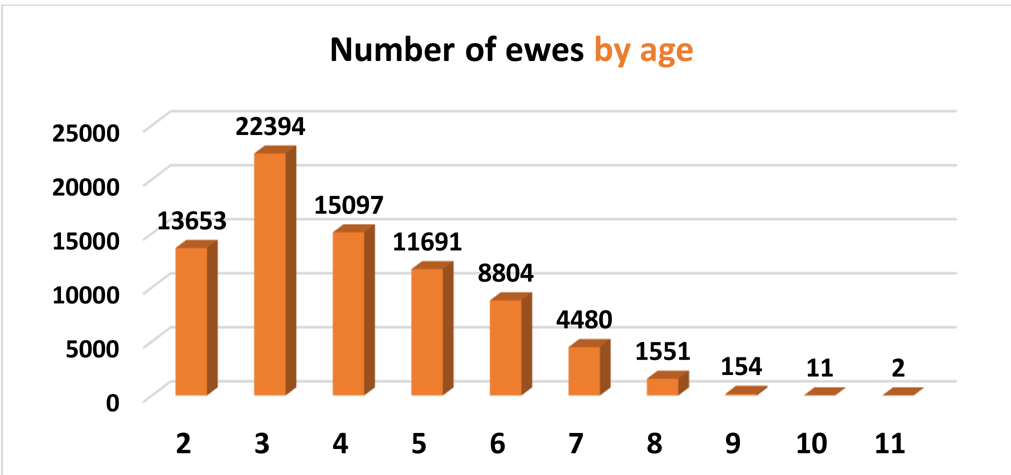

Figure 4.1 Number of ewes by age

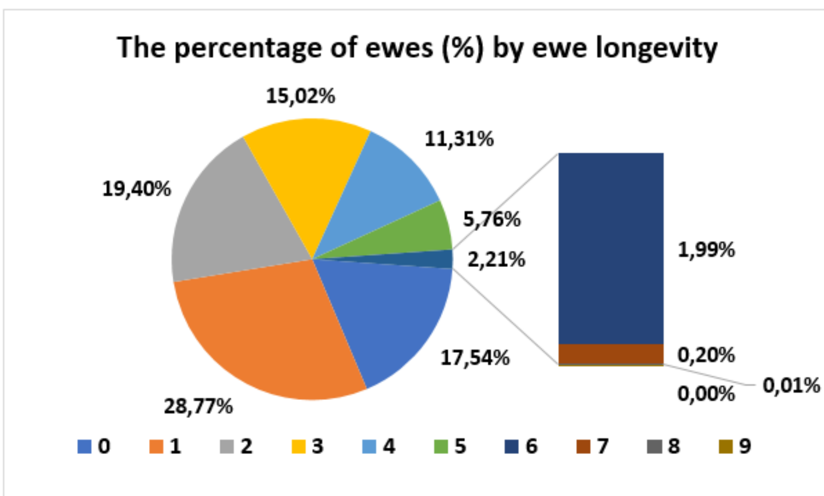

Figure 4.2. Percentages (%) of ewes by ewe longevity

4.3.1 Heritability estimate for ewe longevity

The heritability estimate for the ewe longevity obtained by using the single trait model was 0.14 ± 0.01. This was in the range of values reported previously which ranged from 0 to 0.33 depending on the species, breeds, production system, and trait definition (Conington et al. 2001; El-Saied et al. 2005). Besides, the obtained heritability for ewe longevity was very close to the reported heritability for both the seedstock and commercial flocks in New Zealand sheep populations which were reported as 0.10 and 0.13 by Lee et al. (2015). On the contrary, the obtained heritability for ewe longevity was found smaller than the reported 0.44 that was estimated using a survival analysis model for Suffolk sheep by Milerski et al. (2018). This difference probably can be explained by the nature of survival analysis (they are famous for producing higher heritability estimations than other analysis methods (probably need a citation for the over-estimation of heritability using this approach)) used for the evaluation of ewe longevity as well as the breed differences.

4.4 Conclusion

The results of this study supported the suggestions by McLaren et al. (2020) that when the culling date is not available in the database, it is possible to capture and define longevity by using last production records as a proxy for culling date. Conversely, due to the fact that ewe longevity is highly dependent on culling policies, it should be evaluated within flock or country that apply the same management policies. This study suggested that ewe longevity is a lowly heritable trait which coincides with the previously reported results, implying that direct selection on ewe longevity will result in slow genetic improvement. Conversely, this does not mean that we cannot select for long-lived sheep. We can benefit from the recent development, genomic selection, which is highly suitable for difficult-to-measure traits like ewe longevity.

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CHAPTER 5 - MULTI TRAIT MODEL ANALYSIS FOR ESTIMATING THE GENETIC RELATIONSHIP BETWEEN EWE LONGEVITY, AND STRUCTURAL FOOT AND LEG TRAITS IN SHEEP

Summary

The ideal ewe is the one that is both productive and long-lived. While ewe longevity is a very important trait, it has been often overlooked from a genetic perspective. Increased ewe longevity can lower culling rates and female replacement costs while increasing the number of marketable lambs. Unfortunately, due to the limited amount of culling date and/or culling reason data recorded, ewe longevity has not been widely evaluated for genetic improvement. According to the limited studies focused on the longevity of ewes, it has a low heritability. Moreover, the time lag is challenging as one must wait for the animal or its relatives to leave their respective flocks for an observation of longevity, conversely, structural foot and leg traits can be recorded relatively early in life and are more highly heritable than longevity, which makes a selection for these traits more efficient. Genetic evaluations based on the number of culled ewes could be combined with indirect information based on early predictors such as structural foot and leg scores. Knowledge of genetic relationships between structural foot and leg scores and longevity is required, and therefore, proper identification of structural foot and leg traits to be used as early predictors is essential. The goals of this chapter were 1) to estimate the genetic and phenotypic correlations between ewe longevity and structural foot and leg traits, 2) to determine if structural foot and leg scores can be a potential early predictor for longevity in sheep, and 3) to determine if the structural foot/leg traits can be used as potential predictors of longevity and which ages of foot and leg score are most predictive of ewe longevity. Based on the results of correlations from multi-

trait analyses and the correlated response analyses, we conclude that structural foot and leg scores recorded at early ages in sheep can be used as early life predictors for the ewe longevity. According to the correlated response analyses outputs (we expect a negative response due to score 1 standing for the best one and 5 being the worst one), the best and earliest age should be 3 years old for using the structural foot and leg scores as an early life predictor for ewe longevity. Moreover, the best scores that can be used were found as OFS and BPAS. Breeders may choose one of them, probably, being as an overall evaluation OFS, would be the best and easiest choice for the breeders.

5.1 Introduction

Information on the lifespan of sheep and therefore longevity in a flock is critical to the economic outcomes of production. Unfortunately, due to the limited amount of culling and/or or reason data recorded, ewe longevity has not been widely evaluated. According to the small number studies on ewe longevity, it has a low to moderately heritability (Conington et al. 2001; El-Saied et al. 2005). Another challenge is that producers must wait for the animal or its relatives to leave their respective flocks to obtain a direct measurement of longevity. Alternatively structural foot and leg traits can be recorded relatively early in life and are more highly heritable than longevity, which could enhance rate of genetic change. Genetic evaluations based on the number and ages of culled ewes could be combined with indirect information based on early predictors such as structural foot/leg scores to improve accuracy of selection for longevity. Knowledge of genetic relationships between structural foot and leg scores and longevity is required and, therefore, proper identification of structural foot/leg traits to be used as early predictors is essential. The goals of this chapter were 1) to estimate the genetic and phenotypic correlations between ewe longevity and structural foot and leg traits, 2) to determine if structural foot and leg scores can be a potential early predictor for longevity in sheep, and 3) to determine if the structural foot/leg traits can be used as potential predictors of longevity and which ages of foot and leg score are most predictive of ewe longevity.

5.2 Materials and Methods

The present study utilized data obtained from Focus Genetics flocks which is stored in Sheep Improvement Limited New Zealand's (SIL) database; however, animals within the experimental locations were managed according to the AgResearch Animal Ethics Committee guidelines.

5.2.1 Data collection and description

Pregnancy, performance, and structural foot and leg traits performance data were extracted from SIL's database that was collected between 2000 and 2020 and consisted of information on 77,836 ewes (progeny of 2,466 sires and 41,260 dams). Longevity observations were assigned to ewes according to the difference (in years) between their first lambing (at 2 years old) and their last lambing records. Multi-trait analyses were run separately for each recording age (2 through 7) to see the correlations between ewe longevity and structural foot and leg traits for identifying the ideal recording time for these traits. Additionally, to determine which of the structural foot and leg scores could be best used as an early-life predictor for the ewe longevity, correlated responses were calculated and compared. Summary statistics for the datasets used for the multi-trait analysis for each age can be found in Table 5.1.

Table 5.1 Summary statistics for the datasets used for the multi-trait analysis for each of the ages

Ages	Trait	N	Average	SD	Min	Max
As a rising 2 years old	OFS[1]	1,369	2.60	0.91	1	5
	BPAS[2]	1,369	1.89	0.69	1	5
	FPAS[3]	1,369	1.91	0.75	1	5
	BCHS[4]	1,369	2.59	0.82	1	5
	FCHS[5]	1,369	2.11	0.86	1	5
	LONG[6]	**59,840**	**1.82**	**1.57**	**0**	**9**
	LIFESPAN	**59,840**	**3.82**	**1.57**	**2**	**11**
As a rising	OFS[1]	10,753	2.69	0.69	1	5

3 years old	BPAS[2]	10,753	2.32	0.60	1	5
	FPAS[3]	10,753	2.32	0.60	1	5
	BCHS[4]	10,753	2.38	0.65	1	5
	FCHS[5]	10,753	2.30	0.58	1	5
	LONG[6]	**62,410**	**2.39**	**1.40**	**1**	**9**
	LIFESPAN	**62,410**	**4.39**	**1.40**	**3**	**11**
As a rising 4 years old	OFS[1]	6,942	2.73	0.74	1	5
	BPAS[2]	6,942	2.32	0.56	1	5
	FPAS[3]	6,942	2.36	0.60	1	5
	BCHS[4]	6,942	2.48	0.68	1	5
	FCHS[5]	6,942	2.37	0.58	1	5
	LONG[6]	**41,134**	**3.18**	**1.16**	**2**	**9**
	LIFESPAN	**41,134**	**5.18**	**1.16**	**4**	**11**
As rising 5 years old	OFS[1]	5,024	2.87	0.76	1	5
	BPAS[2]	5,024	2.38	0.60	1	5
	FPAS[3]	5,024	2.38	0.60	1	5
	BCHS[4]	5,024	2.64	0.73	1	5
	FCHS[5]	5,024	2.49	0.61	1	5
	LONG[6]	**26,563**	**3.86**	**0.93**	**3**	**9**
	LIFESPAN	**26,563**	**5.86**	**0.93**	**5**	**11**
As a rising 6 years old	OFS[1]	2,948	2.92	0.81	1	5
	BPAS[2]	2,948	2.43	0.63	1	5
	FPAS[3]	2,948	2.38	0.60	1	5
	BCHS[4]	2,948	2.72	0.78	1	5
	FCHS[5]	2,948	2.55	0.51	1	5
	LONG[6]	**14,797**	**4.52**	**0.71**	**4**	**9**
	LIFESPAN	**14,797**	**6.52**	**0.71**	**6**	**11**
As a rising 7 years old	OFS[1]	1,246	3.01	0.87	1	5
	BPAS[2]	1,246	2.47	0.68	1	5
	FPAS[3]	1,246	2.40	0.63	1	5
	BCHS[4]	1,246	2.80	0.84	1	5
	FCHS[5]	1,246	2.56	0.66	1	5
	LONG[6]	**6,110**	**5.29**	**0.52**	**5**	**9**
	LIFESPAN	**6,110**	**7.29**	**0.52**	**7**	**11**

[1]OFS = overall foot score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score, [6]LONG = ewe longevity

5.2.2 Genetic evaluations for ewe longevity and structural foot and leg traits in sheep

The analyses for the genetic evaluations of ewe longevity (LONG) and structural foot and leg traits in sheep were performed using the statistical software package ASREML 3.0 (Gilmour et al., 2009) by using a multi-trait animal model.

In the multi-trait models used for determining the relationship between ewe longevity and each of the structural foot/leg traits, age of dam, birth rank, rearing rank, and heterosis (as a covariate) were used as fixed effects. Contemporary groups were defined separately for ewe longevity (cg_LY) and structural foot and leg traits (cg_FL) as follows:

cg LY: the combination of birth year and birth flock

cg FL: for structural foot and leg scores: the combination of birth year, birth flock, and structural foot and leg scores' recording mob.

In the model, the subscripts $_1$ and $_2$, reference "trait 1" and "trait 2", respectively. The models for each trait were specified as follows:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} \mathbf{x_1} & 0 \\ 0 & \mathbf{x_2} \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} \mathbf{z_1} & 0 \\ 0 & \mathbf{z_2} \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where $\mathbf{y_i}$ represented a vector of observations for ith trait, $\mathbf{b_i}$ corresponded to a vector for fixed effects including the contemporary groups for ith trait, $\mathbf{u_i}$ was a vector containing the animal random genetic effects for the ith trait, $\mathbf{e_i}$ was a vector of random residual effects for the ith trait. $\mathbf{X_i}$ and $\mathbf{Z_i}$ were incidence matrices that relates observations in $\mathbf{y}$ to levels of fixed effects in $\mathbf{b}$ and random animal genetic effects in $\mathbf{u}$, respectively.

Whereas the variances in general can be represented as follows:

$$\text{Var}\,[u_1] = [G^*] \quad = \quad \text{Var}\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} \sigma^2_{u_1} & \sigma_{u_1 u_2} \\ \sigma_{u_2 u_1} & \sigma^2_{u_2} \end{bmatrix} \otimes \text{A}$$

where $\sigma^2_{u_1}$ represents the additive genetic variance of trait 1, $\sigma_{u_1 u_2}$ and $\sigma_{u_2 u_1}$ corresponds to the additive covariances among the two traits and, $\sigma^2_{u_2}$ was the additive genetic variance for trait 2. In the above, $\mathbf{A}$ again represents the Wright's numerator relationship matrix and $\otimes$ indicates the Kronecker product.

The variance and covariance matrix for the residual effects were represented individually as follows:

$$R^{*} = \text{Var}\begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} \sigma_{e_1}^2 & \sigma_{e_1 e_2} \\ \sigma_{e_2 e_1} & \sigma_{e_2}^2 \end{bmatrix}$$

where $\sigma_{e_1}^2$ represented the residual variance of trait 1, $\sigma_{e_1 e_2}$ and $\sigma_{e_2 e_1}$ were the residual covariances between the two traits and, $\sigma_{e_2}^2$ was the residual variance for trait 2.

Finally, the mixed model equations (MME) for this example of a bivariate analysis can be presented as follows:

$$\begin{bmatrix} X'_1R^{11}X_1 & X'_1R^{12}X_2 & X'_1R^{11}Z_1 & X'_1R^{12}Z_2 \\ X'_2R^{21}X_1 & X'_2R^{22}X_2 & X'_2R^{21}Z_1 & X'_2R^{22}Z_2 \\ Z'_1R^{11}X_1 & Z'_1R^{12}X_2 & Z'_1R^{11}Z_1 + g^{11}A^{-1} & Z'_1R^{12}Z_2 + g^{12}A^{-1} \\ Z'_2R^{21}X_1 & Z'_2R^{22}X_2 & Z'_2R^{21}Z_1 + g^{21}A^{-1} & Z'_2R^{22}Z_2 + g^{22}A^{-1} \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} X'_1(R^{11}y_1 + R^{12}y_2) \\ X'_2(R^{12}y_1 + R^{22}y_2) \\ Z'_1(R^{11}y_1 + R^{12}y_2) \\ Z'_2(R^{12}y_1 + R^{22}y_2) \end{bmatrix}$$

And solving for $\hat{b}_i$ and $\hat{u}_i$ we have:

$$\begin{bmatrix} \hat{b}_1 \\ \hat{b}_2 \\ \hat{u}_1 \\ \hat{u}_2 \end{bmatrix} = \begin{bmatrix} X'_1R^{11}X_1 & X'_1R^{12}X_2 & X'_1R^{11}Z_1 & X'_1R^{12}Z_2 \\ X'_2R^{21}X_1 & X'_2R^{22}X_2 & X'_2R^{21}Z_1 & X'_2R^{22}Z_2 \\ Z'_1R^{11}X_1 & Z'_1R^{12}X_2 & Z'_1R^{11}Z_1 + g^{11}A^{-1} & Z'_1R^{12}Z_2 + g^{12}A^{-1} \\ Z'_2R^{21}X_1 & Z'_2R^{22}X_2 & Z'_2R^{21}Z_1 + g^{21}A^{-1} & Z'_2R^{22}Z_2 + g^{22}A^{-1} \end{bmatrix}^{-1} \begin{bmatrix} X'_1(R^{11}y_1 + R^{12}y_2) \\ X'_2(R^{12}y_1 + R^{22}y_2) \\ Z'_1(R^{11}y_1 + R^{12}y_2) \\ Z'_2(R^{12}y_1 + R^{22}y_2) \end{bmatrix}$$

5.2.3 Prediction of the correlated response of ewe longevity to structural foot and leg traits

Correlated response was calculated using the formula below, and in Eq 5.1 (Walsh, 2018) the subscripts y and x, reference "ewe longevity" and "structural foot and leg trait", respectively:

$$CR_y = i_x \, h_x \, h_y \, r_A \, \sigma_{P(y)}$$

(Eq. 5.1)

where CR_y was the correlated response in trait y when selection was based on trait x, i was the selection intensity on x, h_x and h_y are the square roots of heritability of traits x and y, respectively. r_A was the additive genetic correlation between x and y and $\sigma_p(y)$ was the appropriate phenotypic standard deviation for trait y.

Correlated responses for each recording age and structural foot and leg traits (simulated based on the assumption of 20% replacement ewe.

5.3 Results and discussion

5.3.1 Genetic and phenotypic correlations between ewe longevity and structural foot and leg traits

5.3.1.1 Based on the recorded scores at approximately 2 years old (some animals were 18 months old or younger)

The estimates of phenotypic and genetic correlations between ewe longevity and structural foot/leg traits, based on the recorded scores at approximately 2 years of age (some animals may be 18 months old or younger) are shown in Table 5.2. The genetic correlations between ewe longevity and BPAS, FPAS, and FCHS were negative with values ranging between -0.39 to -0.59 in the case of genetic effects but the genetic correlations between ewe longevity and OFS and BCHS were positive with values 0.45 and 0.70, respectively. Regarding the OFS and BCHS, these results were unexpected when considering that in the scoring scale 1 represents the best and 5 represents the worst score for structural traits. These unexpected correlations may be related to due to the scoring being done before animals have reached sufficient maturity, so body weight may not be affecting the scores at this early age whereas body weight may play a larger role on structural foot and leg scores later in life. Admittedly the first opportunity for scoring occurs at a relatively young age and scoring only occurs on a selected set and accordingly there are a small number of observations for this age. As can be seen from the number of observations portrayed on Table 5.1, most of the sheep farmers who provided data to the database that we used for the analyses did not score their animals at this age. According to Martini et. al. (2001), although the sheep reach sexual maturity at approximately 7-12 months of age, depending on breed, the closure of the physeal plates of the long bones may still occur as late as 36 months, meaning that they are still not mature. In addition to this, American Angus Association that has used foot scoring for cattle, providing evidence about the appropriate time for foot and leg scoring (Retallick, 2020). Considering the similarities between sheep and cattle, they reported that yearling age for cattle (similar to sheep that are rising 2 year olds, regarding growing) may not be a good time for foot scoring because of low variation in scores. Scoring at 2, 3, or 4 years of ages, due to the increased variability, or expression in variation on foot and leg structure, could be more beneficial (Retallick, 2020). Our results from the analysis based on recorded scores at approximately 2 years old confirm these previous findings and we speculate that, the best age is for scoring is when the animals are fully mature, which is at or after 3 years old for sheep.

Table 5.2 Heritability on diagonal (boldfaced), genetic (above diagonal), and phenotypic (below diagonal) correlations between structural foot and leg traits and ewe longevity (based on the structural scores recorded **at approximately 2 years old – some animals were 18 months old or younger)**

Traits	**OFS[1]**	**BPAS[2]**	**FPAS[3]**	**BCHS[4]**	**FCHS[5]**	**LONG[6]**
OFS[1]	**0.18**					0.45
BPAS[2]		**0.04**				-0.59
FPAS[3]			**0.09**			-0.40
BCHS[4]				**0.14**		0.70
FCHS[5]					**0.08**	-0.39
LONG[6]	0.34	0.46	0.40	0.34	0.34	**0.13**

[1]OFS = overall foot/leg score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score, [6]LONG = ewe longevity

5.3.1.2 Based on the recorded scores at approximately 3 years old

The estimates of phenotypic and genetic correlations of ewe longevity and structural foot/leg traits, based on the recorded scores at approximately 3 years old are shown in Table 5.3. In general, all the correlations between ewe longevity and structural foot/leg scores were negative with values ranging between -0.17 to -0.42 in the case of phenotypes and between -0.29 to -0.52 for genetic effects.

Table 5.3 Heritability on diagonal (boldfaced), genetic (above diagonal), and phenotypic (below diagonal) correlations between structural foot and leg traits and ewe longevity (based on the structural scores recorded **at approximately 3 years old)**

Traits	OFS[1]	BPAS[2]	FPAS[3]	BCHS[4]	FCHS[5]	LONG[6]
OFS[1]	**0.11**					-0.52
BPAS[2]		**0.12**				-0.49
FPAS[3]			**0.18**			-0.29
BCHS[4]				**0.06**		-0.45
FCHS[5]					**0.06**	-0.51
LONG[6]	-0.42	-0.28	-0.27	-0.23	-0.17	**0.12**

[1]OFS = overall foot/leg score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score, [6]LONG = ewe longevity

5.3.1.3 Based on the recorded scores at approximately 4 years old

The estimates of phenotypic and genetic correlations of ewe longevity and structural foot/leg traits, based on the recorded scores at approximately 4 years old are shown in Table 5.4. In general, all the correlations between ewe longevity and structural foot and leg scores were negative with values ranging between -0.21 to -0.46 in the case of phenotypes and between -0.42 to -0.61 for genetic effects.

Table 5.4 Heritability on diagonal (boldfaced), genetic (above diagonal), and phenotypic (below diagonal) correlations between structural foot and leg traits and ewe longevity (based on the structural scores recorded **at approximately 4 years old)**

Traits	OFS[1]	BPAS[2]	FPAS[3]	BCHS[4]	FCHS[5]	LONG[6]
OFS[1]	**0.12**					-0.61
BPAS[2]		**0.11**				-0.43
FPAS[3]			**0.19**			-0.42
BCHS[4]				**0.11**		-0.52
FCHS[5]					**0.06**	-0.43
LONG[6]	-0.46	-0.28	-0.21	-0.35	-0.22	**0.10**

[1]OFS = overall foot/leg score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score, [6]LONG = ewe longevity

5.3.1.4 Based on the recorded scores at approximately 5 years old

The estimates of phenotypic and genetic correlations of ewe longevity and structural foot/leg traits, based on the recorded scores at approximately 5 years old are shown in Table 5.5.

In general, all the correlations between ewe longevity and structural foot/leg scores were favorable with values ranging between -0.18 to -0.41 in the case of phenotypes and between -0.04 to -0.60 for genetic effects.

Table 5.5 Heritability on diagonal (boldfaced), genetic (above diagonal), and phenotypic (below diagonal) correlations between structural foot and leg traits and ewe longevity (based on the structural scores recorded **at approximately 5 years old**)

Traits	OFS[1]	BPAS[2]	FPAS[3]	BCHS[4]	FCHS[5]	LONG[6]
OFS[1]	**0.06**					-0.45
BPAS[2]		**0.06**				-0.60
FPAS[3]			**0.21**			-0.05
BCHS[4]				**0.08**		-0.21
FCHS[5]					**0.08**	-0.04
LONG[6]	-0.41	-0.26	-0.18	-0.29	-0.19	**0.09**

[1]OFS = overall foot/leg score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score, [6]LONG = ewe longevity

5.3.1.5 Based on the recorded scores at approximately 6 years old

The estimates of phenotypic and genetic correlations of ewe longevity and structural foot/leg traits, based on the recorded scores at approximately 6 years old are shown in Table 5.6. In general, all the correlations between ewe longevity and structural foot/leg scores were negative with values ranging between -0.12 to -0.32 in the case of phenotypes and between -0.20 to -0.69 for genetic effects.

Table 5.6 Heritability on diagonal (boldfaced), genetic (above diagonal), and phenotypic (below diagonal) correlations between structural foot/leg traits and ewe longevity (based on the structural scores recorded **at approximately 6 years old)**

Traits	OFS[1]	BPAS[2]	FPAS[3]	BCHS[4]	FCHS[5]	LONG[6]
OFS[1]	**0.07**					-0.69
BPAS[2]		**0.18**				-0.40
FPAS[3]			**0.14**			-0.20
BCHS[4]				**0.10**		-0.49
FCHS[5]					**0.06**	-0.50
LONG[6]	-0.32	-0.20	-0.12	-0.24	-0.16	**0.13**

[1]OFS = overall foot/leg score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score, [6]LONG = ewe longevity

5.3.1.6 Based on the recorded scores at approximately 7 years old

The estimates of phenotypic and genetic correlations of ewe longevity and structural foot/leg traits, based on the recorded scores at approximately 7 years old are shown in Table 5.7. In general, all the phenotypic correlations between ewe longevity and structural foot/leg scores were not found favorable with values ranging between -0.12 to -0.21 but for the genetic effects, just BPAS and FPAS have the negative values, -0.15 and -0.22, respectively. The genetic correlations for OFS, BCHS, and FCHS were positive which were unexpected, but these results may be biased by being exposed to high selection pressure regarding the structural foot and leg score-related culling or due to having not being able to enough observation for the animals for a proper evaluation at this age.

Table 5.7 Heritability on diagonal (boldfaced), genetic (above diagonal), and phenotypic (below diagonal) correlations between structural foot and leg traits and ewe longevity (based on the structural scores recorded **at approximately 7 years old)**

Traits	**OFS[1]**	**BPAS[2]**	**FPAS[3]**	**BCHS[4]**	**FCHS[5]**	**LONG[6]**
OFS[1]	**0.23**					0.22
BPAS[2]		**0.29**				-0.15
FPAS[3]			**0.15**			-0.22
BCHS[4]				**0.15**		0.43
FCHS[5]					**0.12**	0.28
LONG[6]	-0.21	-0.16	-0.12	-0.14	-0.07	**0.08**

[1]OFS = overall foot/leg score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score, [6]LONG = ewe longevity

5.3.1.7 Correlated responses for each recording age and structural foot and leg traits

For the comparison of the structural foot and leg traits regarding which one can ideally be used as an early-life predictor for ewe longevity, we simulated correlated responses by using the assumption of 20% replacement rate (selection intensity (*i*)=0.35) for the ewes. Correlated responses for each recording age and structural foot and leg trait can be seen in Table 5.8. According to these results, 3 years appeared most favorable (earliest and most appropriate one) for scoring the structural foot and leg scores. Moreover, considering the highest correlated responses (we expect a negative response due to score 1 stands for the best one and 5 is the worst one), if a breeder wants to use these traits as an early life predictor of ewe longevity, probably OFS or BPAS would be the best choices at 3 years recording.

Table 5.8 Correlated responses for each recording age and structural foot and leg traits (simulated based on assuming that 20% replacement ewe = selection intensity (i)=0.35)

Recording Ages	Trait	Correlated response
As a rising 2 years old	OFS	0,038
	BPAS	-0,023
	FPAS	-0,024
	BCHS	0,052
	FCHS	-0,022
As a rising 3 years old	OFS	**-0,029**
	BPAS	**-0,029**
	FPAS	-0,021
	BCHS	-0,019
	FCHS	-0,021
As a rising 4 years old	OFS	-0,027
	BPAS	-0,018
	FPAS	-0,024
	BCHS	-0,022
	FCHS	-0,014
As rising 5 years old	OFS	-0,011
	BPAS	-0,014
	FPAS	-0,002
	BCHS	-0,006
	FCHS	-0,001
As a rising 6 years old	OFS	-0,016
	BPAS	-0,015
	FPAS	-0,007
	BCHS	-0,014
	FCHS	-0,011
As a rising 7 years old	OFS	0,005
	BPAS	-0,004
	FPAS	-0,004
	BCHS	0,009
	FCHS	0,001

[1]OFS = overall foot/leg score, [2]BPAS = back pastern angle score, [3]FPAS = front pastern angle score, [4]BCHS = back feet claw and hoof shape score, [5]FCHS = front feet claw and hoof shape score, [6]LONG = ewe longevity

5.4 Conclusion

Based on the results of correlations from multi-trait analyses and the correlated response analyses, we conclude that structural foot and leg scores recorded at early ages in sheep can be used as early life predictors for the ewe longevity. According to the correlated response analyses outputs (we expect a negative response due to score 1 standing for the best one and 5 being the worst one), the best and earliest age should be 3 years old for using the structural foot and leg scores as an early life predictor for ewe longevity. Moreover, the best scores that can be used were found as OFS and BPAS. Breeders may choose one of them, probably, being as an overall evaluation OFS, would be the best and easiest choice for the breeders.

5.5 Literature cited

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