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AGE OF THE DAM, PERMANENT ENVIRONMENTAL AND MATERNAL GENETIC EFFECTS ON WEIGHT AT 90 DAYS OF PIRENAICA CALVES.

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Summary

1. ABSTRACT

In beef cattle, dams play a crucial role in providing a pre and postnatal environment for their offspring. This environment directly impacts the performance of the offspring and is known as the maternal effect. The maternal effect can be divided into two distinct components: the maternal genetic effect and the permanent maternal environment effect. These maternal effects are particularly important for weaning weight, which is a trait considered in the selection criteria of the Pirenaica breed. The specific trait associated with weaning is the weight at 90 days, which is used to isolate the effect of the environment on calf feeding and make the calves solely dependent on maternal milk production. However, the age of the dam can influence the genetic and environmental maternal effects throughout the productive lifespan of the cow. The objective of this study is to describe the changes in genetic and environmental maternal effects throughout the productive lifespan of the cows. To achieve this, various random regression models were used, linking the age of the dam, the maternal genetic and the environmental permanent effects to a several orthogonal polynomials calculated from the age of the cow at calving. Additionally, the model of analysis also included a covariate with the calf recording age, a two-level sex effect, a random herd-year-season effect, and an additive genetic effect associated with the calf. The dataset was filtered to include only data from dams aged between 600 and 6,600 days, resulting in a final database that included weight records of 85,670 calves from 21,673 dams. A total of 27 random regression models were implemented, varying the number of regression coefficients (4 to 6) for the age of the dam, the environmental maternal effect, and the maternal genetic effect. These models were compared using the AIC criteria after estimating the (co)variance components with REML. The results indicated that the most suitable model for describing the covariance structure of the data was the one that used 5 orthogonal polynomials for the age of the dam, the environmental maternal effect, and the maternal genetic effect. Using this model, the analysis revealed that the maternal heritability ranged from 0.059 to 0.12. Heritability was lower at younger ages

and increased as the dam aged. In contrast, the influence of maternal environmental effects remained relatively stable throughout the productive life of the cows. Furthermore, maternal genetic correlations among different ages of the dam in days decreased to values below 0.5 for distant lactations (e.g., 1000 days compared to 4000 days). The maternal permanent correlations were even lower, approaching values close to zero (e.g., 1500 days compared to 5000 days). These findings provide valuable insights for optimizing the selection schemes of future dams based on their expected longevity and milk production.

2. PIRENAICA BREED

The Pirenaica beef cattle breed is an autochthonous Spanish breed that is found in several Autonomous Communities, such as Navarre, Basque Country, Aragon, Cantabria, Catalonia, La Rioja, and in the provinces of Soria, Cáceres, Burgos, Castellón, and Madrid. However, the highest population of this breed is concentrated in Navarre and the Basque Country (Mendizabal, 1998). This breed holds significant importance in the northern regions of Spain and its meat is recognized and categorized under the Protected Geographic Indication (PGI) markers, along with various other types of meat. The Pirenaica breed, owing to its historical living conditions, possesses the ability to utilize resources that would otherwise go to waste or become degraded. Its robustness and adaptability allow it to exploit resources that may not be accessible to other cattle breeds (Loza san martín, 2012).

Figure 1 and figure 2. Sire and cow of Pirenaica breed. Web page: Pirenaica_breed

2.1. Origins

This ancient native breed of cattle is named after the geographical area of its current origin and major settlement: the western part of the Pyrenees Mountain range. In the past, it was also known by other names such as "Raza Vasca" or "Raza del País" (Echeverría & Asarta, 1975). The breed's phylogeny is closely linked to the origins of European bovine breeds, and two main theories have been proposed: monophyletic and polyphyletic. The monophyletic theory suggests that all breeds descended from the "*Bos Taurus Namáricus*", which was an Asian aurochs closely resembling the European primitive bovine. On the other hand, the polyphyletic theory argues that the population originated from both the "*Bos Taurus Primigenius*" and the "*Bos Taurus Brachycesos*" (Echeverría & Asarta, 1975).

2.2. Historical evolution of the breed

In the 19th century, the Pirenaica cattle breed was widespread across the entire northern region of Navarra, stretching from the Roncal valley to Ameskoa. This encompassed various valleys such as Salazar, Anezka, Arce, Erro, Anué, Ulzama, Imoz, Guez, and the Metauten district (CONASPI, 2020). The breed's presence also extended into the Basque Country and the southern slopes of the Pyrenees in Aragon, and there is a possibility that it reached Catalonia as well. During the mid-19th century, the Basque provincial councils made modest attempts to promote the breed. Contests were organized during this period, and the population of the breed reached around 80,000 cows. Towards the end of the 19th century, after the Carlist wars, renewed efforts were undertaken, which included the establishment of annual exhibitions and the regulation of numerous farms in Navarra. In 1905, the breed's herd-book was created, and this resulted the first cattle herd-book in Spain (CONASPI, 2020).
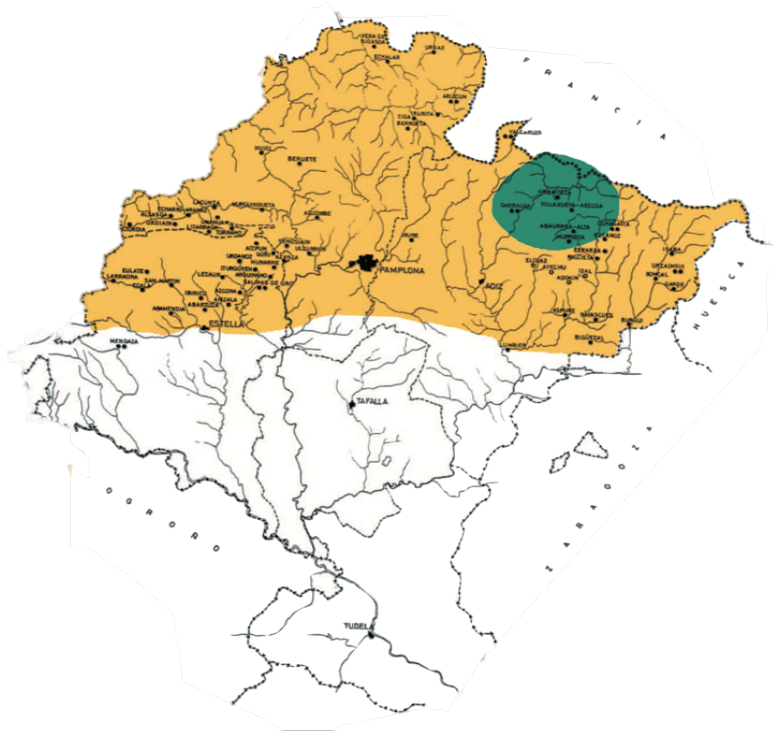
Figure 3. Geographical location of the Pyrenean cattle (province of Navarra) stables in 1940.

Until the mid-20th century, the Pirenaica cattle breed was renowned for its triple aptitude, as the animals were utilized for meat production, milk production, and as working animals (CONASPI, 2020) . However, during this period, significant economic development and industrialization brought about substantial changes in the rural areas where the Pirenaica cattle were predominantly diffused. A considerable number of people in these regions migrated to cities, resulting in a significant decline in farming activity (Echeverría & Asarta, 1975). Furthermore, deliberate efforts were made to introduce animals from other breeds to enhance specialized performance. Specifically, the Brown Swiss and Holstein-Friesian populations were extensively introduced into the geographic area of the Pirenaica breed. The Brown Swiss breed was used for crossbreeding with the Pirenaica to improve meat production, while the Holstein-Friesian breed was introduced to establish specialized dairy farms focused on milk production near urban areas. As a result, the Pirenaica breed faced a critical period during the 1960s and 1970s and was ultimately classified as endangered (Echeverría & Asarta, 1975). In the Basque Country, the breed was nearly extinct, with only 40 registered cows in Guipuzkoa, while in Navarra, there were approximately 1,500

purebred cows remaining. In response to the situation, the provincial council of Navarra took action to promote the Pirenaica breed (Mendizabal, 1998). In 1974, the Ministry of Agriculture, Fisheries, and Food (M.A.P.A.) established the Movera Censyra, a reproductive and selection center located in Zaragoza. Subsequently, cattle breeder associations were formed in various provinces, and the confederation CONASPI was established as an umbrella organization to oversee these associations. CONASPI's activities included regulating the breed's herd-book, supervising yield performance recording, and implementing a genetic improvement program (CONASPI, 2020). Several additional factors contributed to the breed's repopulation. Subsidies were provided to farmers to encourage the breeding of primiparous cows and support the purchase of sires. Veterinarians also received grants for insemination using semen from purebred sires (CONASPI, 2020). Traditional butchers played a crucial role by consistently purchasing and offering higher prices for Pirenaica meat. This was made possible through the establishment of the Protected Geographic Indication (PGI) "Ternera de Navarra," which recognized and protected meat produced by native breeds labeled as "Raza Autóctona", the labels are shown in Figure 4 and 5. (CONASPI, 2020).

Figure 4 and Figure 5 display distinct labels. On the right side, the labels indicate the Protected Geographic Indication (PGI) for "Ternera de Navarra," signifying its regional designation and quality assurance. On the left side, the labels indicate the autochthonous breeds, denoted as "Raza Autóctona".

As of now, the use of purebred bulls has been reinstated, and we can confidently state that the Pirenaica breed has made a remarkable recovery. The 2022 census reported a population of 26,312 Pirenaica heads. The geographic distribution of the breed is depicted in Figure 6
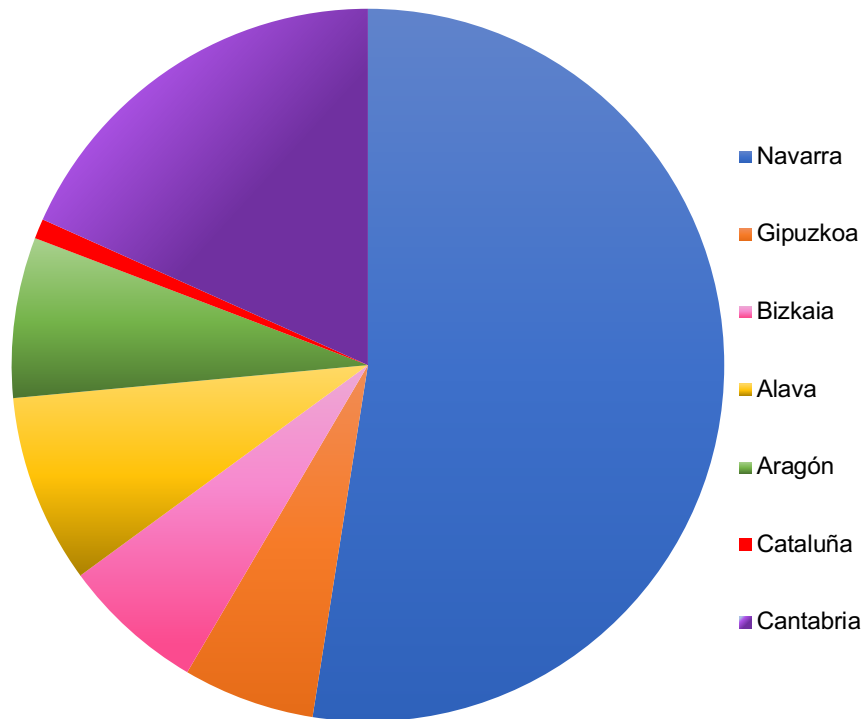
Figure 6. Shows the census of Pirenaica cattle in 2022, categorized by their geographical distribution.

3. MORPHO-FUNCTIONAL CHARACTERISTICS

3.1. Ancestral morphology of the breed

Traditionally, the Pirenaica breed was known for its triple aptitude for work, meat, and milk, as documented by Echeverría & Asarta, 1975 .The original description of the ancestral individuals, provided by Echeverría & Asarta in 1975, included several distinctive morphological traits. These traits encompassed a compact yet deep chest, a dorsal line that sloped upward, a tail base of moderate height, slightly raised loins, hindquarters that were less developed compared to the forequarters, a high but narrow back, a small udder, and thick skin (see Figure 8). In terms of size, the Pirenaica breed was relatively small, with an average height of around 120 cm.

Figure 7. Representative of the ancient Pirenaica cow type. Web page:antigua-vaca-Pirenaica

Since 1920, the Pirenaica breed has undergone significant changes that have resulted in substantial improvements in meat production. The breed's original triple-purpose nature has gradually shifted towards a stronger emphasis on meat production, leading to corresponding changes in the animals' morphology (CONASPI, 2020).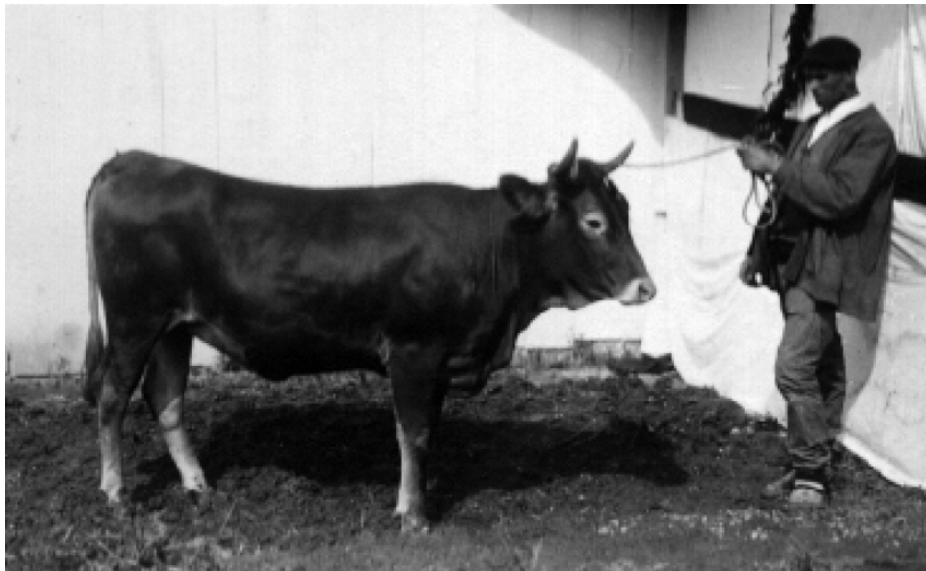 A comparison of the main characteristics of Pirenaica animals in 1926 and 1997 was conducted by Mendizabal (1998), and the results are presented in Table 1 and Figure 8. It is evident that the animals from the 1970s were taller and larger in size compared to the original animals from the 1920s.

Table 1. Zoometric values of adult cows obtained for 2 groups of Pirenaica: first column represents ancient breed (1926), and the last one cows of the improved breed (1997). (Adapted by Mendizabal, 1998)

TRAITS	ANCIENT BREED (1926)	IMPROVED BREED (1997)
Height at withers (cm)	117 ±3	132±7
Back height (cm);		131±7
Rump height (cm)	122±4	139±6
Tail height (cm	123±4	142±7
Body length (cm)	138±5	167±11
Chest depth (cm)	63±2	88±33
Rear width (cm);		53±5
Back width (cm)	36±3	53±5
Rump length (cm)		53±5
Interiliac width (cm);	45±2	56±4
Coxofemoral width (cm)		55±5
Thoracic circumference (cm);	163±7	201±13
Cannon circumference (cm);	16±0.7	21±1.2
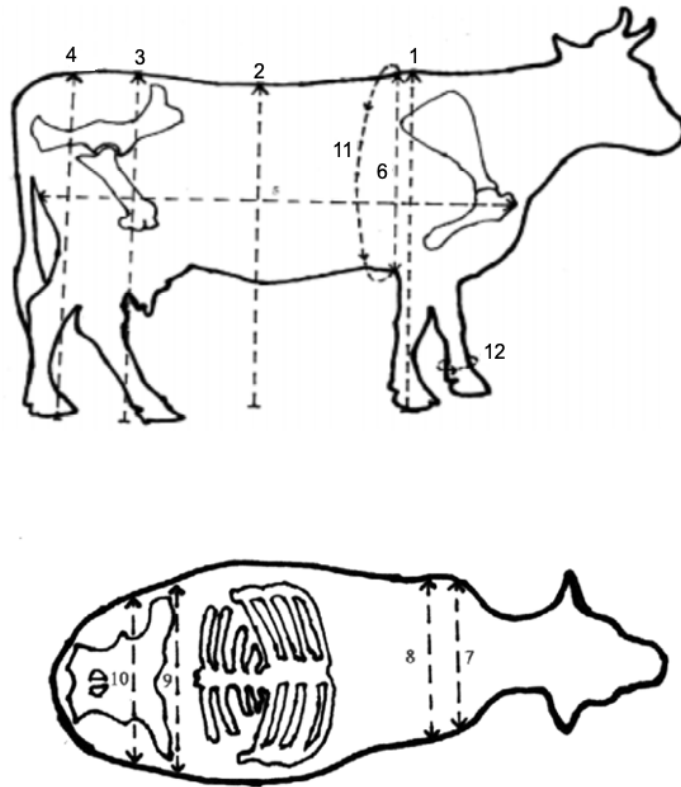
Figure 8. Morphological measurements 1. Height at withers; 2. Back height; 3. Rump height; 4. Tail height; 5. Body length; 6. Chest depth; 7. Width of bouts; 8. Back width; 9. Interiliac width; 10. Coxofemoral width; 11. Thoracic circumference; 12. Back width.

3.2. Current morphology of the breed

The morphological description of the animals in the Pirenaica population was provided by CONASPI (2020) and can be summarized as follows:

♦ General appearance: The animals of the Pirenaica breed are recognized for their lively, harmonious, and well-developed appearance, featuring a muscular build. They demonstrate relatively early development, with a prolonged growth period that leads to maturity at a later stage. These animals exhibit a good body length, and their bellies maintain proportionality without excessive folding.

14

- Skin, coat, and mucous membranes. The Pirenaica breed is characterized by a coat of uniform colour and grain, which can range from the lightest to the brightest shade. Discolorations may appear on the throat, perineum, armpits, limbs, muzzle, and orbital region, but there should be no hairs of any other colour present. The skin of these animals is typically white or yellowish, and the flesh is visible with a flesh-coloured or pinkish hue. The tongue and inner mucous membranes are light in colour.

- Head and neck. The Pirenaica breed is characterized by a head of medium proportions, featuring wide nostrils, a broad forehead, and strong jaws. The ears are of medium size and covered with fine hair. The breed is known for its expressive eyes, which are slightly protruding and surrounded by a clear halo, commonly referred to as the "Partridge eye" trait. In both males and females, the lyre-shaped horns are prominent, with a slight spiral and circular base. They are pearly white, with yellowish tips. The neck of the Pirenaica breed is of medium length, slender, and muscular. In females, the upper line of the neck is straight, while in males, it exhibits a pronounced muzzle. Both genders may have a slight dewlap. The breed is characterized by correct insertions of the neck and head, as well as a straight back.

- Chest, back and thorax. The males of the Pirenaica breed are known for their deep and muscular chests. They have a well-developed back that is well connected to both the neck and trunk. The thorax is deep, and the ribs are arched, contributing to the overall muscular and robust build of the breed.

- Back and withers. The withers of the Pirenaica breed are broad and well joined to both the neck and trunk. The trunk itself should be long, and the back-lumbar line is characterized by being muscular, broad, and straight. The limbs are of medium length, with wide and strong joints that are correctly developed. The hooves are well developed, hard, and strong, with a moderate level of openness, and they typically have a light-yellow colour.

- Rump and tail. The Pirenaica breed is characterized by a long, wide, and horizontally aligned croup. In females, the croup may exhibit marked bony

prominences. The tail is moderately high, long, and abundantly tasselled, adding to the breed's distinctive appearance.

♦ Thighs and gluteal muscles. The thighs and buttocks of the Pirenaica breed are well developed and have a significant let down. They exhibit a moderate convexity, without pronounced intermuscular grooves.

♦ Genital organs and udders. The Pirenaica breed is characterized by normally developed testicles in males, which are well descended and have correct anatomical conformation. In females, the breed is known for well-formed udders, with correct insertion and separation of teats. The udders exhibit an appreciable venous system and are well-developed. The nipples are correctly implanted and have a pinkish colour.

♦ Body development. The conformation of the Pirenaica breed is characterized by being medium-sized and proportionate. The animals exhibit a balanced and harmonious overall appearance, with no extreme or disproportionate features.

♦ Limbs and flanks. Medium-length limbs with wide and strong articulations, correct pasterns, well developed, hard and strong, moderately open, and light-yellow hooves.

The Pirenaica breed is characterized by dominant straight profiles, which may vary in prominence due to the frontal depression affecting the shape of the orbits. The breed's size falls within moderate limits, transitioning from subhypermetric to mesolinear proportions, which are typical of beef cattle (Mendizabal, 1998). These morphological characteristics highlight the breed's perfect adaptability to its production environment, particularly its ability to thrive in areas with challenging climatic and geographical conditions, thanks to its rusticity. Moreover, the Pirenaica breed is known for ease of calving, both in purebred and crossbred individuals, owing to its long and slender structure. It also exhibits sufficient milk production to nourish the calves until weaning, a high maternal index, low incidence of infertility problems, and remarkable longevity during the productive period (CONASPI, 2020).

The appearance of the Pirenaica breed reflects liveliness, harmony, and a well-developed muscular conformation. The breed experiences relatively early development, with a prolonged growth period that reaches completion at a later stage. This developmental process contributes to a notable body length and a proportionate abdomen (P. Aranguren et al., 2009). These characteristics remain consistent traits of the breed and are described in further detail below.

Figure 9. Grazing herd of Pirenaica https://pirenaicasdelnansa.com/galeria-imagenes-vaca-raza-pirenaica

3.3. Productive characteristics

The main productive traits for meat production have been summarized by (CONASPI, 2020) and are reflected in Table 2.

Table 2. Average performance for the main productive traits in the Pirenaica population.

Birth weight	*42-43 kg*
Weaning weight	*250-300 kg*
Daily average growth	*1,600 kg/d*
Conversion rate of concentrate	*4,1 kg/kg*
Slaughter live weight	*555 kg*
Cold carcase weight:	*350 kg*
Carcass yield	*63%*
Carcass composition	
Muscle	*75,1%*
Extra	*2,1%*
First	*4,1%*
Second	*7,0 %*
Third	*21,6 %*
Fat	*8,4%*
Bone	*16,4%*
Muscle/bone	*4,6*
Carcass conformation	*U-2*
Degree of fattening: (1 = less fat to 15 = more fat)	*4,65*
Carcass colour: (1 = light pink to 15 = dark red)	*4,83*
Fat colour: (1 = white y 15 = dark yellow)	*4,31*
Fat distribution: (1 = irregular to 5 = uniform)	*4,25*
Fat texture: (1 = firm y 9 = oily)	*2,75*
Meat quality	
- *Ph*	*5,44*
- *Meat colour*	*5,42*
- *Water retention capacity: (% water expelled)*	*22,73%*

4. LIVESTOCK SYSTEM

Traditionally, Pirenaica animals were typically found in small, family-owned farms, with approximately ten individuals per farm. However, the current trend has shifted towards larger farms that accommodate between twenty to a hundred or more head of cattle (Echeverría & Asarta, 1975). The breeding system of the Pirenaica breed is closely tied to the climate and landscape conditions of the Pyrenees region. The distribution of the breed is primarily concentrated in two main climatic regions: the Alpine region and the Cantabrian region (Figure 10).

Figure 10. The map highlights the geographical areas of northern Spain where the Pirenaica breed is predominantly found. These areas include the Cantabrian region and the Alpine region corresponding to the Pyrenees.

The Alpine region is characterized by continuous and persistent snowfall in autumn and winter, with occasional occurrences in April and May. The area frequently experiences sub-zero temperatures during winter, while summer temperatures do not exceed 35°C. Forests dominate the landscape, and grazing is prevalent during the summer months (CONASPI, 2020). The Pirenaica population has achieved remarkable adaptation to the harsh conditions of the Alpine regions, demonstrating excellent acclimatization, robust health, and a strong aptitude for meat production. It also exhibits precocity when regular feeding is provided, which acts as a barrier to the introduction of foreign breeds. The breed's resilience, ability to mobilize body reserves,

and strong maternal aptitude, accompanied by appreciable milk production, make it a perfect fit for the climatic and geographical conditions of the mountains. The breed's rusticity contributes to relatively smooth calving experiences, with healthy calves being born without major issues. Once naturally weaned, the calves become self-sufficient in feeding (Picot et al., 2000). In the Cantabrian region, rainfall is evenly distributed throughout autumn, winter, spring, and mid-summer. Spring frosts are rare, and during harsh winters, temperatures do not drop below 5°C. The maximum temperatures never fall below 0°C, and in summer, they can reach up to 40°C. The climate in this region is generally temperate and characterized by abundant rainfall, constant humidity, and a predominance of forested hills. The Cantabrian region is known for its rich pasture lands (Calafell & Bertranpetit, 1994). In this area, the Pirenaica breed may face competition from other breeds that are also well-suited to the region's climate and conditions.

4.1. Nutrition

The livestock production system of the Pirenaica breed follows a semi-extensive grazing approach. During the summer months, the herds graze in the mountainous areas, typically on plots owned by the municipality. In spring and autumn, the cattle are moved to meadows in the valleys. In winter, the animals are fed with hay produced during the summer, cereal straw, and sometimes supplementary feed (CONASPI, 2020). Calves are typically weaned between 4 and 6 months of age. During this period, depending on the time of year, the cows are taken out to pasture and given a supplement of concentrate. Starting from the beginning of winter, which coincides with the first snowfall, the cows are moved to closed stables with a fixed housing system. They are provided with a diet rich in silage and hay, usually sourced from the farm. If necessary, supplements may be administered before calving to address any deficiencies in energy, protein, phosphorus, trace elements, or vitamins. Towards the end of winter, from mid-April to June and from November until weather conditions allow, the herds are taken

to pasture at lower altitudes in the surrounding valleys of the farms (Echeverría & Asarta, 1975). During this period, the animals are fed a mixed diet, and grazing is limited to a few hours, allowing for acclimatization. From approximately June to November, the animals undergo transhumance and are taken to higher altitudes for grazing. During this time, their food requirements are met by the vegetation present in the Pyrenean pastures. Calves feed on their mother's milk and remain with the suckling-cow until they start grazing, continuing to consume maternal milk (CONASPI, 2020). This practice is advantageous as it prepares the microbial flora in the rumen and develops the pre-stomachs, enabling the calves to assimilate feed at weaning. After weaning, which typically occurs around four to five months of age, the calves are provided with feed and hay until the end of the fattening phase, which takes place around 12 months of age on the same farm. The animals are then slaughtered at approximately 12 to 14 months of age (Aranguren et al., 2009).

4.2. Reproduction

Most dams in the Pirenaica breed are inseminated either through artificial insemination or natural mating by introducing bulls into the herd during the spring months, typically from March to May. Calving occurs during the winter period, starting in November. The number of registered births in 2022 is depicted in Figure 11. Currently, there is a growing trend to synchronize the heat cycles of the dams to concentrate calving within the most favourable period (CONASPI, 2020). This practice offers advantages as it improves control and management of the herd's reproductive function. The age at first calving varies depending on breeding conditions and ranges from 30 to 36 months. The first oestrus generally occurs around the time of weaning, while the first viable oestrus for insemination or natural mating typically takes place between 18 and 24 months of age when the cow's live weight reaches approximately 60% of the adult weight. With proper nutrition and management, it is common to achieve an average of one calf per cow per year in many herds. The breed's low incidence of fertility problems, effective

health control measures, and increased use of artificial insemination contribute to enhanced productivity (CONASPI, 2020). Currently, embryo transfer is conducted on an experimental basis, only.
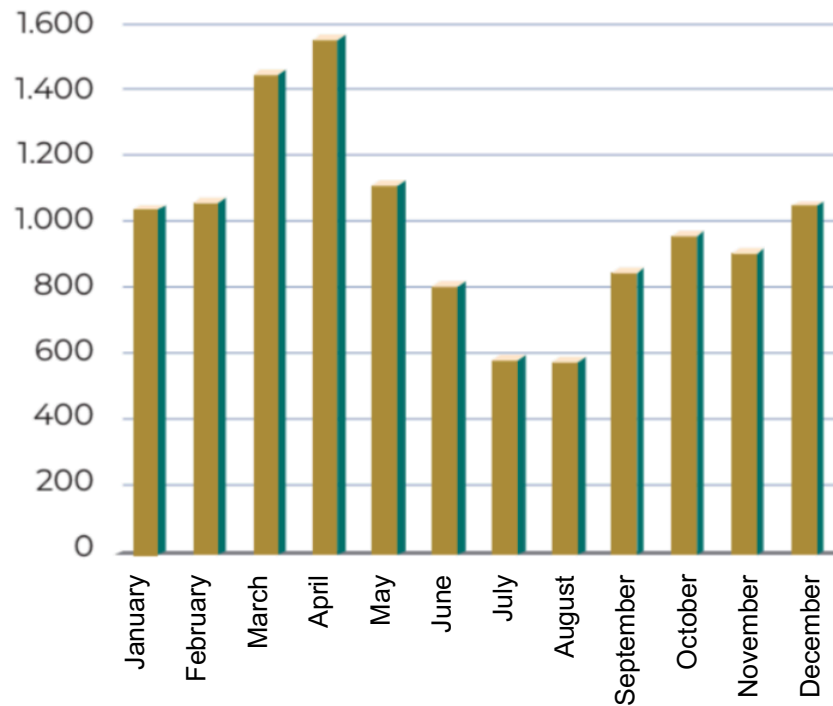

Figure 11. Number of births recorded by CONASPI in the year 2022.

Figure 12. Pirenaica cow with calf grazing. http://www.conaspi.es.

5. GENETIC SELECTION IN PIRENAICA BREED

5.1. The breeding association.

The Confederation of Associations of Pirenaica Cattle Breeders (CONASPI) was established in 1986 through the collaboration of several provincial and regional associations, including ASPINA (Navarra), ASAGAPIR (Bizkaia), ASAPI (Aragón), ASPIC (Cataluña), HEBE (Gipuzkoa), and ARPIEL (Álava). Following its foundation, CONASPI developed a new herd book regulation and proposed a genetic improvement program for the breed. On December 7, 1988, CONASPI received official recognition from MAPA (Ministry of Agriculture, Fisheries, and Food) as a collaborating institution responsible for managing and controlling the Herd Book, as well as verifying the performance of the Pirenaica cattle breed. The primary objectives of CONASPI are to preserve the breed's purity and implement a selection program while promoting its expansion (CONASPI, 2020).

CONASPI also holds the responsibility of establishing and maintaining the herd book, verifying the performance yields, and collaborating in its ongoing management and development. It aims to promote the adoption of practices that contribute to increased productivity and profitability for farmers. Over the years, CONASPI has accumulated a wealth of information in its herd book, with reliable data dating back to 1928 (Mendizabal, 1998). Additionally, the association plays a crucial role in the selection of breeders designated for the collection of semen for artificial insemination. CONASPI, together with the participating associations, actively contributes to the recognition and awarding of the Protected Geographic Indication (PGI) mark "Ternera de Navarra." The organizational structure of CONASPI is illustrated in Figure 13.
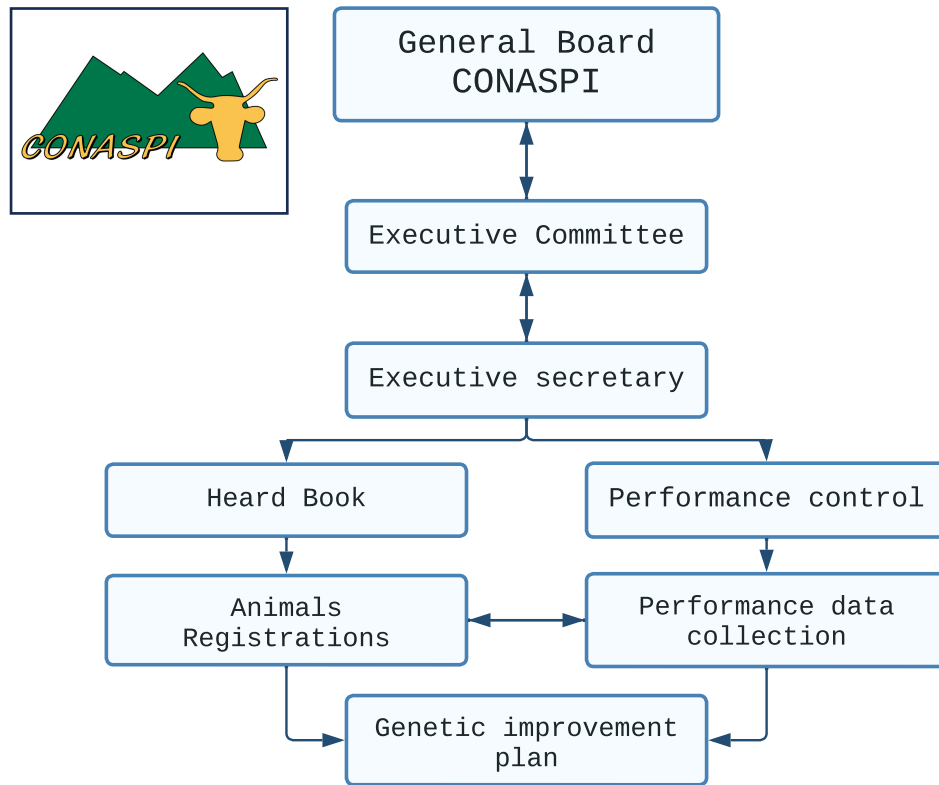
Figure 13. Organigram of the breed association.

5.2. The breeding program.

The breeding program for the Pirenaica cattle breed aims to enhance the profitability of both purebred Pirenaica farms and those involved in industrial crossbreeding. This is achieved by focusing on improving meat production and maternal traits (Makkar, 2012). The genetic improvement of the Pirenaica breed is conducted by selection, which involves identifying the individuals with the highest predicted additive genetic merit within the breed and ensuring their intensive reproduction to produce a succeeding generation superior to the previous one (CONASPI, 2020).

The genetic evaluation, which identifies individuals with desirable traits and transmits them to their offspring, is a fundamental aspect of this process. For the Pirenaica breed, the evaluation and qualification of animals are based on information gathered through

a genealogical and performance control system. This system operates within the farms themselves and the future sires' test station (Sabaiza Test Centre), under management and environmental conditions similar to those found in conventional breeding farms. The ultimate objective is to produce cows that can consistently produce one calf per year under their rearing environment. These calves, after undergoing fattening, should reach 12-13 months of age with optimal growth and desirable carcass and meat characteristics that align with market demands. The breeding program, therefore, encompasses the simultaneous improvement of both meat production and maternal aptitudes, considering the specific environmental conditions in which the cattle are bred (CONASPI, 2020).

The selection programme has the following objectives:

- Ensuring profitable calf production within a breeding cow production system by optimizing the percentage of calves produced. This is achieved by focusing on factors such as calving ease, improving fertility by reducing calving intervals, increasing milk yield, and enhancing the viability of calves.
- Obtaining harmonious animals that enable the maximum expression of productive and performance traits. This includes improving calf growth, optimizing slaughter weight, and enhancing carcass characteristics to maximize meat production.

Additionally, there are other traits of importance, such as forage intake capacity, functional abilities, and rusticity (adaptation to the environment). These traits are also considered in the selection program to ensure the overall resilience and suitability of the Pirenaica breed in its specific production environment (CONASPI, 2020).

5.3. *The Herd book.*

Each animal registered in any of the sections comprising the Herd Book will receive an individual identification using the Bovine Identification Code (BIC), in accordance with the existing regulations on animal health for bovine species in both the European Union and Spain. The BIC will serve as the animal's registration number in the official Herd Book for its entire lifespan, fulfilling all necessary purposes (Echeverría & Asarta, 1975). The Pirenaica cattle Herd Book encompass various sections and categories to ensure comprehensive record-keeping and management.

MAIN SECTION

In the main section of the Pirenaica cattle Herd Book, animals are eligible for entry if they have both parents and grandparents registered in the main section of the breed's herd book. Furthermore, they must meet the morphological criteria for entry and comply with the specific requirements of pedigree control.

The main section is further divided into subsections to facilitate organization and categorization (CONASPI, 2020).

Birth category: All offspring, regardless of sex, that are born to parents registered in the main section of the Pirenaica cattle Herd Book must be recorded in this register.

Definitive category: Animals in the *Birth category* may be eligible for entry if they meet the following criteria:

- Females must be at least two years old and have at least one proven birth. Males must be at least fourteen months old.
- They should exhibit appropriate body development relative to their age and the ecological environment they are raised in.
- They should not display any of the genetic defects identified in the linear morphological qualification.

- They should not have any functional or other impediment that would hinder their reproductive capability for future use (CONASPI, 2020).

Basic category: This category may encompass animals from the main section whose linear type of evaluation reveals the presence of genetic defects or dysfunctions that render them unsuitable as breeding animals. It also includes animals that have undergone a progeny test, which identified their transmission of genetic defects to their offspring (CONASPI, 2020).

Merit Category: Animals in the Definitive category that exhibit exceptional genetic, morphological, productive, or functional characteristics, in alignment with the breed-specific regulations and selection objectives, will be included in this category. These animals have demonstrated outstanding traits that contribute to the breed's genetic improvement and meet the defined selection criteria (CONASPI, 2020).

ANNEXED SECTIONS

In these sections, females that possess the characteristics specified in the breed standard but lack complete genealogical documentation to prove their ancestry may be entered. To ensure compliance with these requirements, these females must fulfill the following criteria (CONASPI, 2020):

- They should be at least 2 years old and have a verified record of calving.
- Their body development should correspond to their age.
- They should not exhibit any of the genetic defects specified in the linear morphological qualification conducted during registration.
- They should not have any functional or other impediment that would hinder their future use as breeding animals.

5.4. Genetic breeding programme

The structure of breeding program of the Pirenaica beef cattle population is presented in Figure 14.

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                    │  GENETIC BREEDING SCHEME     │
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          ┌──────────────────┬──────────────────┬──────────────────┐
    ┌───────────┐      ┌───────────────┐   ┌─────────────┐
    │ SLAUGHTER │      │ CONTROL OF    │   │  GENEALOGY  │
    │ HOUSE DATA│      │ FARM YIELDS   │   └─────────────┘
    └───────────┘      └───────────────┘
                    ┌─────────────────────────┐
                    │ GENETIC EVALUATION       │
                    │                          │
                    │ GENETICS INDEX           │
                    │  · PM10                  │
                    │  · 210 DAYS              │
                    │  · CARCASS WEIGHT        │
                    │  · CONFORMATION          │
                    │  · FATNESS               │
                    │  · MEAT INDEX(ICC)       │
                    │  · LIFE INDEX(ICV)       │
                    └─────────────────────────┘
    ┌──────────────────────┐        ┌──────────────────────┐
    │ BEST SELECTION OF     │        │ List of best animals  │
    │ COWS                  │        │ with genetic indexes  │
    │  Best 500 ICC         │        │ to farmers            │
    │  Best 500 ICV         │        └──────────────────────┘
    └──────────────────────┘
    ┌──────────────────────────────────────────────────┐
    │ Morphological evaluation and reproductive data    │
    └──────────────────────────────────────────────────┘
                │── Rejected
    ┌──────────────────────────────────────────────────┐
    │ Mothers of future breeders                        │
    └──────────────────────────────────────────────────┘
                │── Rejected
    ┌──────────────────────────────────────────────────┐
    │ Male progeny for Sabaiza                          │
    └──────────────────────────────────────────────────┘
    ┌──────────────────────┐        ┌──────────────────────┐
    │ Auction for natural   │        │ Artificial            │
    │ mating                │        │ insemination          │
    └──────────────────────┘        └──────────────────────┘
```
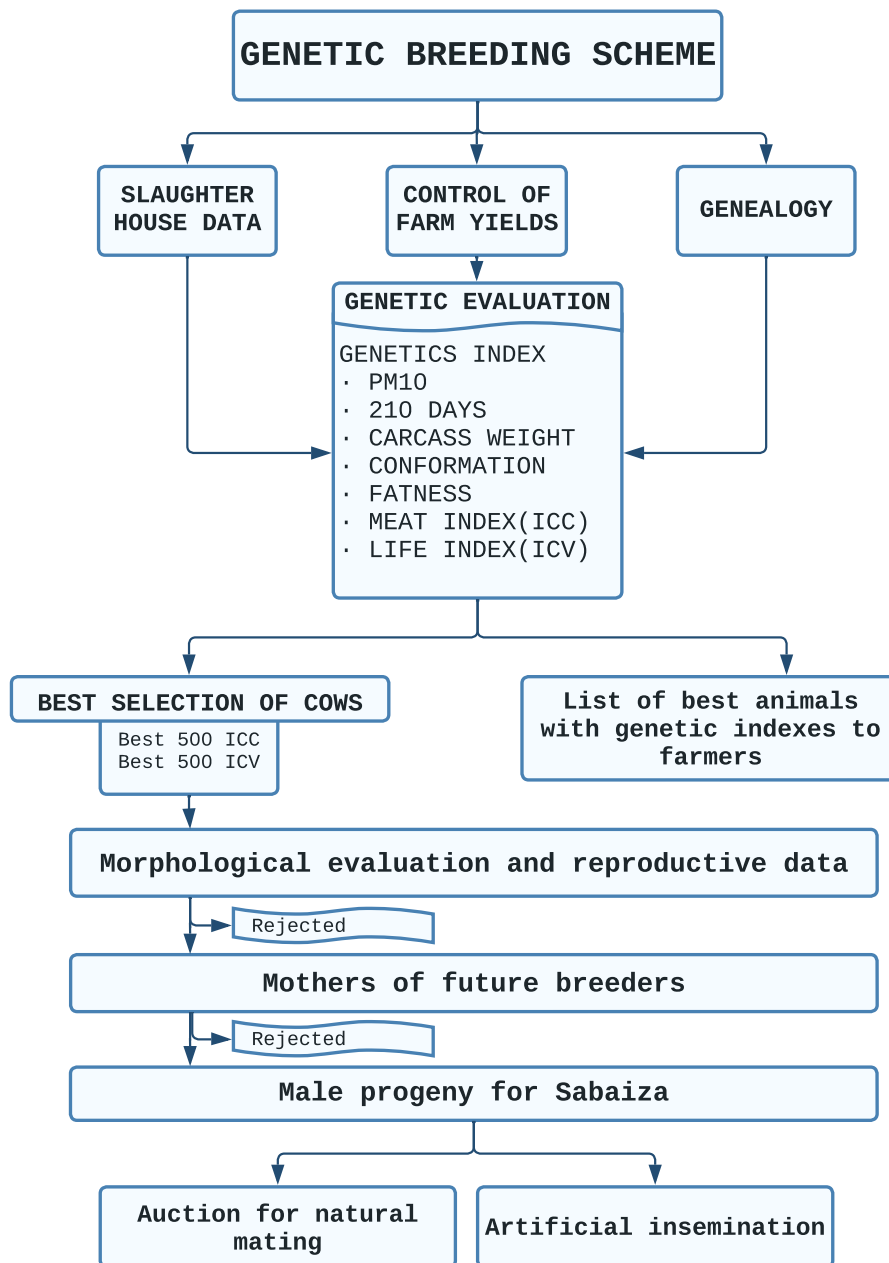
Figure 14. Genetic breeding programme used in genetic improvement plan in the Pirenaica breed.

The initial phase of the breeding program entails assessing the genetic merit of potential breeding candidates. This evaluation is based on the phenotypic information obtained from various sources, including data collected from farms as well as the slaughterhouse.

At the farms, several traits are considered for genetic evaluation, including:

- *Birth weight (BW):* This trait has significant implications for the calving process and impacts various aspects of farm management. It is associated with calf mortality within the first 48 hours, placenta retention, maternal fertility, and subsequent calf growth (Echeverría & Asarta, 1975).

- *Maternal effect at day 90 (M90):* The weight of the calf at 90 days serves as an indicator of the cow's maternal abilities (CONASPI, 2020). It reflects the cow's capacity for breeding and milk production, as the calf is primarily dependent on maternal milk during this period.

- *210-day weight (W210):* This trait is chosen for its practicality and ability to be directly measured in most farm animals. It serves as a reliable predictor of the calves' subsequent performance, with a strong genetic correlation observed between 210-day weight and slaughter weight at 12-14 months.

Moreover, the phenotypic information recorder at the slaughterhouses includes:

- *Cold Carcass Weight (CCW):* This trait is directly linked to the selection objective; however, it can only be measured in animals that have been slaughtered. As a result, it is used primarily to estimate the genetic merit based on information obtained from relatives (CONASPI, 2020).

- *Carcass Conformation (CON):* This characteristic is assessed at the slaughterhouse using the SEUROP scale, which assigns a rating ranging from S (indicating the best conformation) to P (representing the poorest conformation), as depicted in Figure 15. In genetic evaluation, this rating is converted into a numerical scale as reported in the picture. Conformation within the SEUROP

scale is associated with the price paid by the slaughterhouse per kilogram (Heggli et al., 2023).
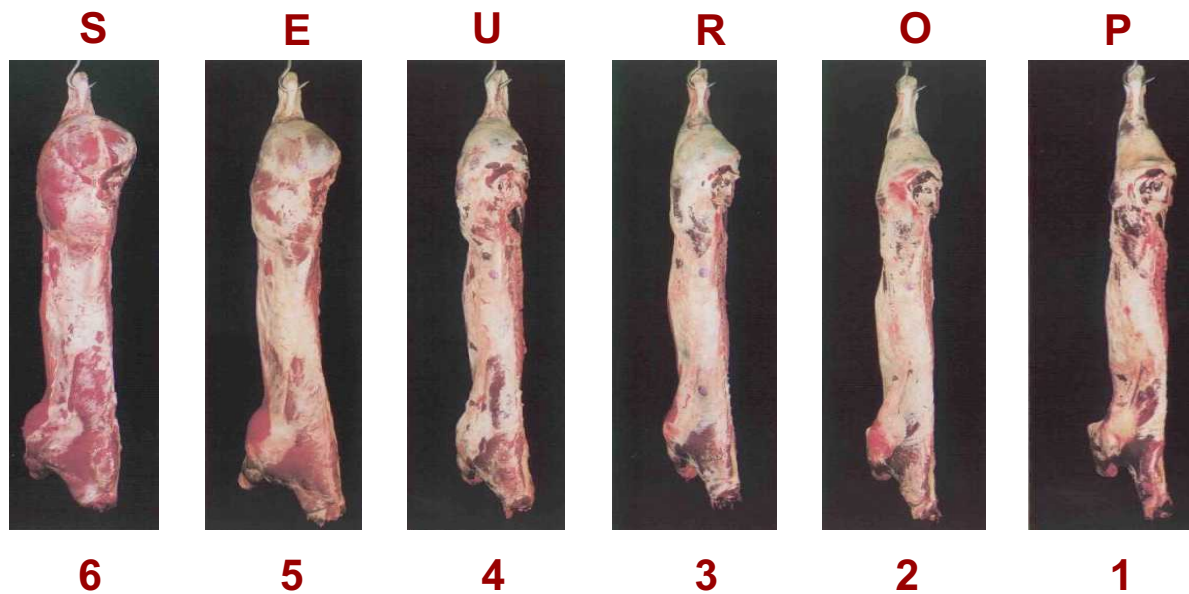

Figure 15. SEUROP scale for carcass conformation.

- *Carcass Fattening (FAT):* This trait is assessed at the slaughterhouse using the SEUROP scale, which spans from 1 (indicating low fat) to 5 (representing high fat), as shown in Figure 16. Similarly, for genetic evaluation purposes, it is transformed into a numerical scale. The fat level in the carcass is linked to the cow's capacity to mobilize energy reserves required for pregnancy and lactation (Nogalski et al., 2012).
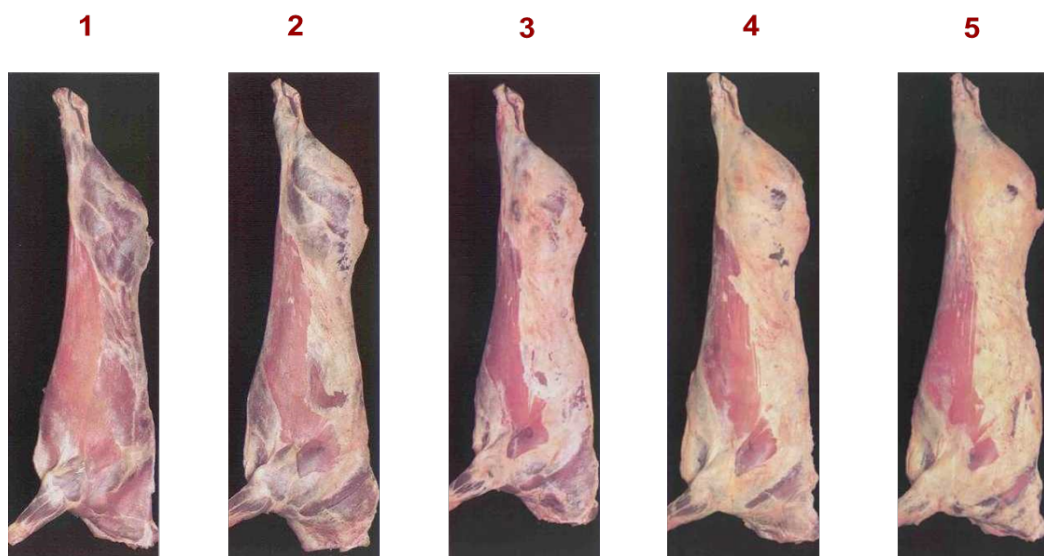
Figure 16. SEUROP scale for evaluation the carcass fattening.

The genetic evaluation was conducted using BLUP (Best Linear Unbiased Prediction) methodology, as proposed by Henderson (1984). The breeding values were predicted and standardized to a mean of 100 and a standard deviation of 10. These standardized breeding values were then integrated into two composite selection indexes. The purpose of these composite selection indexes is to maximize the profitability of the breed in future generations by effectively selecting breeding animals (Wellmann, 2023).

In the Pirenaica breeding program, two composite selection indexes are utilized: the Composite Meat Index (CMI) and the Composite Life Index (CLI) (Table 3).

Table 3.

SELECTION INDEX	*DESCRIPTION*
Composite meat index (CMI)	It combines selection for weight at 210 days, cold carcass weight and carcass conformation. **CMI = 0.25 W210 + 0.25 CCW + 0.50 CON**
Composite life index (CLI)	It combines selection for the maternal capacity of cows, conformation and fattening of the carcass. **CLI = 0.20 CON + 0.50 M90 + 0.30 FAT**

The Composite Meat Index (CMI) aims to identify the most suitable individuals for meat production, whether for purebred or crossbreeding purposes. On the other hand, the Composite Life Index (CLI) focuses on selecting the optimal individuals to establish the next generation of purebred cows (Altarriba et al., 2009). Once the genetic evaluations are obtained, farm-specific reports are prepared and provided to farmers, serving as an additional tool for decision-making. These reports include information about inbreeding levels and offer recommendations or guided mating suggestions. Additionally, a ranking system is established to identify cows of merit based on their achievements in both meat and overall life indexes. These exceptional cows undergo

morphological classification and assessment of their reproductive performance. The top-performing cows are then selected as potential dams for future sires (i.e., bull-dams). Ideally, they are paired with recommended sires through targeted mating, with the goal of producing genetically superior male calves and advancing the breeding program. In the case of the Composite Meat Index (CMI), the top 500 females that have calved at least once are selected based on a combination of factors. These selection criteria include calving ease, conformation, and carcass weight. These females are recognized for their ability to produce high-quality beef calves, ensuring optimal meat production (CONASPI, 2020).

Regarding the Composite Life Index (CLI), cows with a minimum of two instances of calving are considered for selection. Various factors are considered, such as calving ease, conformation, milk production, and fatness, which serves as an indicator of robustness. These cows are known for producing superior heifers suitable for breeding. All selected mothers undergo inspection by breed qualifiers, and those that meet the criteria are entered into the breed's Register of Merit (CONASPI, 2020).

5.5. Breeding center for selected sires

The genetic center primarily consists of grazing parcels and serves as a facility for rearing calves for a length of 6-8 months, from their arrival until they reach 14-15 months of age. To ensure appropriate development and growth, the calves' diet is supplemented with concentrate. The center is currently located on the Sabaiza land, which is owned by the Government of Navarre. Every quarter, 6-8-month-old calves from controlled herds are admitted to the center (CONASPI, 2020). These calves are the offspring of carefully selected mothers registered in the herd book, ensuring their prior qualification. They must be in good health and free from bovine viral diarrhea (BVD) and infectious bovine rhinotracheitis (IBR), which are diseases associated with respiratory ailments and abortions (Potgieter et al., 1984). Upon arrival at the center,

the calves undergo weighing and undergo a series of sanitary, quarantine, and acclimatization treatments for approximately one month, following strict biosecurity guidelines. Throughout their stay at the genetic center, the animals are weighed monthly, and at around 13 months of age, they undergo a new morphological qualification and specific zoometric measurements. An Evaluation Committee then reviews all available data for each animal and pre-selects candidates for offspring testing through artificial insemination. Typically, 2-4 animals per year are selected for this purpose. The remaining calves, which may demonstrate lower performance, are designated for natural mating, and distributed among herds (Ooi et al., 2023). However, animals deemed unsuitable during the evaluation process will be sent for slaughter.

5.6. Catalogues of breeding stock

The sires selected for artificial insemination are featured in the breeding stock catalogue (Figure 17). This comprehensive catalogue provides essential information for each sire, including genetic predictions for various traits such as birth weight (ICO nacimiento), carcass merit index (ICO aptitud cárnica), and livability index (ICO aptitud vida) (P.Aranguren et al., 2009). The catalogue also indicates the accuracy of these predictions (Fiabilidad), providing an indication of the reliability of the estimated values. Additionally, the catalogue includes the pedigree of the sires, tracing their lineage up to grandparents. It also provides information on the ease of calving for their offspring (Facilidad de parto), the fertility of their semen (Fertilidad del toro), and morphological characteristics (CONASPI, 2020). This information serves as a valuable resource for breeders to make informed decisions when selecting sires for artificial insemination.

HATXIKI		
Nº Reg: **ES061520380153**	Nombre: **HATXIKI**	Código I.A.: **A-29-064**
C.I.B.: **ES061520380153**	Criador: **Bizkaiko Foru Aldundia-Gorliz (Bizkaia)**	Fecha Ncto.: **26/01/2017**

P.	VIRUS - ES021520394735
Ab.	NA146095 - ES081402509978
Ab.	SOTA - ES021520355890
M.	UTERQUE - ES081520380097
Ab.	NESTOR - ES061402466067
Ab.	KINTA - ES091520186347

Facilidad de parto	7	Fácil	
Fertilidad del toro	100	Normal	

Índices Genéticos	
ICO Nacimiento	91
ICO Aptitud Cárnica	100
ICO Aptitud Vida	108
Fiabilidad	96 %

Índice de Crecimiento	79	
Desarrollo Muscular	79	
Aptitud Funcional	79	
Caracter Racial	76	
P. Total	78	

Datos Zoométricos a los 1-08 años

134 cm.   177 cm.   197 cm.

62 cm.   75 cm.   40 cm.

Peso	Peso Nac.	Peso 120 días	Peso 210 días	Peso 365 días	Ganancia media diaria
723 kg	43 kg	180 kg	245 kg	411 kg	1371 gr

✳Animal de tipo mixto con mucho carácter racial.
✳Línea maternal con mucha capacidad criadora. Madre de pelvis amplia y bien emplazada.
✳De línea paterna de muy fácil parto.

HATXIKI

Padre de HATXIKI

Figure 17. Example of a breeding sire of Sabazia test center with all traits in description highlighted (catalogue of CONASPI).

6. MATERNAL EFFECTS IN BEEF CATTLE

One of the traits included in the breeding program of the Pirenaica population is the genetic effect for weight at 90 days. Maternal effect refers to the direct influence of the phenotype of the mother on the phenotype of her offspring (Arnold, 1994). In the case of cows, the maternal influence on the expression of traits in calves occurs through both the environmental conditions provided by the mother during a portion of the calf's life and the transmission of genes from the mother to the calf. The influence of the maternal environment can be observed in two phases of the calf's life. The first phase is the intrauterine period, which spans from conception until birth (Abuelo, 2020). During this period, the mother's environmental conditions, such as nutrition and overall health, can affect the development and growth of the calf. The second phase occurs from birth to weaning, during which the mother's care, milk production, and nurturing behavior can significantly impact the calf's growth and overall development. Considering the maternal effect in the breeding program allows for a comprehensive understanding of the factors influencing the performance and traits of the Pirenaica population (Altarriba et al., 2005). By selecting cows with desirable maternal qualities, such as high milk production and excellent mothering abilities, breeders can improve the genetic potential and overall productivity of the offspring.

Dickerson (1947) and Willham (1963) proposed a comprehensive quantitative genetic model that incorporates both direct effects and maternal effects on a trait (Speidel et al., 2010). According to Willham's model, when there is only one offspring per dam, the observed phenotype of an individual (P_i) is determined by the sum of its own phenotypic direct effect ($P_{D,i}$) and the phenotypic maternal effect due to its dam ($P_{M,j}$) where i represents the individual and j represents the dam of the individual (Bijma, 2006; Willham, 1963).

$$P_i = P_{D,i} + P_{M,j}$$

The direct and maternal effects are not directly observed; rather, they represent the underlying phenotypic effects of the offspring and dam on the observed phenotype, P_i. It is important to note that the maternal effect itself is a phenotypic effect, which can be further decomposed into an additive genetic effect and a non-genetic effect, often referred to as the permanent environmental effect. The maternal genetic effect refers to the influence of the dam's genes on specific traits, particularly those related to milk production and other factors relevant to offspring development (Iwaisaki et al., 2005; Koch, 1972). In contrast, the environmental maternal effect is associated with the environment in which the dam was raised, including aspects such as diet and management practices. These non-genetic factors can include aspects such as the maternal care provided, the quality of the dam's milk, or other environmental conditions that persistently affect the offspring's phenotype (González-Recio et al., 2012).

Weaning weight is a trait that has been extensively studied regarding these significant influences (Garrick, 1990). Numerous studies have demonstrated the clear influence of maternal genetic effects on beef cattle weaning weight (Garrick, 1990; Koch, 1972; Meyer, 1994; Rumph et al., 2004). Consequently, weaning weight can be modified by genetically increasing the pre-weaning growth capacity of calves, using dams with higher maternal capacity, or improving management practices to create a better environment (Koch, 1972). However, the importance of maternal effects tends to diminish with age as post-weaning genetic and environmental factors become more prominent, thereby reducing their overall impact (Garrick, 1990). By considering both the additive genetic and permanent environmental effects, breeders can gain a better understanding of the contributions of genetics and the maternal environment to the observed phenotypes (Räsänen & Kruuk, 2007). This knowledge is valuable for making informed breeding decisions aimed at improving the desired traits.

7. GENETIC EVALUATION OF MATERNAL GENETIC EFFECTS

The estimation of (co)variance components and the prediction of breeding values are crucial steps in the implementation of breeding programs aimed at facilitating genetic improvement (Bijma, 2006). Selecting individuals based on estimated breeding values is more reliable as it considers not only the individual's own phenotypic information but also information from their relatives (Mwansa et al., 2002). By considering the genetic information from both the individual and its relatives, more accurate predictions can be made about an individual's genetic merit and their potential to pass on desirable traits to future generations (Kruuk, 2004). This allows breeders to make informed decisions and effectively accelerate genetic progress in their breeding programs.

7.1. Best linear unbiased prediction (BLUP)

In the genetic evaluation of most livestock populations, the preferred method is best linear unbiased prediction (BLUP) based on an animal model (Nimbkar et al., 2008). This methodology, developed by Henderson, (1984) allows for the simultaneous estimation of fixed effects and breeding values for both animals with or without phenotypes (i.e., through the relationship matrix). BLUP shares similarities with a selection index in terms of its properties and can be considered a form of selection index when no adjustments for environmental factors are necessary (Seid & Endris, 2020).

The term "BLUP" encompasses the fundamental characteristics of the methodology, which are aimed at achieving the best estimation of breeding values while ensuring linearity and unbiased:
- Best – BLUP aims to maximize the correlation between true breeding values and estimated breeding values or minimize the variance of prediction errors.

- Linear – The predictors in BLUP are linear functions of the available data, allowing for efficient estimation.
- Unbiased – BLUP ensures that the average value of the estimated breeding values is equal to the average value of the true breeding values being estimated. This guarantees an unbiased estimation (Cantoni & Hastie, 2002).
- Prediction – The term "prediction" in BLUP distinguishes it from estimators of fixed effects. BLUP focuses on predicting the true breeding values of individuals based on available data, allowing for accurate assessment of their genetic merit (Koivula et al., 2012; Pal & Chakravarty, 2020).

The basic implementation of BLUP involves a mixed linear model represented by the equation:

$$y = Xb + Zu + e$$

In this model, **y** is a vector of phenotypic records, **b** is a vector of systematic or fixed environmental effects, **u** is a vector of additive genetic effects for each animal (Animal model), and **e** is a vector of residuals. **X** and **Z** are incidence matrices. $E(\boldsymbol{u}) = 0, E(\boldsymbol{e}) = 0$ and

$$Var\begin{bmatrix} \boldsymbol{u} \\ \boldsymbol{e} \end{bmatrix} = \begin{bmatrix} A\sigma_u^2 & \mathbf{0} \\ \mathbf{0} & I\sigma_e^2 \end{bmatrix}$$

where **A** is the numerator relationship matrix, **I** is the identity matrix, σ_u^2 is the additive genetic variance and σ_e^2 is the residual variance (G. K. Robinson, 1991).

The animal model BLUP provides several advantages in genetic evaluation:

- Handling unbalanced designs: BLUP can handle datasets with unbalanced designs, meaning it can accommodate variations in the availability of data for

different individuals. This allows for more efficient and accurate estimation of genetic values, even when data is missing or unevenly distributed.

- Utilizing information from all measured relatives: BLUP incorporates information from all measured relatives, improving the accuracy of estimates. This means that the genetic values of an individual are influenced not only by its own performance but also by the performance of its relatives, leading to more reliable predictions (Muir, 2007), even for animals without registered phenotypes.

- Estimating various genetic values: BLUP is versatile and can be used to estimate a variety of genetic values, including breeding values, genetic effects, genotype-environment interactions, and environmental effects (Koivula et al., 2012). This broadens its applicability and provides a comprehensive understanding of the genetic contributions to phenotypic traits.

- Removal of non-genetic biases: BLUP aids in removing non-genetic biases in breeding value estimation. It considers factors such as non-random mating and the genetic merit of mothers, allowing for more accurate and unbiased breeding value estimates. This ensures that the estimated genetic values primarily reflect the true genetic potential of individuals.

- Facilitating selection: BLUP assists in assessing the genetic merit of individuals and enables informed selection decisions based on estimated breeding values. By identifying superior individuals for breeding purposes, BLUP contributes to genetic improvement within a population, leading to enhanced performance and desirable traits in future generations. (Henderson, 1984; G. K. Robinson, 1991).

However, it must be noted that the animal model BLUP equations requires of estimates of the variance components, that are usually achieved using REML (Restricted Maximum Likelihood) of Bayesian Analysis with McMC methods (Henderson, 1984).

7.2   *Maternal Animal model*

The maternal animal model is an extension of the simple BLUP animal model that incorporates an additional genetic effect specifically for the dam (Crews & Wang, 2007). This maternal genetic effect aims to capture the influence of the dam's genes on the maternal environment experienced by the offspring.

The statistical linear model is:

$$y = Xb + Zu_d + Wu_m + Wp + e$$

where **y** is the vector of phenotypic records, b is the vector of "fixed" environmental effects, u_d is the direct genetic effect that express the effect of the genes of the calf in the trait, u_m is the maternal genetic effect that reflect the contributions of the dam genes into the maternal environment affecting the phenotype, p is the permanent maternal effect that express the non-genetic contributions of the dam to the maternal environment, and **e** is the residual (Crews & Wang, 2007). Further, **X**, **Z** and **W** are the incidence matrices that links u_d, u_m and **p** with the data. The variances of the random effects are:

$$Var \begin{bmatrix} u_d \\ u_m \\ p \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_u^2 & 0 & 0 & 0 \\ 0 & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I\sigma_p^2 & 0 \\ 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

Where **A** is the numerator relationship matrix, **I** is the identity matrix, σ_u^2 is the additive genetic variance, σ_m^2 is the maternal additive genetic variance, σ_p^2 is the permanent environmental variance and σ_e^2 is the residual variance. Moreover, in some cases, the

direct ($\boldsymbol{u_d}$) and the maternal ($\boldsymbol{u_m}$) can be related trough the additive genetic covariance σ_{um}.

In the maternal animal model, certain assumptions are made, including the independence of maternal permanent environmental effects and residual effects from direct and maternal genetic effects (Meyer, 1994). By solving the equations of the maternal animal model, estimates of the direct and maternal genetic effects can be obtained (Crews & Wang, 2007).

In addition to the advantages offered by the animal model BLUP, the maternal animal model allows for the distinction between direct and maternal effects. It achieves this by separating the estimation of direct effects, which are attributed to an individual's own genetic makeup, from maternal effects, which are influenced by the mother (Meyer, 1997). This is particularly useful for traits where the mother has a direct impact on calf performance, such as weaning weight (Mallinckrodt et al., 1993). The maternal breeding value is only expressed in mothers, but the genes responsible for this value are carried by both parents and inherited by all animals. Therefore, the maternal animal model enables the prediction of maternal values of reproduction for all animals (Crews & Wang, 2007). The prediction of maternal breeding values is of great importance for making informed selection decisions and advancing traits influenced by maternal effects (Gerstmayr, 1992, Williams et al., 2022). Breeders can use these predictions to make selection decisions for young cows, considering their expected performance. This enables the retention of genetically superior cows without hindering overall genetic progress (Bonifazi et al., 2021).

The maternal animal model BLUP also incorporates systematic or fixed effects that contribute to the phenotypic expression, such as sex, age of the dam, or management group effects (Misztal et al., 2018). These effects are included to eliminate non-genetic sources of variation and improve the prediction of breeding values across multiple

generations (Dominik et al., 2017). By accounting for these factors, the model can more accurately estimate the genetic component of the traits under consideration, leading to more reliable and informative breeding value predictions.

7.3. Maternal effect and age of the dam

One of the systematic effects commonly included in the maternal animal model is the age of the dam. This effect is considered because the age of the dam has a significant impact on the growth of its offspring. Mature beef cows typically wean heavier calves compared to younger cows (Stewart & Martin, 1981). This difference can be attributed to various factors. Firstly, heifers, which are still growing themselves, tend to produce less milk compared to mature cows. Additionally, older cows may also produce less milk, resulting in lower weaning weights for their offspring (Szabó et al., 2006). In the Pirenaica population, for instance, there is an approximately 15 kg variation in weaning weight between cows aged 8 years and cows aged 16 years or more.

The traditional maternal animal model assumes that both the genetic and permanent environmental effects remain constant throughout the lifespan of the cows. However, when considering weaning weights as "longitudinal" traits, it is important to acknowledge that the genetic and environmental influences, particularly those related to milk production and maternal care, may vary over the productive life of cows (Daniels & Pourahmadi, 2002). In animal breeding, the usual approach for analyzing such "longitudinal" traits, where the genetic or environmental influence may change over time, is the use of random regression models (Schaeffer & Jamrozik, 2008). These models allow for the incorporation of the age of the dam as a covariate and provide a more comprehensive understanding of the genetic and environmental effects on weaning weights throughout the cows' productive lifespan (Arthur et al., 1993).

8. ESTIMATING (CO)VARIANCE FUNCTION WITH RANDOM REGRESSION MODEL

Traits that are measured multiple times throughout an animal's lifetime are referred to as repeated measurements (Speidel et al., 2010). These repeated measurements can provide valuable information about how certain characteristics change over time and may exhibit varying degrees of correlation. Analyzing these traits requires a specific statistical approach due to the structured covariance model associated with them (Arango et al., 2004).

The change over time in these traits can be of particular interest as it can help us gain a better understanding, explanation, or manipulation of how the characteristic evolves over time (Canter et al., 1988). By studying the function that describes this change, we can uncover valuable insights into the dynamics of the trait and its underlying genetic and environmental factors. This knowledge can contribute to more effective management practices and genetic improvement strategies in animal breeding programs.

In animal breeding, random regression models have been widely used to analyze longitudinal traits such as milk production during lactation or growth in beef cattle (Schaeffer & Jamrozik, 2008). These models are valuable because they allow for the description of the mean and variance of traits across the parametric space, accounting for the changing structure of correlations over time. Some studies have demonstrated that the inclusion of random regression models in the analysis of longitudinal traits improves prediction accuracy (Meyer, 1997). By incorporating the changing nature of these effects over time, random regression models provide a more comprehensive and accurate assessment of the trait's genetic and environmental components.

The estimation of changes in genetic variances and correlations over time within a trait or between traits can be achieved using a random regression model with Legendre polynomials as the basis functions (Haile-Mariam & Pryce, 2015). The choice of the best model involves finding a balance between model complexity and the amount of available information. In the case of random regression models, the orthogonality of Legendre polynomials leads to smaller covariances among the coefficients compared to other types of covariates (Schaeffer & Jamrozik, 2008).

In the context of beef cattle, previous studies utilizing random regression models have primarily focused on adult weights (Arango et al., 2004; De Albuquerque & Meyer, 2001; Meyer, 1994, 1997; Nephawe et al., 2004) or weights from birth to approximately 2 years of age (De Albuquerque & Meyer, 2001; Nobre et al., 2003). These studies have provided valuable insights into the genetic aspects of growth patterns and developmental trajectories in beef cattle.

However, to the best of our knowledge, no study has specifically examined the weaning weights of offspring as a "longitudinal" trait within the context of a dam (Speidel et al., 2010). Such an analysis could provide valuable insights into the dynamics of calf growth and the influence of maternal effects on weaning weights. Future research focusing on the longitudinal aspect of weaning weights would contribute to a more comprehensive understanding of the genetic and environmental factors affecting beef cattle production (Yin & König, 2018). To our knowledge there are not any study that consider the weaning weights of the offspring of a dam as a "longitudinal" trait.

9. MATERNAL EFFECTS ON WEIGHT AT 90 DAYS OF PIRENAICA CALVES

9.1. Introduction and aim of the study.

In beef cattle, cows play a crucial role in providing their offspring with both a prenatal and postnatal environment, including milk supply. Therefore, weaning weights of beef cattle can be improved through selection for the growth ability of calves or by enhancing the maternal environment and milk production of the dam (Garrick, 1990). The variation in a cow's ability to provide this environment or produce milk has a genetic basis proportional to maternal heritability (Crews & Wang, 2007). Consequently, maternal genetic effects are utilized in beef cattle breeding to select future dams and improve maternal ability. These effects are predicted using the solutions derived from the maternal animal model, which incorporates both direct and maternal genetic effects and is commonly applied in the analysis of weaning weight traits (Koch, 1972).

The maternal animal model also includes systematic effects such as sex, age of the dam, herd-year-season, as well as a permanent environmental effect associated with the dam, an additive genetic effect linked to the calf, and a residual effect. The standard maternal animal model assumes that both the maternal genetic effect and the permanent environmental effects remain constant throughout the cow's lifespan. However, it is known that milk production varies with age, with some cows maintaining a consistent level of production throughout their productive life while others experience a decline as they age (López et al., 2015). Therefore, milk production (or maternal effect) can be considered a longitudinal trait that is measured multiple times throughout a cow's productive life.

Longitudinal traits, where measurements are taken at different time points over an individual's lifetime, require specific statistical approaches for genetic evaluation, such

as random regression models (Schaeffer & Jamrozik, 2008). These models allow for the modeling of maternal effects using a regression approach with the age of the dam as the associated covariate. By using this model, it becomes possible to describe the evolution of maternal genetic variances across the productive lifespan of the cows and predict the maternal genetic effect at different age points for each individual (cow or dam). Therefore, the objective of this study is to employ a random regression model to model maternal effects, specifically focusing on the association with the age of the dam for recorded calves. This model will enable the characterization of the maternal genetic variances over the cows' productive lifespan and the prediction of the maternal genetic effect at different age points.

The maternal effect at 90 days serves as a crucial indicator of a cow's maternal abilities and represents a key objective in the breeding program for the Pirenaica breed. All data and results presented in this study pertain to this specific trait. The study aims to investigate the relative contributions of genetic and environmental components to maternal effects and determine if there is any covariation between maternal capacity and environmental factors that influence the phenotypic expression of weight at 90 days.

9.2. Material and methods

9.2.1. Description and filtering of data

In this study, we considered and analysed two types of datasets. The first dataset comprises a collection of weaning weights, with each record containing the following information:

- Sex of the calves, identified with numerical levels: 1 for males and 2 for females.
- Age of the calf in days at the time of registration. The recorded data ranged from 46 and 134 days, with an average ± standard deviation of 94.67 ± 2.45 days (Figure 18).
- Age of the dam of each registered calf. The age varied from 548 days to 11627, with mean of 2606.96 ± 1297.87 days. Outliers were removed, and the age values were restricted to a parametric space between 600 and 6000 days (Figure 19).
- Herd-year-season levels, comprising a total of 9689 levels. Each level consists of calves born in the same season and within the same herd. This grouping reflects the specific farm conditions, husbandry practices, feeding regime, and other relevant factors that are unique to each group.
- Identification code (ID) of the calf as registered in the pedigree.
- Phenotype, which represents the weight of the calf at the time of registration in kilograms (90 days), values ranging from 45 kilograms to 390, with mean of 134.9 ± 39.27 kilograms (Figure 20).
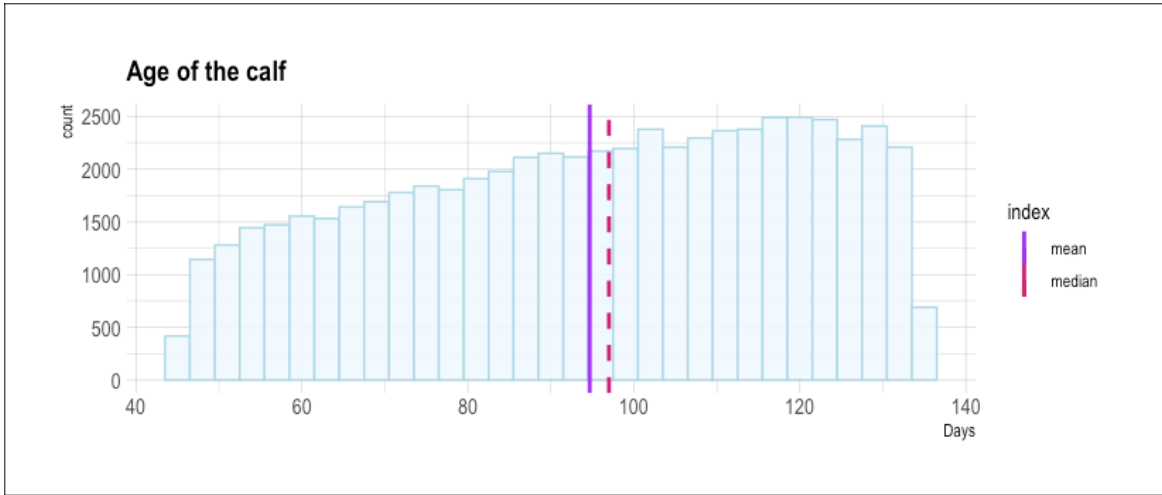
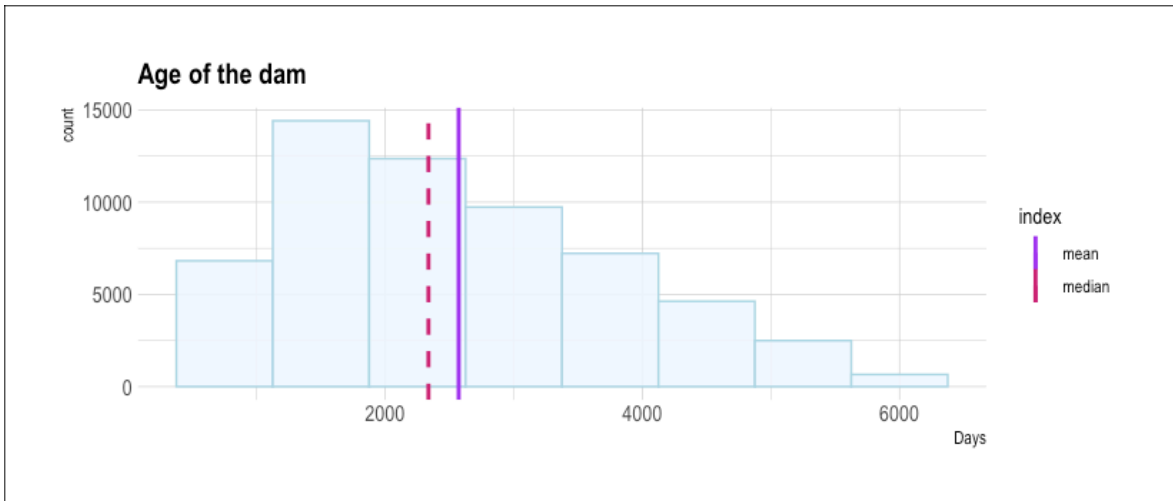*Figure 18. Age of the calf in days at the time of registration.*
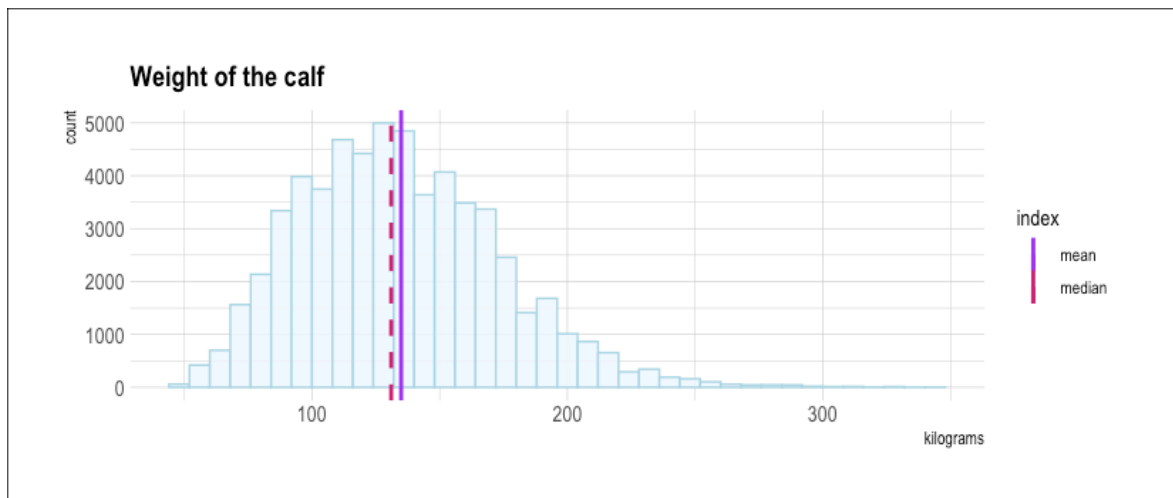

Figure 19. Age of the dam of each registered calf.

Figure 20. Weight of the calf at the time of registration.

48

The second file corresponds to the pedigree data, which comprises a total of 370,568 entries. The columns in the file represent the ID of the calf, the sire (father), and the dam (mother) respectively. These entries document the offspring of 356,688 sires and 358,306 dams, with 13,880 sires and 12,262 dams listed as unknown. To ensure genetic linkage with the phenotypic records for weight at 90 days, the pedigree was filtered using the renumf90 software (Misztal et al., 2018). As a result, only the individuals that had a genetic connection to animals with recorded weight at 90 days data were retained in the pedigree. The final number of animals included in the pedigree was 85,670.

9.2.2. Data editing

In first place, the variable *age of the dam* was filtered between 600 and 6000 days to eliminate outliers. Secondly, it was transformed into the scale $(-1 \leq x \leq 1)$ as:

$$sa_i = [2(a_i - a_{min}) / (a_{max} - a_{min})] - 1 \qquad (1)$$

where sa_i is the scaled age of the dam of the *ith* record, a_{min} and a_{max} were the smallest (600 days) and the largest age of dam (6000 days). This scaled age of dam was decomposed into up to 6 normalized Legendre Polynomials using the following transformation:

$$\phi_j(s_i) = \frac{1}{2^j} \sqrt{\frac{2j+1}{2}} \sum_{m=0}^{j/2} (-1)^m \binom{j}{m} \binom{2j - 2m}{j} s^{j-2m} \qquad (2)$$

A summary of the Legendre Polynomial transformations presented in Table 5.

Table 5.

Polynomial   Transformation

ϕ_0	$0.7071 \times s^0$
ϕ_1	$1.2247 \times s^1$
ϕ_2	$-0.7906 \times s^0 + 2.3717 \times s^2$
ϕ_3	$-2.8062 \times s^1 + 4.6771 \times s^3$
ϕ_4	$0.7955 \times s^0 - 7.955 \times s^2 + 9.2808 \times s^4$
ϕ_5	$4.3973 \times s^1 - 20.5206 \times s^3 + 18.4685 \times s^5$

9.2.3. Statistical analyses

Once the normalized Legendre Polynomials were calculated for the age of dam of all records. Data were analyzed using the following model:

$$y = Xb + Z_1h + Z_2p + Z_3m + Z_4u + e$$

where:

- y is a vector of weights at 90 days.
- b is a vector of systematic effects that include:
  - a covariate with age of calves at recording.
  - a sex effect (2 levels).
  - one regression coefficient for each normalized orthogonal polynomial for the age of the dam.
- h is a vector of herd year season effects (9,689 levels).
- p is a vector of random regression coefficients for the maternal permanent. environmental effects (21,673 levels x number of orthogonal polynomials).

- **m** is a vector of random regression coefficients for the additive genetic maternal effects (85,670 levels x number of orthogonal polynomials).
- **u** is a vector of additive genetic direct effects (85670 levels).
- **e** is a vector of residuals.
- **X, Z₁, Z₂, Z₃** and **Z₄** are the corresponding incidence matrices.

The vector **h** was treated a random variable, assuming a Gaussian distribution as follows:

$$\boldsymbol{h} \sim N(0, \boldsymbol{I}\sigma_h^2),$$

where σ_h^2 represents the variance associated with the herd-year-season effects, and **I** denote the identity matrix. The assumption of randomness was made due to the limited availability of phenotypic information for the majority of herd-year-season groups.

The assumed distribution of the vector **u** was:

$$\boldsymbol{u} \sim N(0, \boldsymbol{A}\sigma_u^2),$$

where **A** represents the numerator relationship matrix and σ_u^2 denotes the direct additive genetic variance.

The assumed distributions of the random regression coefficients for the permanent environmental effects (p) were as follows:

$$\boldsymbol{p} \sim N(0, \boldsymbol{I} \otimes \boldsymbol{P}),$$

where $\otimes$ is the Kronecker product, **P** is the matrix of the permanent environmental (co)variances associated with the normalized orthogonal polynomials.

Similarly, the assumed distribution of the random regression coefficients for the maternal genetic effects (**m**) was:

$$\boldsymbol{m} \sim N(0, \boldsymbol{A} \otimes \boldsymbol{M}),$$

where the matrix **M** represents the maternal genetic (co)variances associated with the normalized orthogonal polynomials. Furthermore, the residuals (e) were assumed to

follow a Gaussian distribution with zero mean and variance σ_e^2. It is important to note that the dimensions of the **P** and **M** matrices, as well as the **p**, **m**, and **b** vectors, depend on the number of orthogonal polynomials included in the analysis.

A total of 27 models were implemented by defining the number of regression coefficients (4 to 6), the number of random regression coefficients for the permanent maternal environmental effects (4 to 6) and for the random regression coefficients for the maternal genetic effect (4 to 6). The estimation of the variance components was carried out with aireml algorithm (Gilmour et al., 1995) after 100 iterations with the EM algorithm (Dempster et al., 1977). It was performed with the BLUPF90+ software (Misztal et al., 2018). To adapt the data to the format used by this software and to create the parameter file for this purpose the software RENUMF90 was used.

The variance components were estimated by restricted maximum likelihood (REML) using the VCE function of BLUPF90+ and models were compared with the Akaike information criterion (AIC) (Akaike, 1974). AIC is an information criteria-based relative fit index that was developed as an approximation of out-of-sample predictive accuracy of a model given the available data. Like BIC, AIC's deviance term is based on the log-likelihood (also known as the log predictive density; Boykin et al., 2023) given the maximum likelihood point estimate (Akaike, 1974).

9.2.4. Interpretation of the results

Once the best model has been selected, the effects of the age of dam, as well as the permanent environmental and maternal genetic variances, can be calculated for each point within the parametric space (600 to 6000 days). For each age point (a_i), equations (1) and (2) can be used to generate the set of coefficients $\boldsymbol{\Phi_i} = (\Phi_{1i}, \Phi_{2i}, \ldots, \Phi_{Nbi})$, where *Nb* represents the number of orthogonal polynomials for that age. Subsequently, the effect the age of dam at *ith* age (ad_i) linked to that particular point can be obtained by performing a matrix product between the vector of the estimates of the covariates associated with each orthogonal polynomial ($\hat{c}_i$) and the vector $\boldsymbol{\Phi_i}$ as:

$$\widehat{ad_i} = (\widehat{c_1} \quad \widehat{c_2} \quad . \quad \widehat{c_{Nb}}) \begin{pmatrix} \Phi 1i \\ \Phi 2i \\ . \\ \Phi Nbi \end{pmatrix} \qquad (3)$$

Further, the permanent environmental ($var(p)_i$) and maternal genetic variance ($var(m)_i$) at the *ith* age points was:

$$var(p)_i = (\Phi 1i \quad \Phi 2i \quad . \quad \Phi Npi) \begin{pmatrix} \widehat{\sigma_{p_1}^2} & \widehat{\sigma_{p12}} & . & \widehat{\sigma_{p1Np}} \\ \widehat{\sigma_{p12}} & \widehat{\sigma_{p_2}^2} & . & \widehat{\sigma_{p2Np}} \\ . & . & . & . \\ \widehat{\sigma_{p1Np}} & \widehat{\sigma_{p2Np}} & . & \widehat{\sigma_{p_{Np}}^2} \end{pmatrix} \begin{pmatrix} \Phi 1i \\ \Phi 2i \\ . \\ \Phi Npi \end{pmatrix} \qquad (4),$$

and

$$var(m)_i = (\Phi 1i \quad \Phi 2i \quad . \quad \Phi Nmi) \begin{pmatrix} \widehat{\sigma_{m_1}^2} & \widehat{\sigma_{m12}} & . & \widehat{\sigma_{m1Np}} \\ \widehat{\sigma_{m12}} & \widehat{\sigma_{m_2}^2} & . & \widehat{\sigma_{m2Np}} \\ . & . & . & . \\ \widehat{\sigma_{m1Np}} & \widehat{\sigma_{m2Np}} & . & \widehat{\sigma_{m_{Np}}^2} \end{pmatrix} \begin{pmatrix} \Phi 1i \\ \Phi 2i \\ . \\ \Phi Nmi \end{pmatrix} \qquad (5)$$

In this equation, $\widehat{\sigma_{p_i}^2}$ and $\widehat{\sigma_{m_i}^2}$ represent the estimated values of the permanent environmental and genetic maternal variances associated with the *ith* orthogonal polynomial. Additionally, $\widehat{\sigma_{p_{iJ}}}$ and $\widehat{\sigma_{m_{iJ}}}$ denote the estimated values of the permanent environmental and genetic maternal covariances between the *ith* and *jth* orthogonal polynomials.

Further, the calculation of the permanent environmental ($cov(p)_{ij}$) and maternal genetic covariance ($cov(m)_{ij}$) between to age points (i and j) is as follows:

$$cov(p)_{ij} = (\Phi 1i \quad \Phi 2i \quad . \quad \Phi Npi) \begin{pmatrix} \widehat{\sigma_{p_1}^2} & \widehat{\sigma_{p12}} & . & \widehat{\sigma_{p1Np}} \\ \widehat{\sigma_{p12}} & \widehat{\sigma_{p_2}^2} & . & \widehat{\sigma_{p2Np}} \\ . & . & . & . \\ \widehat{\sigma_{p1Np}} & \widehat{\sigma_{p2Np}} & . & \widehat{\sigma_{p_{Np}}^2} \end{pmatrix} \begin{pmatrix} \Phi 1j \\ \Phi 2j \\ . \\ \Phi Npj \end{pmatrix} \qquad (6)$$

And

$$cov(m)_{ij} = (\varPhi 1i \quad \varPhi 2i \quad . \quad \varPhi Nmi)\begin{pmatrix} \widehat{\sigma_{m_1}^2} & \widehat{\sigma_{m12}} & . & \widehat{\sigma_{m1Np}} \\ \widehat{\sigma_{m12}} & \widehat{\sigma_{m_2}^2} & . & \widehat{\sigma_{m2Np}} \\ . & . & . & . \\ \widehat{\sigma_{m1Np}} & \widehat{\sigma_{m2Np}} & . & \widehat{\sigma_{m_{Np}}^2} \end{pmatrix}\begin{pmatrix} \varPhi 1j \\ \varPhi 2j \\ . \\ \varPhi Nmj \end{pmatrix} \quad (7)$$

These variances and covariances was used to calculate the permanent environmental $(Cor(p)_{ij})$ and maternal genetic correlation $(Cor(m)_{ij})$ between two specific age points (i and j) as:

$$Cor(p)_{ij} = \frac{cov(p)_{ij}}{\sqrt{var(p)_i var(p)_j}} \quad (8)$$

and

$$Cor(m)_{ij} = \frac{cov(m)_{ij}}{\sqrt{var(m)_i var(m)_j}} \quad (9)$$

Finally, the prediction of maternal breeding value $(\widehat{bv(m)}_{ij})$ for the *ith* individual at the *jth* age was calculated as:

$$\widehat{bv(m)}_{ij} = (\widehat{m_{\iota 1}} \quad \widehat{m_{\iota 2}} \quad . \quad \widehat{m_{\iota Nn}})\begin{pmatrix} \varPhi 1j \\ \varPhi 2j \\ . \\ \varPhi Nmj \end{pmatrix}$$

Here, $\widehat{m_{\iota J}}$ represents the prediction of the maternal additive genetic effect associated with the *jth* orthogonal polynomial and for the *ith* individual.

9.3. Results and discussion

9.3.1. Model comparison

The results of the model comparison, based on the Akaike information criteria (Akaike, 1974) calculated using the blupf90+ software, are presented in Table 6 for the 27 proposed models.

Table 6. Results of the AIC criteria for the 27 proposed models.

Nb	Np	Nm	AIC
4	4	4	537595.97
4	4	5	537591.53
4	4	6	537586.06
4	5	4	537551.11
4	5	5	537549.29
4	5	6	537562.24
4	6	4	537556.95
4	6	5	537550.26
4	6	6	537556.21
5	4	4	537560.48
5	4	5	537552.72
5	4	6	537547.63
5	5	4	537547.09
5	5	5	**537538.86**
5	5	6	537543.32
5	6	4	537553.41
5	6	5	537549.14
5	6	6	537551.88
6	4	4	537560.78
6	4	5	537542.98
6	4	6	537548.11
6	5	4	537548.08
6	5	5	537539.84
6	5	6	537544.28
6	6	4	537545.75
6	6	5	537545.63
6	6	6	537552.63

The model that showed the best fit included 5 orthogonal polynomials for the age of dam effect, the permanent environmental effect, and the maternal genetic effects. It is important to note that the choice of model depends on the data, as the AIC procedure selects the best model by balancing model complexity and the available information. From this point onwards, all the results will refer to this selected model.

9.3.2. Age of Dam effect

The impact of the age of the dam on the weight at 90 days was determined using equation (3), utilizing the solutions for the covariates associated with the 5 orthogonal polynomials of the selected model. Figure 21 displays the plot depicting the age of the dam effect across the entire range of possibilities (600-6000).
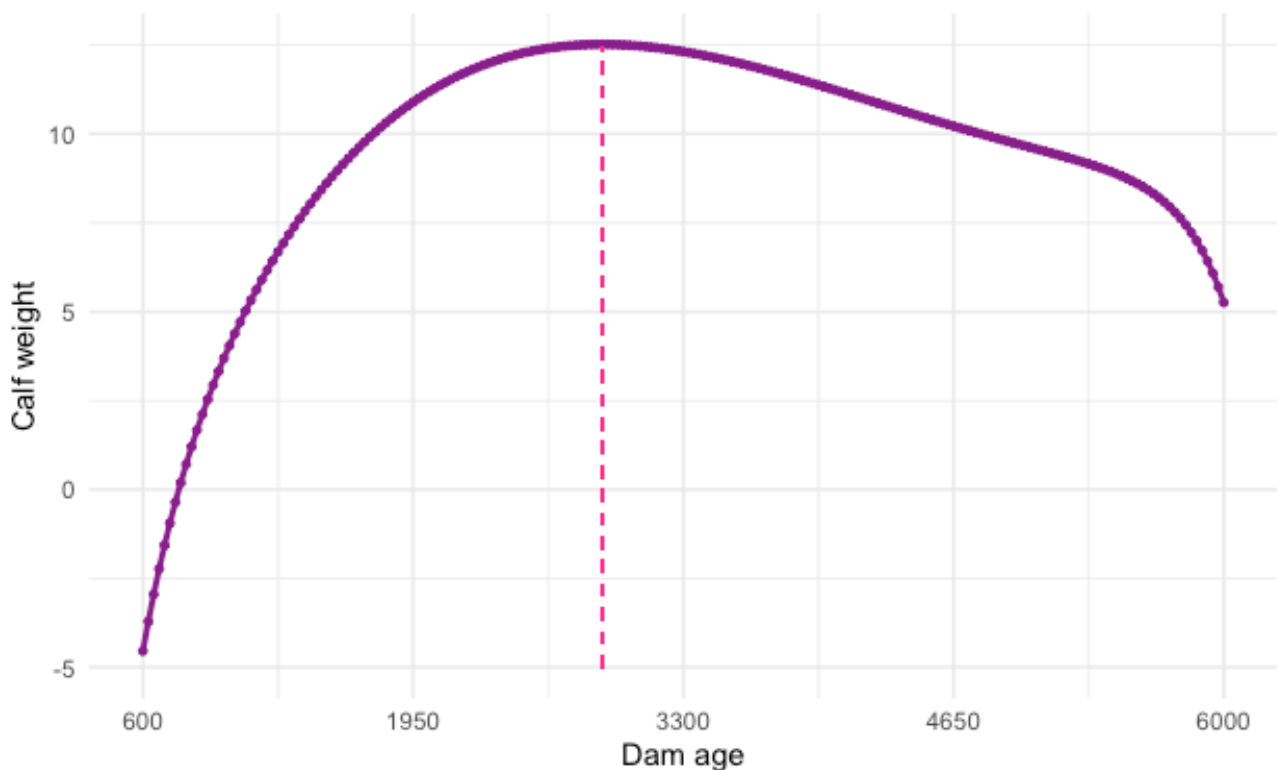

Figure 21. Evolution of dam's age effect: The graphic represents in axes y the dam performance over lactation decomposed into 5 normalized Legendre polynomials, in axes x the range of age considered in days.

The figure reveals that the age of the dam effect is worst in very young dams and rapidly increases until reaching a peak at around 2900 days (approximately 8 years), followed by a gradual decline. These findings align closely with previous studies in the field. For instance, age-of-dam effects were found to be statistically significant (P < 0.01) for weaning weight of calves born to 4- to 9-year-old Angus and Hereford cows bred with different sires such as Hereford, Angus, Red Poll, Brown Swiss, Galabieh, Maine-Anjou, and Chianina (Gregory et al., 1978). Additionally, it was observed that cows between the ages of 7 to 10 years old produced the highest weaning weight calves, with the age of the dams showing a significant correlation (p<0.05) (Bahashwan, 2016). Furthermore, milk supply has been identified as the most influential factor impacting weaning weight (Davis et al., 1983). Various studies have indicated that milk production increases with the age of the dam and decreases in older dams (Arthur et al., 1993). Therefore, the observed changes in calf weight with the age of the dam can likely be attributed to variations in milk production throughout the dam's lifespan (Robison et al., 1978; Swali & Wathes, 2006).

9.3.3. Variance component estimation

Estimates of variance and covariance components were obtained using the Restricted Maximum Likelihood (REML) method, employing the aireml algorithm (Gilmour et al., 1995). An animal model was fitted, incorporating all available pedigree information (Meyer, 1994). The REML estimates for the additive genetic, herd-year-season, and residual variances were 237.08 Kg^2. 174.18 Kg^2 and 252.10 Kg^2, respectively. Furthermore, the estimates for the maternal permanent environmental and maternal genetic (co)variances were:

$$\hat{P} = \begin{pmatrix} 51.167 & 10.999 & -13.060 & 3.7216 & -2.0283 \\ 10.999 & 25.178 & -4.9197 & -5.7162 & -10.030 \\ -13.060 & -4.9197 & 3.7580 & 1.4905 & 0.57489 \\ 3.7216 & -5.7162 & 1.4905 & 16.914 & -4.0961 \\ -2.0283 & -10.030 & 0.57489 & -4.0961 & 7.1427 \end{pmatrix},$$

And

$$\widehat{M} = \begin{pmatrix} 99.499 & 17.273 & -4.9133 & -5.1928 & -0.91938 \\ 17.273 & 19.138 & -5.2222 & -3.2590 & -2.8784 \\ -4.9133 & -5.2222 & 12.269 & -4.5427 & 2.2107 \\ -5.1928 & -3.2590 & -4.5427 & 5.1312 & -2.6334 \\ -0.91938 & -2.8784 & 2.2107 & -2.6334 & 3.7733 \end{pmatrix},$$

All of these estimates need to be converted into the maternal permanent environmental variance and the maternal genetic variance corresponding to each specific age.

9.3.4. Maternal permanent environmental variance

The variation of the maternal permanent environmental variance across the parameter range (600-6000 days) is depicted in Figure 22. It was computed using formula (4), utilizing the REML estimates of the maternal permanent environmental (co)variance linked to the 5 Legendre polynomials.
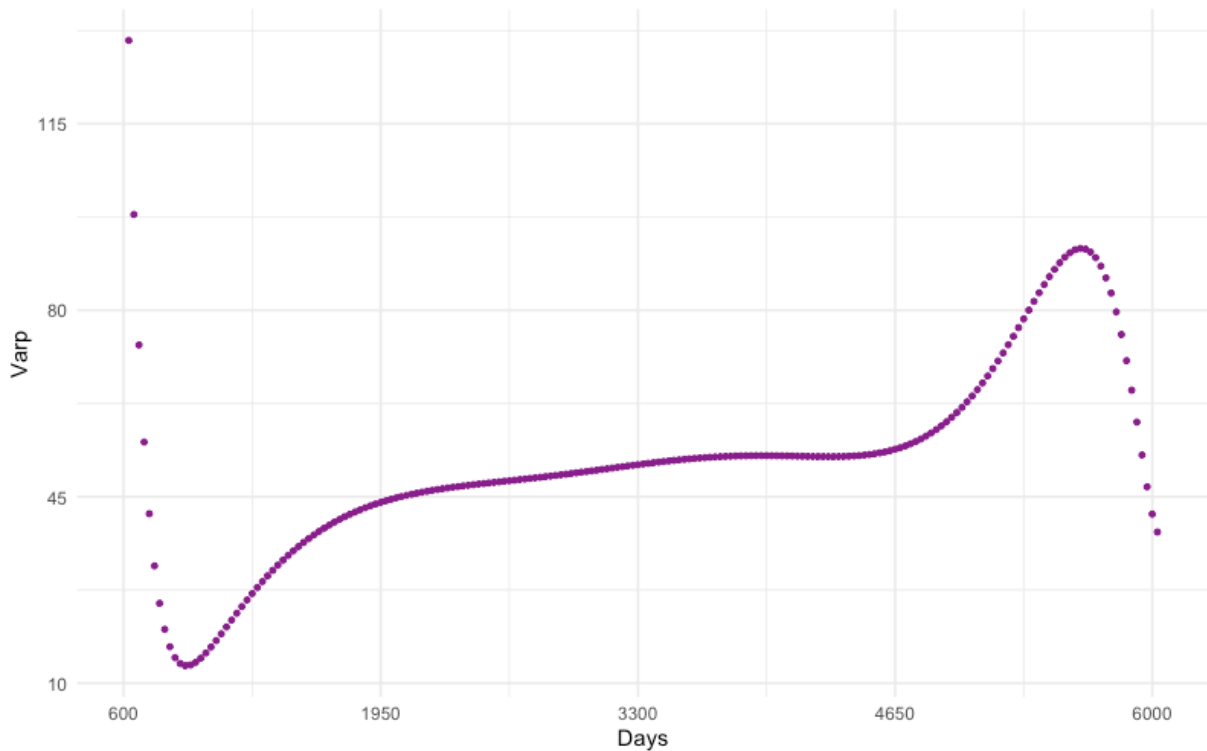

Figure 22. Estimates of the maternal permanent environment variance between 600 to 6000 days of age.

It is important to observe that the maternal permanent environmental variance remains relatively stable between approximately 1900 to 4600 days (around 5 and 13 years). In younger dams, there is a decreasing negative trend, while from around 650 days of age (around 2 years), it experiences a rapid initial increase followed by a continuous growth. In older dams, it sharply increases from 4700 days (around 13 years) and then starts to decrease again. However, it is essential to note that the estimates near the boundaries of the parameter range provide less reliable information. This outcome suggests that the magnitude of the non-genetic influence from the dam remains relatively constant within a broad range of the parameter space.

9.3.5. *Maternal genetic variance*

Similarly, equation (5) was utilized to compute the maternal genetic variance across the range of ages, employing the REML estimates of the maternal genetic (co)variances associated with the 5 Legendre polynomials. The resulting plot is presented in Figure 23.
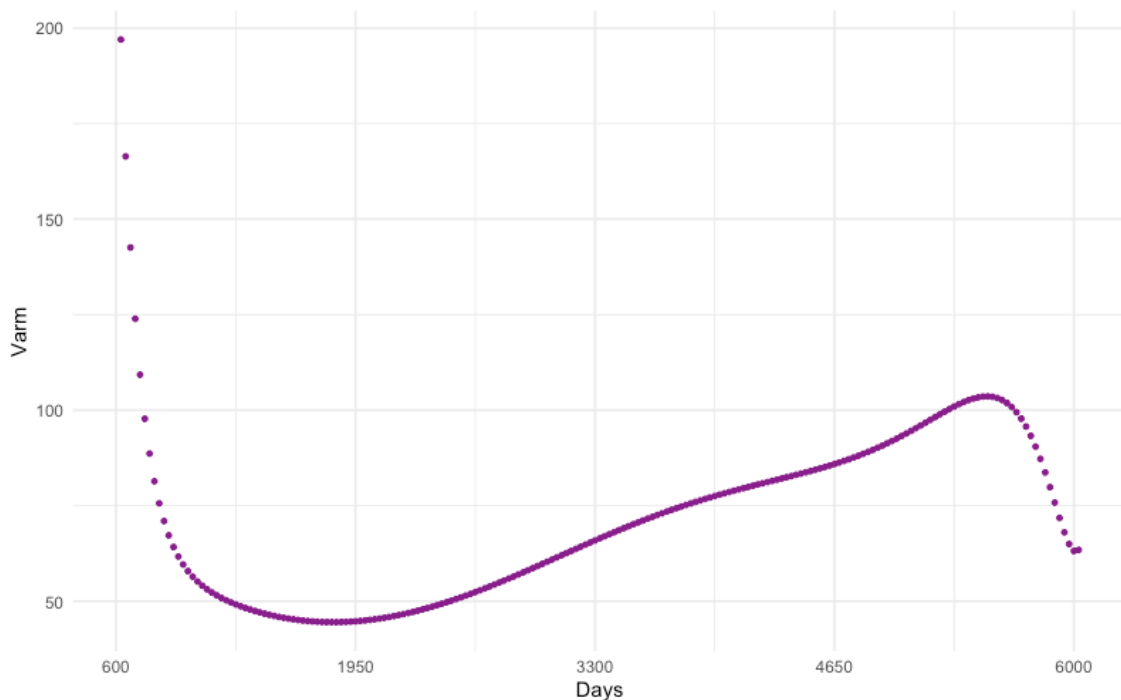

Figure 23. Estimates of the maternal genetic variance in according of dam age.

Despite the extreme values observed at the beginning and end of the parameter range, it is evident that the maternal genetic variance exhibits a consistent upward trend with the age of the dam. Specifically, it increases steadily from around 1900 days (approximately 5 years) to 5500 days (approximately 15 years) in very old dams, and then starts to decline again. This rise in the maternal genetic variance signifies that the genetic variability of the maternal genetic effect is smaller when cows are young compared to when they are older. The increase in variability can be attributed to the greater genetic diversity associated with maintaining milk yield as cows age.

9.3.6. Heritability

Given these estimates, the evolution of the direct (h^2) and maternal heritability (m^2) along the parametric space are presented in Figures 24 and 25.
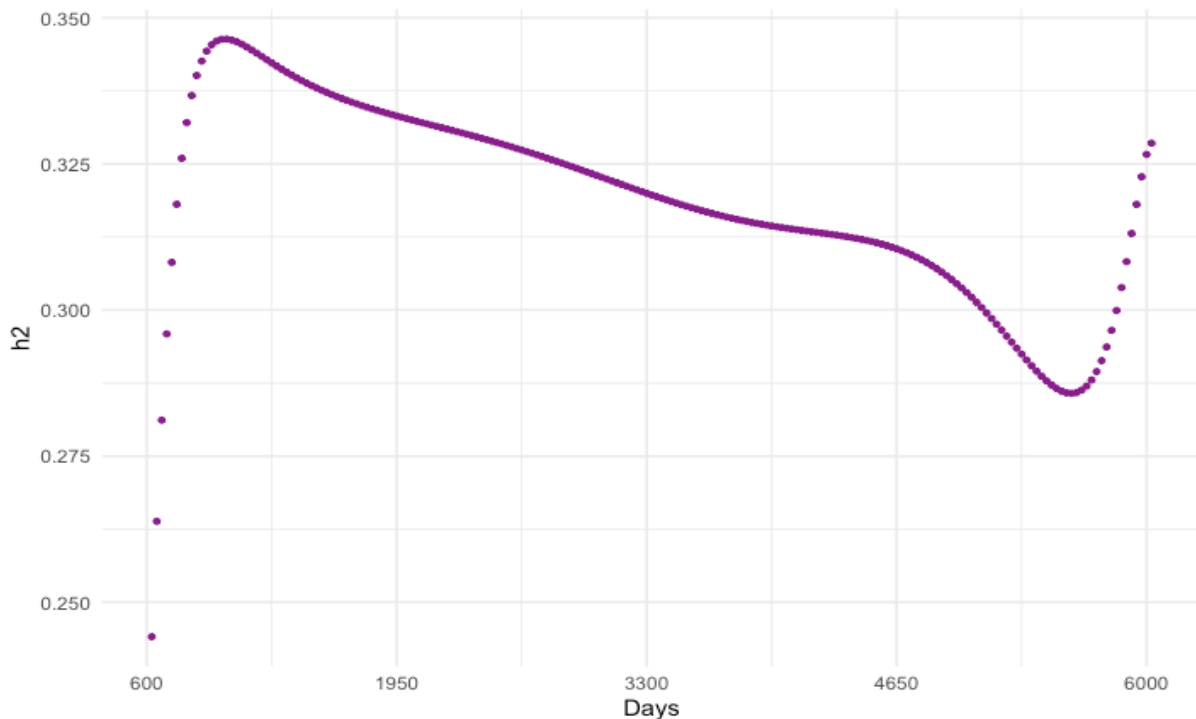

Figure 24. Estimation of direct hereditability in according of dam age.

The direct heritability showed a slight decline with dam's age, resulting from an increase in maternal genetic variance. Its values ranged between 0.24 at 600 days and 0.35 at 1030 days, but it remained above 0.30 across most of the studied parameters. These findings align with other estimates of direct heritability for weight at 90 days (Cortés-Lacruz et al., 2017) and weaning weight (Gutiérrez et al., 2007) in Spanish populations and international populations (Chud et al., 2014; Meyer, 1997; Rumph et al., 2004; Santana Jr. et al., 2013; Van Vleck et al., 1996) while not reaching the same magnitude as the ones acquired through Kaps et al (2000) and Lopez et al (2020).
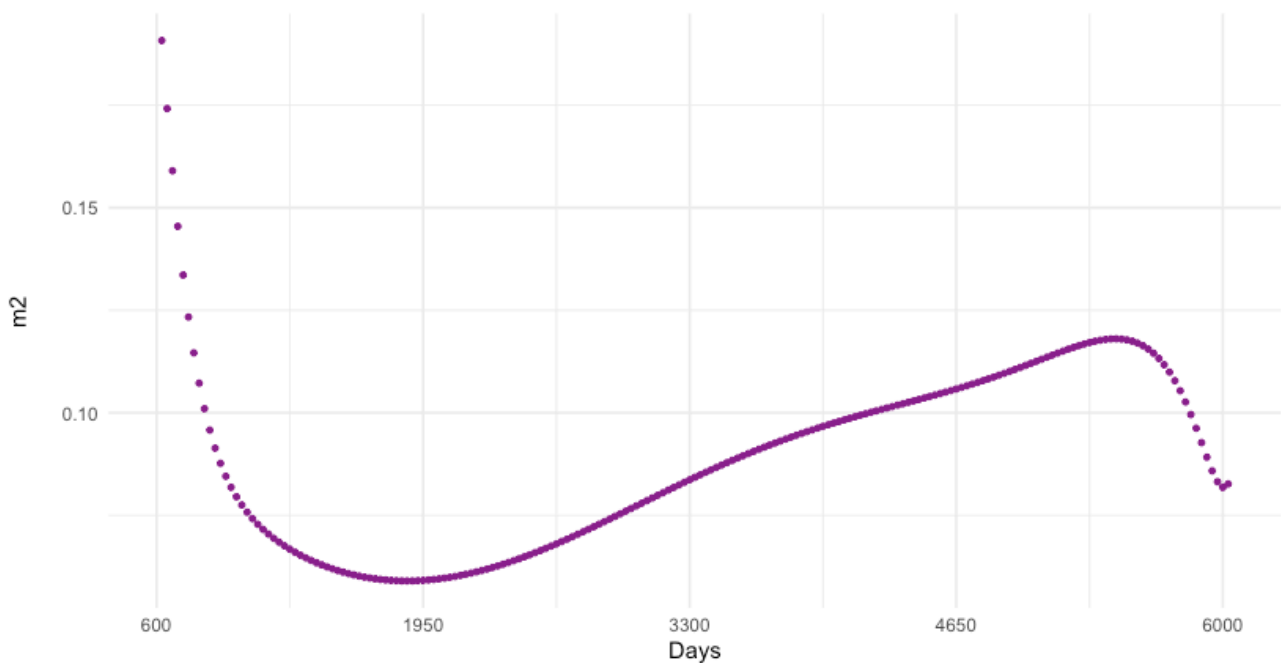

Figure 25. Estimation of maternal heritability (m^2) in according of dam age.

Regarding maternal heritability, it increases as the cow ages. The average estimate was approximately 0.08, with a range from 0.06 to 0.13. These results are consistent with estimates from other beef cattle populations (Chud et al., 2014; Gutiérrez et al., 2007; Meyer, 1992, 1997; D. L. Robinson, 1996; Tosh et al., 1999). The estimates were larger than those reported by Cortés-Lacruz (2017) but smaller than the ones obtained by Choi (2005) for the Hanwoo population. Our findings indicate that weight at 90 days is influenced by both the genetic composition of the calf and the genetic effects associated with the dam. The direct heritability is greater than the maternal heritability, but

61

potential improvements can be achieved by selecting either for the direct breeding values or the maternal ones.

9.3.7. Genetic Correlations

Based on the REML estimates of M and P, equations (6) and (7) were utilized to calculate the covariance between points of the dam's age. Furthermore, formulas (8) and (9) were applied to compute the maternal genetic and permanent environmental correlations between all points of the dam's age, which are presented in Figures 26 and 27.
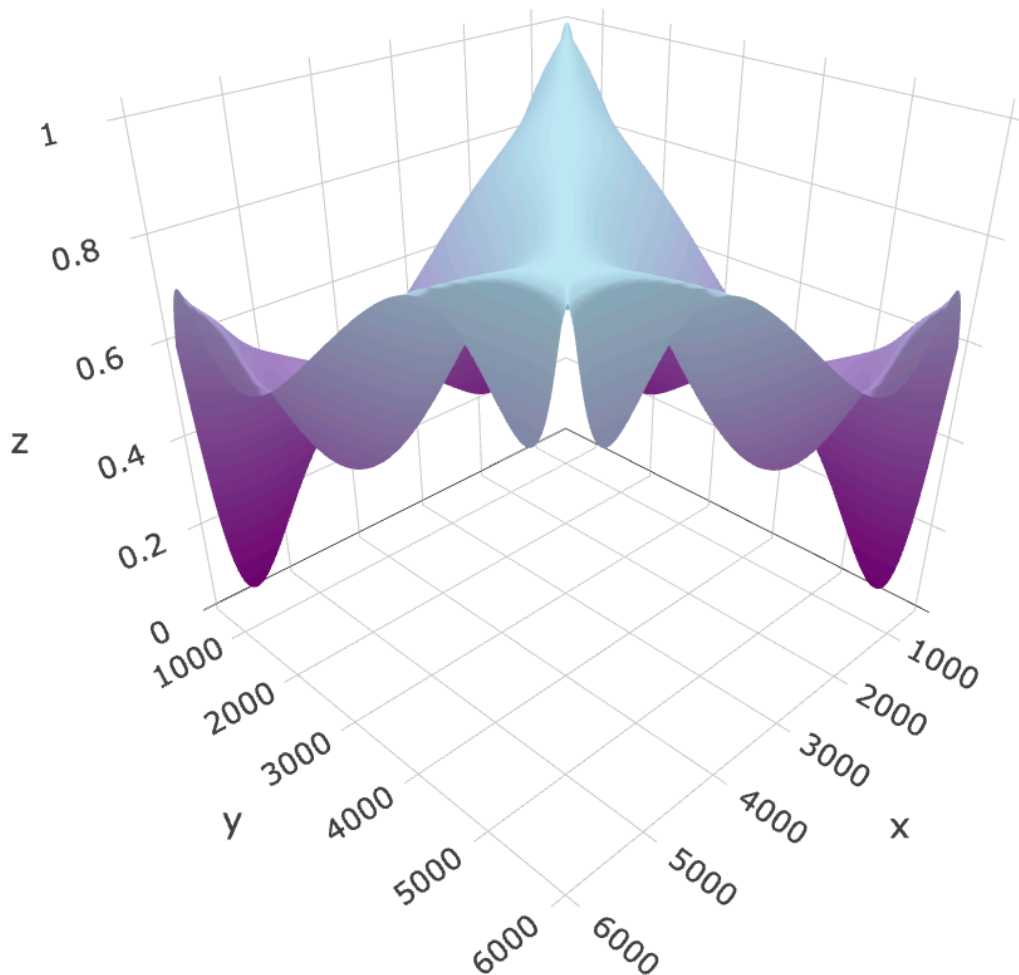

Figure 26. Correlation between all maternal genetic variance possibilities. Web page: Variance_correlation(m)
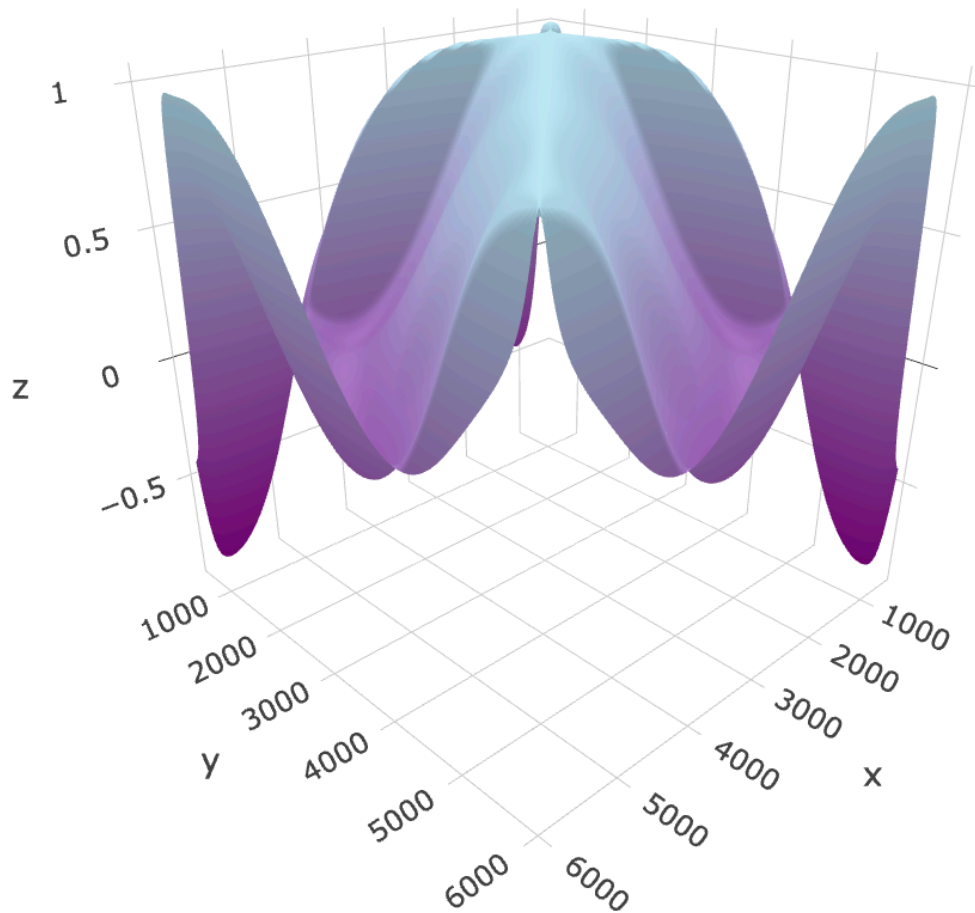
Figure 27. Correlation between all maternal permanent environmental effect variance possibilities. Web page
Variance.correlation(p)

As expected, the correlations were perfect (1) between adjacent ages but decreased as the distance between ages increased. Specifically, Table 2 displays the maternal genetic and permanent environmental correlations for 10 pre-defined ages ranging from 500 to 5500 days, with intervals of 500 days.

Table 7. Maternal genetic correlation (upper side) and maternal permanent environmental correlation (lower side) between 10 ages of dam (1000, 1500, 2000, 2500, 3000, 3500, 4000, 4500, 5000 and 5500 days of age).

	1000	1500	2000	2500	3000	3500	4000	4500	5000	5500
1000	1	0.8764	0.7145	0.5726	0.4733	0.4207	0.4075	0.4232	0.4546	0.4835
1500	0.9376	1	0.9399	0.8080	0.6689	0.5627	0.5030	0.4891	0.5134	0.5576
2000	0.9977	0.9627	1	0.9544	0.8566	0.7553	0.6757	0.6243	0.5959	0.5771
2500	0.9764	0.8332	0.9501	1	0.9687	0.9029	0.8307	0.7611	0.6892	0.6045
3000	0.8534	0.6199	0.7995	0.9453	1	0.9794	0.9320	0.8662	0.7750	0.6483
3500	0.6543	0.3708	0.5803	0.7951	0.9474	1	0.9841	0.9376	0.8507	0.7103
4000	0.4342	0.1517	0.3513	0.5932	0.8104	0.9523	1	0.9824	0.9184	0.7898
4500	0.2394	0.0135	0.1612	0.3796	0.6145	0.8140	0.9478	1	0.9743	0.8806
5000	0.1040	0.0013	0.0487	0.1783	0.3631	0.5661	0.7578	0.9199	1	0.9634
5500	0.0704	0.1422	0.0571	0.0357	0.0898	0.2147	0.3986	0.6321	0.8792	1

In table 7, it can be observed that the maternal genetic correlations decrease to values lower than 0.5 (for example, between 1000 days and 4000 days), and the maternal permanent correlations were even lower, reaching values very close to zero (for instance, between 1500 days and 5000 days).

The reduction of genetic correlations between maternal genetic effects at distant age points aligns with the findings of previous studies (Espinoza, 2014; Jakobsen et al., 2002; Wellnitz et al., 2022; Williams et al., 2022) that demonstrated similar trends in genetic correlations for milk yield traits across the dam's lifespan over time. It is important to note that the genetic correlation between early age points (i.e., 1000 days) and older age points reached lower values (around 0.40-0.50). This consistency is in line with the results of Carlén et al (2004) and Mrode & Swanson (2003), which also showed that the genetic correlation between the first lactation and subsequent ones was

lower compared to the correlation between lactations over the second. The reason for this difference can be attributed to the fact that cows are not fully mature during their first lactation.

9.3.8. *Maternal Breeding values*

The structure of maternal genetic variances and covariances described above implies that the maternal genetic breeding values of individuals change along the parametric space. Estimated breeding values (EBVs) differ at each age of dam point, and with this information, it is possible to modify the selection criteria, particularly when selecting sires of dams. The choice of a dam from a given sire in a particular herd depends on the productive system employed (Bijma, 2006). In other words, maternal performance can vary depending on the expected longevity of future cows. To illustrate this phenomenon, Figure 28 displays the estimated maternal EBV estimates of seven selected sires as a function of Legendre polynomial estimates.
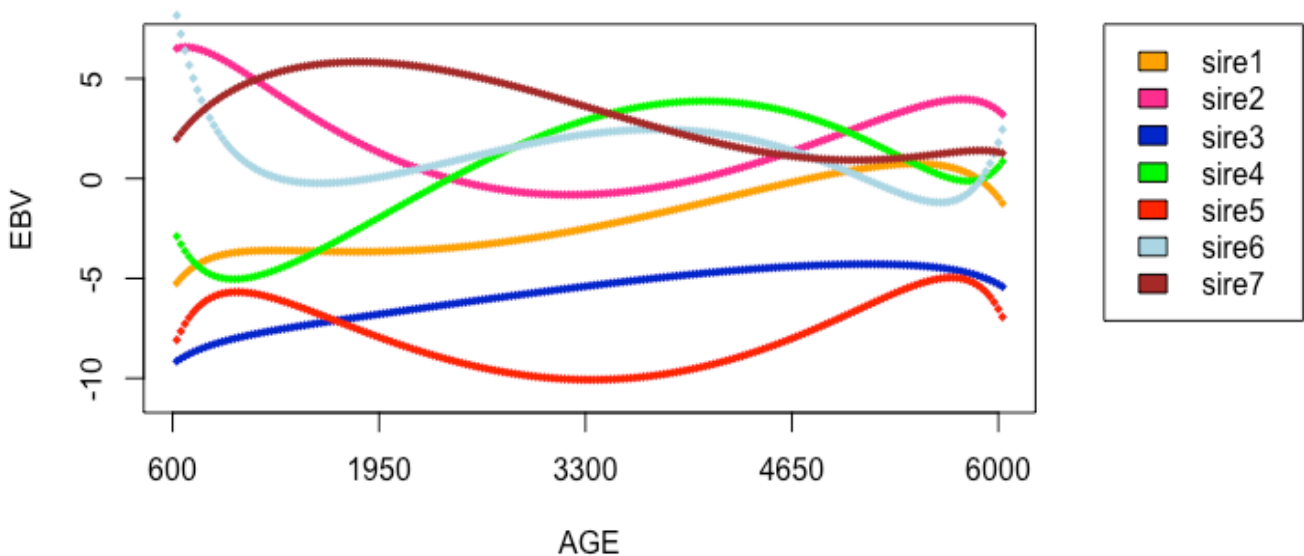

Figure 28. EBV variation, along the y-axis, of seven different sires, for maternal genetic effects, adjusted for different ages recorded in days, along the x-axis.

The weaning weight maternal Estimated Breeding Value (EBV) of a bull indicates his daughters' ability to produce calves with higher weight at 90 days. In Figure 28, it is evident that the EBV values vary at each age point and do not follow the same pattern for all sires. For example, sire 4 exhibits a negative slope during the early ages, with an inflection point around day 1000 where the trend changes to a positive one, continuing until it reaches a peak near day 4500, and then displaying a slow decline. On the other hand, sire 5 shows an opposite pattern, with an initial rapid increase in EBV, followed by a decreasing phase from day 1000 to the midpoint of our parameter range, around day 3300, and finally, an increase again afterwards. These varying trends in the maternal EBV of different sires suggest that their daughters' maternal abilities to produce heavy calves differ across different age points. It highlights the importance of considering the specific characteristics of each sire's progeny and how they perform at various stages of the dam's age, which can inform more targeted and effective breeding decisions to enhance weight at 90 days in the herd. At this point, to optimize selection for maternal effects, it is essential to study the age distribution at calving of the cows in each specific case. Let's consider a hypothetical scenario with two herds, where only the semen of bulls 2 and 4 from Figure 28 is available. Different selection decisions can be made based on the specific characteristics of each farm.

In one of the farms, if cows are typically removed from the third calving (around 2000 days), the best selection decision would be to use bull "2." This is because bull "2" exhibits a positive trend in EBV from the early ages and continues to show improvement until the midpoint of the parametric space, which aligns better with the calving pattern of the cows. On the other hand, if calving is more frequent in older animals in the other farm (e.g., in a mountain or traditional cattle system), the best selection decision would be to use bull "4", that shows a negative slope during the early ages, a change in trend at around day 1000, an EBV that increases until around day 4500, which allow this bull to be more suitable for the older animals' calving pattern.

These considerations demonstrate the importance of tailoring the selection decisions based on the specific age distribution at calving in each farm, and how it can be influenced by factors like management practices, environmental conditions, and the overall reproductive strategy implemented. Nevertheless, the distribution of calving ages can vary across different herds. As a result, the "total" maternal breeding value is expected to differ between herds with different management practices. The proposed model offers flexibility in selecting new dams based on their specific patterns of parity distributions. This adaptability allows breeders to make more customized and suitable selection decisions depending on the particular characteristics and goals of each herd's management.

10. CONCLUSIONS.

The results of this study lead to the following conclusions:

1. The age of the dam has a non-linear impact on the weight at 90 days of the calves.
2. In the Pirenaica beef cattle population, the direct heritability of weight at 90 days is higher than the maternal heritability.
3. The maternal additive genetic variance (and the maternal heritability) varies along the productive life of the cow, showing a slight increase with age.
4. The genetic correlation between adjacent age points is very high, but it decreases between distant age points.
5. The genetic correlation of maternal effects at early ages with the maternal effects at older ages is below 0.50.
6. The maternal breeding value varies along the age of the dam.
7. The optimization of the selection strategy must consider the age distribution of the herd or the population.

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