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The impact of genetic selection for increased production on fitness traits of small ruminants

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ABSTRACT

Many sheep and goat breeds worldwide are subjected to high levels of selection emphasis to increase production of meat, milk and fibres. The continuous selection on a small number of traits have resulted in unintended consequences, mostly as adverse effects on the fitness of animals. Selection for increased dairy production led to an increase in mastitis incidence, while selection for increased meat yield impacted on the prevalence of *MSTN* and *CLPG* mutations. Reproduction efficiency is the single most important trait in any small ruminant production system. Selection for increased litter sizes in small ruminants has resulted in increased numbers of triplet and quadruplet pregnancies, with an associated increase in mortalities and reproductive wastage. To optimize a genetic response, a balanced approach should be followed to set breeding objectives that include some of these fitness traits. Selection for increased resilience to even one stressor (such as mastitis) could result in an improvement of overall robustness. As the accurate recording of health and welfare traits is currently a limitation, mitigation strategies should include the generation of novel phenotypes which could also be included in genomic solutions to address the current shortcomings of breeding programs.

1. Introduction

Small ruminants, including both sheep and goats, were amongst the first livestock species to be domesticated approximately 10,000–12,000 years ago (Jackson et al., 2020). Their movement followed that of human dispersal to the Far East and westwards to Europe and Africa (Zheng et al., 2020). Early management and selection practices included culling, polling and castration, which resulted in the establishment of new phenotypes suited to human needs. The main production purpose of these species was firstly as a food source, followed by fibre production several hundred years later.

Modern goats are spread across five continents, and exceed 1 billion animals, of which 55.4 % and 38.7 % are respectively found in Asia and Africa (Mazinani and Rude, 2020). This follows the expected dispersion pattern of animals with superior adaptability to harsh environments, that are expected to thrive in extensive production systems (Amills et al., 2017). Similarly, 43.6 % of the 1.1 billion global sheep population is found in Asia, and 30 % in Africa (Mazinani and Rude, 2020). Sheep and goats are some of the most diverse species to be farmed across the world, due to the range of adaptive characteristics that they express and their ability to produce in almost any ecological region, such as deserts, mountainous or tropical areas (Amills et al., 2017). Although small ruminants are found in a wide range of agrological and geographic regions, they are mostly farmed with in the tropical and sub-tropical areas of the world. In Africa and Asia, indigenous goats and sheep are often kept due to their superior adaptive characteristics. These breeds are commonly found in poorly-resourced communities and marginal environments. On the other hand, intensified small ruminant dairy production systems are found in developed countries, such as France and Italy in Europe, Canada as well as the USA.

Both sheep and goats produce a range of products, including meat, milk and fibres and this multifunctionality leads them to contribute to economic development and food security at various levels within the socio-economic structure of different countries (Mazinani and Rude, 2020; Lu, 2023). The roles of small stock in society are manifold, from providing food security and improved livelihoods, to inclusion in cultural rites and religious ceremonies. The high levels of per capita consumption of sheep and goat products underlines the importance of efficient production, continuous genetic improvement and sustainable management of these species.

Indigenous breeds are still mainly kept and farmed with in developing countries in Africa, Asia and South America with the main purpose of providing food security, while commercial breeds are intensively farmed with for meat, milk and fiber production. Additionally, sheep are

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typically more subjected to high selection pressure as they are more commonly found in commercial systems, compared to goats. As artificial selection has had a more pronounced effect on commercial breeds, this review will focus on the effect of intense genetic selection on commercial breeds, and specifically on the unintended consequences of the selection process.

2. Importance of the small ruminant industry

Small ruminant species are primarily kept for meat production. In 2020, the world meat goat population was estimated at 495 million animals. Meat production from goats increased by 20 % from 2010 to 2020, resulting in more than 6 million metric tonnes of goat meat produced in 2020 (Lu, 2023). Although more meat was produced over this period, the efficiency with which it was produced decreased worldwide on average by 0.5 %, while the efficiency increased by 5.3 % in the Americas (Lu, 2023). Some goat breeds, such as the Boer goat, are dispersed across the world, while many smaller indigenous or locally-developed breeds and populations also contribute to this sector. Table 1 gives an indication of the trends in small ruminant meat and dairy production over the past two decades.

Mutton production is the main production focus of most sheep farmers, having replaced wool production. Global sheep meat production is approximately 9 million tonnes, with annual per capita consumption at about 1.7 kg (Mazinani and Rude, 2020). Australia and New Zealand have historically been acknowledged as the major exporters of sheep meat, while China is the top consumer (46 % of all sheep meat) and importer of the product (Mazinani and Rude, 2020; Ramírez-López et al., 2020). Demand for sheep meat is linked to both the size of the Muslim population in a country, as well as the purchasing power of the general population (Ramírez-López et al., 2020).

Approximately 21 % of the 2200 million sheep and goats found worldwide are found in the dairy production industry (Pulina et al., 2018; Mazinani and Rude, 2020). The global dairy goat population exceeded 220 million animals in 2020 (Libera et al., 2021). Global goat milk production has increased by 12 % over the period 2007–2020, with approximately 21 million metric tonnes of goat milk produced in 2020 (Lu, 2023). A small number of goat breeds (including the Toggenburg, Saanen and Alpine) dominate the goat dairy industry. Dairy sheep and goats together produce about 3.5 % of the global milk product (Pulina et al., 2018). Most sheep and goat milk is not consumed directly, but is processed for either self-consumption or to become part of a high-end value chain.

Table 1
Trends in global small ruminant production from 2000 to 2020 (adapted from Dubeuf et al., 2023).

Product	2000	2010	2020
Sheep meat (million tonnes)	7.48	8.35	9.81
Goat meat (million tonnes)	3.8	5.14	6.28
Sheep milk (million tonnes)	8.32	9.98	10.4
Goat milk (million tonnes)	13.5	17.5	21.0

Fibres produced by small stock, including wool, mohair and cashmere, have become niche products due to the global dominance of synthetic fibres in the textile industry. Wool production has become a secondary industry to mutton production, and is dominated by Asia, Australia and New Zealand. The annual global clean wool production amounts to approximately 1.2 million kg (Zenda et al., 2024). Mohair and cashmere are produced in much smaller quantities by goats and are regarded as luxury fibres. These fibres contribute less than 0.1 % to the global fibre production industry, but nonetheless play an important role in the high-value-added apparel market due to their unique characteristics, such as softness and lustre (Hunter, 2020).

3. Genetic improvement of small ruminants

Genetic improvement has made significant contributions to an increase in livestock performance over time. For these improvements to be significant, they need to be cumulative, permanent and sustainable (Berry et al., 2022). Most breeding programs focus on the selection of superior parent stock on the assumption that superior matings will on average result in offspring out-performing the current generation. It is of importance to ensure that these superior matings do not compromise the genetic variation within a population, and that the genetic relatedness between the parents (and thus inbreeding) be managed carefully. The increases in homozygosity that is associated with inbreeding, results in the well-described phenomenon of inbreeding depression, which adversely impacts fitness traits such as reproduction, survivability and adaptation in all livestock species (Visser et al., 2023).

Genetic improvement has historically been based on quantitative principles where individuals with superior phenotypes or trait values

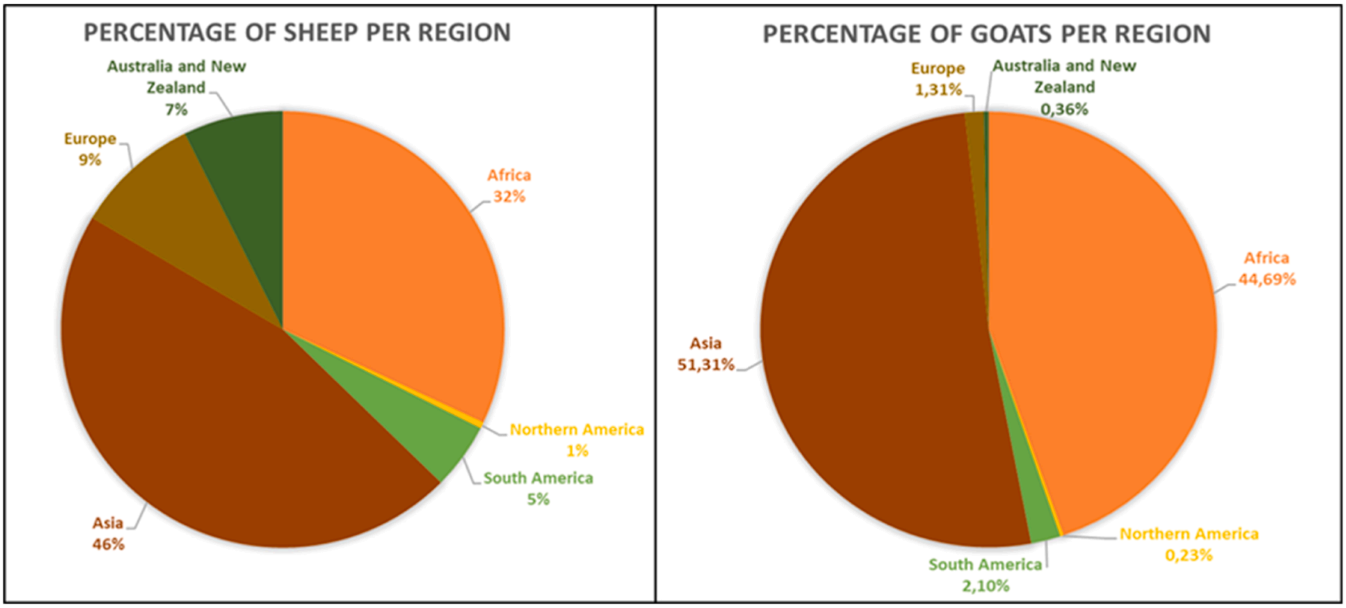

Fig. 1. Dispersal of small ruminants across the six main regions worldwide (based on FAOSTAT, 2024).

were chosen to become parents (Dodds et al., 2007). Some small ruminant breeds have more recently made use of advanced technology to accurately estimate the genetic potential of their animals. However, accurate phenotypic and pedigree information is necessary to be able to apply mixed model procedures to calculate estimated breeding values (EBVs). As such, only seedstock and commercial breeders in countries with animal improvement schemes have been able to reap the benefits of these techniques.

Annual genetic gain within a population is commonly presented using the following equation:

$$\Delta G = \frac{r \times i \times \sigma_g}{lg}$$

Where ΔG is the annual genetic response, r is the accuracy of selection, i is the selection intensity, σ_g is the genetic variance and Ig is the generation interval (Bourdon, 2000). Each of these parameters has an impact on the rate of genetic change. The accuracy of selection is dependent on both the heritability of the trait, as well as the information available. An infinitesimal (and usually additive) model of inheritance is assumed for most traits of economic importance, which means each trait is influenced by a considerable number of genes each with an infinitely small effect. The proportion of the total variance described by these genes are referred to as the heritability of the trait (Dodds et al., 2007). Selection on traits with higher heritability values, such as milk yield or weaning weight (heritability values of 0.27 and 0.32, respectively; Mucha et al., 2022), will show faster progress in a population, and are thus often popular traits for breeders to select for.

Using a data-driven approach by selecting for traits that are moderate to highly heritable, as well as easily and cost-effectively measurable could, however, result in sacrificing traits associated with adaptation and survivability, as highlighted by Garrick and Golden (2009). Although selection emphasis for higher productivity in traits such as milk, wool and carcass yields have resulted in valuable genetic gains, certain adverse consequences such as mastitis, reproductive failure and an increase in diseases have also been observed.

Successful selection programs for sheep and goats are less common than for the cattle industry. Specific countries such as Ireland (Berry et al., 2022), France (Astruc et al., 2022), Australia (Bates et al., 2023) and New Zealand (Johnson et al., 2021), to name a few, has very successful and effective sheep breeding programs. However, well-organized improvement programs in goats are mostly limited to Europe, North America and Australia (Amills et al., 2017 Astruc et al., 2022; Massender et al., 2022). Within meat production systems for both sheep and goat, selection emphasis is typically divided between reproduction and growth traits. Dairy related traits (milk yield, protein and fat content, somatic cell count and udder morphology) are only of consequence in relatively small dairy sheep populations, and in the North American and European milk goat industries. Across all systems, birthing performance also rates high in terms of selection emphasis. Animal health and welfare traits typically rate quite low and are poorly represented in breeding objectives of small ruminants (Berry et al., 2022).

Countries with successful, effective small ruminant recording and improvement programs, have commonly implemented genomic selection for one or both of these species. This practice of incorporating genome wide genotypic information into breeding values estimation, have resulted in a much faster rate of genetic improvement, specifically in hard-to-measure, sex-limited and lowly heritable traits (Berry et al., 2022). Furthermore, genomic information contributes to the improved understanding of the genetics underlying traits of economic importance and the consequences of selection on genomes (Massender et al., 2023). Genomic selection has been successfully implemented in i.e. Australian (Wicki et al., 2024), British (McLaren et al., 2018), Chinese (Wang et al., 2024) and Irish (Berry et al., 2022) sheep for traits ranging from udder conformation to fibre diameter and live weight. In goats, genomic selection has been mostly limited to dairy breeds such as the Alpine and Saanen breeds in Canada (Massender et al., 2022), France (Arnal et al., 2023), Italy (Negro et al., 2024) and New Zealand (Scholtens et al., 2021). Researchers agree that the implementation of genomic selection in small ruminants will improve the accuracy of estimated breeding values, resulting in increased rates of gain across traits. More animals entering the respective reference populations, and cost-efficient higher density SNP arrays will contribute to the impact of genomic selection on this industry.

4. Unintended consequences of artificial selection for production traits

Data-driven selection for production traits resulted in the improvement of diverse traits such as milk yield, body weight and litter size in small ruminants, with little regard to the ability of the animals to cope with environmental stressors, or their general robustness and longevity (Mucha et al., 2022). Previously reported genetic antagonisms between production, fertility and health traits suggest that a balance between selection criteria is necessary to avoid sacrificing the well-being of high producing animals. In general, fewer disorders and causal variants have been identified in small ruminants than in cattle. Table 2 gives an indication of the limited research that has been performed in terms of identifying causal variants for Mendelian traits and diseases in small ruminants, as reported by Online Mendelian Inheritance in Animals (OMIA).

Adverse consequences that are associated with artificial selection differ between the various production types, and will thus be discussed with regards to specific breeding objectives and selection criteria per type.

4.1. Selection for increased milk production

Worldwide, milk produced by sheep and goats have doubled over the last five decades (Pulina et al., 2018). While milk yield ranges widely between breeds, countries and production systems, it remains the most economically important trait within dairy systems and thus the one on which most selection pressure is put. As this data-driven breeding objective for increased yield was pursued, genetic progress of up to 6.0 L/year was reported (Mucha et al., 2022). However, a genetic antagonism between milk yield and mastitis resistance has been well described in dairy cattle (Tolone et al., 2013). As higher milk yields are pursued, the udder health of the cattle is compromised, leading to increased culling and a detrimental impact on longevity (Banos et al., 2019). Tolone et al. (2013) and Martin et al. (2018) confirmed that this unfavourable genetic correlation between milk yield, udder morphology and mastitis also exist in dairy sheep and goats, respectively. Libera et al. (2021) reported that between 70 % and 90 % of ewes presenting with clinical mastitis episodes, were culled.

Although many individual studies report heritability estimates for dairy production traits in small ruminants, little research has been done

Table 2

A summary of inherited disorders, other (single-locus) traits, and associated genes and variants in Taurine cattle, sheep and goats (https://omia.org/home/, accessed 1 October 2024).

	Taurine cattle	Sheep	Goats
Traits (phenes)			
All traits: disease and non-disease	693	324	126
All Mendelian traits: disease and non-disease	310	128	26
With at least one known causal variant	210	64	17
Mendelian diseases	272	92	12
With at least one known causal variant	191	46	8
Variants (mutations)			
All known likely causal variants for all Mendelian traits: disease and non-disease	275	92	21
All known likely causal variants for Mendelian diseases	248	52	9

on the correlations and associations between milk production traits and resilience. Inconsistent results for the genetic correlations between these traits in dairy sheep have been reported, ranging from favourable to unfavourable (Banos et al., 2019). Mucha et al. (2022) performed a meta-analysis of genetic parameters to investigate these, and concluded that an unfavourable relationship exists between milk production traits and somatic cell score (as an indicator of mastitis) in dairy sheep. Although a contradictory result was reported for dairy goats in the same paper, this latter result was based on limited data (only two studies) and need further investigation. It is however important to note that somatic cell count has a lower ability to predict mastitis in goats than in either cattle or sheep (Rupp et al., 2011). Most scientific results conclude that the inclusion of a selection criteria for enhanced resistance to mastitis will not adversely affect milk yield in dairy producing small ruminants.

Mastitis can also have an adverse impact on meat-producing small ruminants. Clinical symptoms such as swelling and pain have a direct economic impact on a meat-producing flock in terms of lighter lambs, premature culling of ewes and increased veterinary costs (McLaren et al., 2018). Yearly economic losses due to mastitis in a UK Texel flock were estimated to be as high as £ 2.7 million (Conington et al., 2008). As somatic cell scores are difficult to measure in meat-producing animals, McLaren et al. (2018) suggested the use of udder and teat conformation scores could be useful in these production environments, as longer and wider udders were associated with higher infection levels.

Apart from the relatively obvious correlation between milk yield and mastitis, an unfavourable genetic correlation between milk yield and fecal egg count has been reported. This has implications as resistance to several anthelmintic drugs has been reported, and only one of them (namely eprinomectin) is allowed during lactation with no withdrawal period for milk (Aguerre et al., 2022). Although contradictory results have again been reported in the limited number of studies investigating this correlation in dairy sheep, unfavourable correlations may indicate a genetic antagonism between milk production and immune response (Aguerre et al., 2022). This highlights the need to include adaptation and welfare traits into a breeding objective, to prevent sacrificing these traits for the sake of increased production.

4.2. Selection for increased meat production

In both meat sheep and goats, increasing meat production is an important economic breeding objective. Webb and Casey (2010) have extensively reviewed the impact of continuous selection for growth on carcass and meat traits. A number of genes have been identified that affects carcass yield and meat quality in sheep (Cockett et al., 2005; Tellam et al., 2012), of which the callipyge (*CLPG*) and myostatin (*MSTN*) loci are the most well-known.

MSTN (also known as growth and differentiation factor 8, *GDF8*) is a well-known major gene causing the double muscling phenotype in a range of species. This highly conserved gene is a negative regulator of skeletal muscle mass, and variants causes the enlargement of muscles (Aiello et al., 2018). The higher incidence observed in mutations in the *MSTN* gene across species (cattle, sheep, goats, dogs, and horses), is indicative of intensive artificial selection for growth and frame size. The double muscling phenomenon has been particularly well-described in cattle, where it is associated with high carcass yield, but also with respiratory disease, lameness, heat stress, longer gestations resulting in higher birth weight, and thus higher incidence of dystocia (Bellinge et al., 2005; Aiello et al., 2018). Naturally occurring variants are rare in both sheep and goats, but has been shown to cause the double muscling phenotype in Texel, Charollais and Norwegian sheep (Tellam et al., 2012; Aiello et al., 2018), as well as in *MSTN*-edited animals (Kalds et al., 2023). Additionally, various *MSTN* variants has been shown to influence growth and carcass yields favourably in i.e. Indian Madras sheep (Sahu et al., 2017), Savak Akkaraman sheep (Kar et al., 2024), Latvian sheep (Trapina et al., 2024) and Tibetan sheep (Zhao et al., 2024). Although an increase in birth weight were reported in these studies, no specific higher incidence of dystocia has been mentioned.

The *CLPG* locus is also associated with muscular hypertrophy in sheep and has been linked to higher dressing percentages and improved lean yield in e.g the American Dorset (Tellam et al., 2012). However, this mutation does not affect all muscle groups, as *MSTN* does – but has the greatest impact on the *longissimus dorsi* and *semimembranosus* muscles (Tellam et al., 2012). As the phenotype only develop after birth, there is also no adverse effect on birthing ease, and no accompanying dystocia. The *CLPG* mutation is however associated with tougher meat (Cockett et al., 2005). Cramer et al. (2018) postulated that this could be linked to anti-apoptotic activities in callipyge lamb meat.

4.3. Selection for increased litter size

Reproductive efficiency is widely recognised as one of the key drivers of profitability in farming systems (Abdoli et al., 2016). Small ruminants globally are kept in a wide range of production systems, but the majority is farmed in harsh, extensive systems with seasonal limitations in terms of nutrition and water availability, as well as generally low managerial inputs. Despite these challenges, the demand for increased intensification and production has led to a drive for increased reproductive performance (Notter, 2012). Although fertility traits such as ovulation rate, age at first parity and litter size are generally lowly heritable (Safari et al., 2005), sufficient genetic variation exists within and between populations to support acceptable rates of genetic improvement. High prolificacy can however be an unfavourable trait under extensive production conditions with limited resources (Gootwine et al., 2006; Notter et al., 2018).

Selection emphasis has focused on increasing maternal production and efficiency by increasing lamb output per ewe (Fetherstone et al., 2021), or other indicators of litter size such as litter size at weaning (Notter, 2012; Cottle et al., 2016) across breeds and production systems. Selection for twinning results in an increase in frequency of triplet and quadruplet pregnancies (Cottle et al., 2016; Notter et al., 2018) and thus, successful selection for prolificacy has resulted in increased mortality rates up to weaning, as well as decreased survival of females during lactation (Cottle et al., 2016). Offspring born from larger litter sizes (more than singles), suffer from a lack of sufficient nutrition, hypoxia and oxidative stress during pregnancy (Gootwine, 2020). These adverse effects result in especially triplet and quadruplet lambs born with low birth weights and decreased chances of survival. Reproductive wastage such as neonatal, perinatal and postnatal mortalities has been reported to be a major welfare concern (Gootwine, 2020; Smith et al., 2023). Offspring that do survive typically take longer to attain target market weights (Cottle et al., 2016).

The introgression of major genes, such as mutations in *BMPR1B* or *GDF9*, in a breeding program in an effort to increase prolificacy has been well documented (Abdoli et al., 2016). Unfortunately, some of these mutations (e.g. $FecG^T$) causes sterility in homozygous ewes (Notter, 2012). Even when this is not the case, breeding with homozygous ewes in commercial flocks could lead to high lamb mortality rates, as it has an unfavourable correlation with birth weight (Gootwine, 2020) as well as a lower mature body size of the ewes (Gootwine et al., 2006). Furthermore, carrier lambs have been reported to have poor post-weaning performance (Gootwine et al., 2006).

5. Future breeding strategies

5.1. Improved breeding objectives and selection criteria

In order to address the fitness issues that have been introduced mainly due to high selection pressures, the breeding objectives of small ruminants need to be balanced to obtain an optimized genetic response across various trait types. Selecting for the latter group of traits does not only aim to address a specific stressor or disease, but also to improve the general wellbeing of the animals. This will especially be true in the climate change environment that will impact production systems at all levels.

Goats are well-known for their superior adaptation and ability to withstand high temperatures. In the face of climate change, their natural ability to adapt to harsh environments might however be challenged, resulting in lowered yields and immune responses (Sejian et al., 2021). Measures that are used to indicate welfare during heat stress include vocalization, skin temperature, rectal temperature and production parameters (i.e. growth, milk yield or reproduction efficiency). Apart from the routinely measured production traits, the other traits are not often recorded and can thus not be used in a general breeding and selection program. The use of novel traits, such as physiological measures (e.g. respiratory rate, body temperature) or biomarkers (e.g. creatinine, glucose levels) are often difficult to measure and expensive – and thus not included in routine animal recording (Ramón et al., 2021). Despite these challenges, Ramón et al., 2021 concluded that breeding strategies should place low to moderate emphasis on weather resilience components to allow animals to maintain homeostasis and limit production losses during climate change.

Care should be taken to align reproductive efficiency goals per breed with the resources available, both in terms of environmental conditions and managerial support (Notter, 2012). The rate of decline in birth weight as litter size increases is influenced by the breed of sheep (Gootwine, 2020). Uterine capacity could thus play an important role in this phenomenon and should be investigated as a source of within-breed variation when selecting for increased prolificacy. Various genetic approaches have been suggested to attain optimal, rather than maximal, reproductive efficiency, such as using a multiple threshold-model by Cottle et al. (2016), or using crossbreeding or major genes to improve prolificacy (Gootwine, 2020).

Despite the enormous financial impact of specific diseases on the small ruminant industry, and the associated adverse effects thereof on the welfare of animals, only a few causative mutations have been identified for which direct selection can be performed. One such example was the successful identification of *CLCN1*, which is the variant causing myotonia congenita in Merino sheep (Manning et al., 2024). As not all diseases are under the control of major genes, the use of accurate, routinely measured phenotypes is necessary for selection based on estimated breeding values or genomic selection for these quantitative traits. A small number of important opportunities for selection for improved animal welfare will be discussed.

Gastrointestinal nematodes (GIN) is a challenging factor for small ruminant production throughout the world. It has an adverse impact on the profitability of production, but also on the increase in anthelmintic resistance and the general welfare of sheep and goats. As resistance to parasites have a genetic basis, selective breeding for improved resistance to GIN have been suggested as a long-term solution (Hayward, 2022). Common traits used to attain this breeding goal include faecal egg count (FEC), FAMACHA© scores and body condition scores (BCS). Of these, FAMACHA© and BCS are easy to measure and are moderately heritable (Dlamini et al., 2019; Hayward, 2022). Selecting for a combination of indicator traits which might differ between varying environments and production systems, could be valuable tool in mitigating the impact of parasites on small ruminants.

The susceptibility of dairy animals to infections of the udder has a genetic component, and it is thus possible to use within-breed selection for improved resilience or resistance. Selection could be performed on indirect measures of clinical mastitis, such as Somatic Cell Scores, but Banos et al. (2017) recommends a combination of these with clinical mastitis measurements. The use of Marker Assisted Selection or genomic selection could result in relatively fast genetic progress, but are also dependent on accurate phenotypic measures per dairy breed. Libera et al. (2021) proposed the use of novel biomarkers, such as acute-phase proteins, miRNAs and cathelicidins to improve the diagnosis of mastitis. However, these need further investigation, in terms of both practicality and financial suitability. Importantly, Ithurbide et al. (2022), reported that improved udder health was closely associated with functional longevity. Selection for increased resilience to a specific stressor could thus possibly provide benefits in terms of overall robustness and improved welfare of animals.

Footrot (primarily caused by *Dichelobacter nodosus*; Cinar et al., 2024) is one of the most common contagious hoof infections that is found in sheep and goats. The severity of the infestation varies greatly, but causes pain and adversely affects the normal behaviour, locomotion and feed intake of the affected animals (Cinar et al., 2024; Gaspar et al., 2024). Although the disease is widespread and has been known for almost two centuries, the genetic basis thereof is still not understood. Currently it is mostly managed using costly treatment and control measures, and a long-term sustainable solution is still needed. Although some genome wide analyses studies have been performed in an effort to investigate footrot susceptibility and identify causal mutations (Mucha et al., 2015; Niggeler et al., 2017; Cinar et al., 2024; Gaspar et al., 2024), it generally only served to highlight the complexity of the trait. Nonetheless, including some footrot phenotypes as routine measurements in breeding strategies (making use of either estimated breeding values or genomic selection), should result in the breeding of animals that are genetically less susceptible to the disease.

Scrapie is deadly contagious disease, belonging to the transmissible spongiform encephalopathies (TSEs) (Pakpahan et al., 2023). The highly conserved *PRPN* gene encodes for the prion protein. Several polymorphisms within the gene have been described and have been closely linked to scrapie susceptibility (Rodríguez-Andrade et al., 2023). Genetic selection for the resistant allele and the eradication of the susceptible alleles has been shown to be highly effective in managing this disease. Based on genotypic classification of the resistant vs. susceptible alleles, five risk groups which are used as several scrapie control measures were identified by the European Union (Bordin et al., 2020). Although the actual prevalence of scrapie in many other countries are not known, knowledge of the functional mutations responsible for susceptibility / resistance to the disease and the successful incorporation of this in breeding programs, has had a favourable impact on the health and welfare of small ruminants.

5.2. Use of new technologies

All successful breeding programs are dependent on the availability of pedigree and performance data. In general, participation of small ruminant producers in animal recording and improvement schemes (especially in developing countries) are less than that of cattle producers. This hampers the implementation of marker assisted as well as genomic selection practices. Although a number of putative QTL and candidate genes have been identified for health and welfare traits such as mastitis (Banos et al., 2017), udder conformation (Vermette et al., 2013) and heat stress (Abioja et al., 2023), their incorporation in routine breeding programs have been limited. Genomic selection has been implemented mostly in dairy goat and sheep populations, such as those in the United Kingdom, France, New Zealand, Spain and Canada. These programs still however mainly focused on milk yield traits, with little focus on inclusion of welfare traits. Genomic selection is challenging in the small ruminant industry, due to small flock / herd sizes, high costs and a lack of industry coordination (Massender et al., 2023), but could contribute significantly to the balanced improvement of small ruminant populations.

New technology to measure a range of different traits, including production, health and behaviour, of small ruminants could provide useful phenotypes to include in balanced breeding objectives. There is a wide range of tools available, including wearable and non-wearable sensors as well as injectable devices. For instance, temperature sensors could measure rectal, vaginal or rumen temperatures indicating fever, while accelerometers could provide feedback on lameness or sick animals (Caja et al., 2020; Odintsov Vaintrub et al., 2021). Caja et al. (2020) provided a comprehensive review on sensing technologies applied in the small ruminant sector. Applications that impacted the welfare of sheep and goats, included the use of rumen boluses to detect heat stress (Castro-Costa et al., 2015), accelerometers to detect lameness (Barwick et al., 2018), and acceleration loggers to estimate nutrient requirements (Miwa et al., 2015). Furthermore, thermal imaging using infrared cameras have been used to detect infectious diseases, such as hoof lesions, bluetongue and mastitis (Caja et al., 2020). Weighing scales were developed by Byrne et al. (2019) to detect foot rot in sheep. However, sensing technology also lags behind in terms of small ruminant applications when compared to that available for cattle. The development of cost-effective and user-friendly technologies for the small ruminant industry is necessary to improve the sustainability of this sector, specifically with regards to welfare management.

6. Concluding remarks

Data-driven selection has resulted in increased performance of most economically important traits in the small ruminant industry. This has however been accompanied by sacrifices to the animals' general fitness and wellbeing. Although a few health traits are included in some routine breeding programs, this is not the case for most systems. Innovative solutions are necessary to mitigate the effects of directional selection, while maintaining efficient production. The use of precision livestock farming technologies to generate novel phenotypes, in combination with genomic selection, could contribute to more optimised, balanced breeding objectives.

CRediT authorship contribution statement

Carina Visser: Writing – original draft, Conceptualization.

Declaration of Competing Interest

I wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome. I confirm that I have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. I am the Corresponding Author and the sole contact for the Editorial process. I have provided a current, correct email address which is accessible by me.

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