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Estimation of genetic parameters and derivation of economic weights for health and welfare indicators to improve breeding strategies in the Merinoland sheep population

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List of Abbreviations

Abbreviation	Full text
AHC	Agglomerative hierarchical clustering
AI	Artificial intelligence
BCS	Body condition score
BW	Birth weight
CAP	Common agricultural policy
CVM	Contingent valuation method
DAG	Dagginess score
EBV	Economic breeding value
EV	Economic value
FZC	Fuzzy clustering
GIN	Gastrointestinal nematodes
MEV	Marginal economic value
MFC	Major farm characteristics
MTM	Multiple-trait model
OBV	Overall breeding value
P	Profit
PAM	Partition around medoids
PR	Profitability ratio
PWW	Post weaning weight
QTL	Quantitative trade loci
REV	Relative economic value
SEM	Structural equation model
SL	Schwanzlänge
STM	Single-trait model
TL	Tail length
WTP	Willingness to pay
WW	Weaning weight

Zusammenfassung

Das Ziel dieser Arbeit ist es, die wissenschaftlichen und praktischen Grundlagen für eine nachhaltige Schafzucht durch die Integration genetischer, phänotypischer und wirtschaftlicher Perspektiven zu verbessern, wobei ein besonderer Schwerpunkt auf Gesundheits- und Tierwohlmerkmalen wie der Schwanzlänge liegt. In drei sich ergänzenden Studien untersucht diese Arbeit die genetische Architektur und die Wechselbeziehungen zwischen Schwanzlänge und Wachstumsmerkmalen bei Merinolandschafen (Kapitel 2), die Heterogenität deutscher Schafhaltungssysteme und ihre Auswirkungen auf die Priorisierung von Zuchtzielen (Kapitel 3) und die Entwicklung eines verbesserten bioökonomischen Modellierungsrahmens zur Ableitung ökonomischer Gewichte für ein breites Spektrum von Zuchtmerkmalen, einschließlich neuartiger Merkmale für Tierwohl und Krankheitsresistenz (Kapitel 4). Zusammen tragen diese Studien zu einem ganzheitlichen Verständnis darüber bei, wie wohlfahrtsorientierte Zuchtstrategien umgesetzt werden können, ohne die Produktionseffizienz oder die Wirtschaftlichkeit zu beeinträchtigen.

Die erste Studie liefert eine detaillierte quantitativ-genetische Analyse der Schwanzlänge (SL) und ihrer Zusammenhänge mit wichtigen Wachstumsmerkmalen. Unter Verwendung von Ein-Merkmal-, Mehrfachmerkmal- und Strukturgleichungsmodellen (SEM) zeigt die Studie, dass die SL in hohem Maße vererbbar ist, was auf ein starkes Potenzial für eine genetische Verkürzung der Schwänze als Alternative zum Schwanzkupieren hinweist. Wichtig ist, dass SEM-Ansätze zeigen, dass sich die phänotypischen Pfade, die die SL mit der Wachstumsleistung verbinden, von den zugrunde liegenden genetischen Korrelationen unterscheiden. Während die genetischen Korrelationen zwischen Schwanzlänge (SL) und Gewichtsmerkmalen positiv sind, was aus züchterischer Sicht auf antagonistische Beziehungen hindeutet, sind die SEM-basierten zeitverzögerten phänotypischen Effekte negativ. Das bedeutet, dass längere Schwänze das Wachstum beeinträchtigen können, da sie eine erhöhte Anfälligkeit für Kontaminationen und Infektionen mit sich bringen. Diese Ergebnisse unterstreichen die Bedeutung der Modellierung von Merkmalsabhängigkeiten nicht nur genetisch, sondern auch durch kausale phänotypische Pfade, die umwelt- und gesundheitsbezogene Risikofaktoren widerspiegeln. Die Studie schafft somit eine methodische und konzeptionelle Grundlage für die Integration von Tierwohlmerkmalen wie der Schwanzlänge in Zuchtprogrammen unter Berücksichtigung ihrer komplexen biologischen Zusammenhänge.

Aufbauend auf dieser genetischen Perspektive verlagert die zweite Studie den Fokus auf die Vielfalt der Haltungssysteme in der deutschen Schafzucht. Durch hierarchisches Clustering von 25 Schafbetrieben werden drei unterschiedliche Haltungssysteme identifiziert, die sich in Herdengröße, Produktionsausrichtung und Wirtschaftsweise (z. B. ökologisch vs. konventionell) unterscheiden. Unter Verwendung eines kontingenten Bewertungsansatzes leitet die Studie

clusterspezifische wirtschaftliche Gewichte für 12 Zuchtzielmerkmale ab, basierend auf der Zahlungsbereitschaft der Landwirte. Während die meisten Merkmale über alle Cluster hinweg eine ähnliche Bewertung aufweisen, zeigt die Futterverwertung erhebliche Unterschiede, was den Einfluss des Haltungssystems auf die wirtschaftliche Relevanz der Merkmale unterstreicht. Bemerkenswert ist, dass alle Cluster der Merkmalskategorie „Gesundheit und Tierwohl", einschließlich der Schwanzlänge, mit Werten zwischen 24% und 29% eine erhebliche Bedeutung beimessen. In einigen Clustern werden Merkmale des Tierwohls und der Tiergesundheit sogar noch vor Leistungsmerkmalen priorisiert. Diese Ergebnisse unterstreichen, dass moderne Zuchtziele auf die Merkmale des Haltungssystems zugeschnitten sein müssen und zunehmend die gesellschaftlichen und von den Landwirten geprägten Erwartungen hinsichtlich des Tierschutzes und funktioneller Robustheit widerspiegeln sollten.

Die dritte Studie vertieft die ökonomische Bewertung der Schafzucht, indem sie das bio-ökonomische Modell mit dem Softwarepaket ECOWEIGHT um Gesundheits- und Tierwohlmerkmale erweitert. Das erweiterte Programm ermöglicht die Integration von Krankheitsinzidenz, Behandlungskosten und Schwanzlänge auf Herdenebene, wodurch marginale und relative ökonomische Gewichte für 15 Zuchtmerkmale bei Merinolandschafen abgeleitet werden können. Fruchtbarkeit und Überlebensmerkmale erweisen sich als die wirtschaftlich einflussreichsten Merkmale, die zusammen den größten Teil des relativen ökonomischen Gewichts ausmachen. Im Gegensatz dazu tragen Gesundheitsmerkmale, Parasitenresistenz, Schwanzlänge und Produktionsmerkmale nur marginal zum ökonomischen Gesamtgewicht der untersuchten Forschungsherde bei, was vor allem auf deren außergewöhnlich hohen Gesundheitszustand zurückzuführen ist. Sensitivitätsanalysen, bei denen der Anteil kurzschwänziger Tiere verändert wurde, zeigen nur geringfügige Verschiebungen der ökonomischen Gewichte, was darauf hindeutet, dass eine auf das Wohlergehen ausgerichtete Züchtung für kürzere Schwänze ohne wesentliche wirtschaftliche Einbußen umgesetzt werden kann.

Zusammenfassend bieten die drei Studien einen umfassenden Rahmen für die Integration von Tierwohlmerkmalen, insbesondere der Schwanzlänge, in Schafzuchtprogrammen. Die genetischen Analysen zeigen die Machbarkeit der Selektion auf kürzere Schwänze und verdeutlichen gleichzeitig, wie wichtig es ist, phänotypische Pfade zu berücksichtigen, die mit Gesundheitsrisiken verbunden sind. Die Charakterisierung der Haltungssysteme unterstreicht, dass Tierschutzmerkmale von Landwirten zunehmend geschätzt werden und sich in den Zuchtzielen widerspiegeln sollten. Schließlich bestätigt die bio-ökonomische Modellierung, dass die Einbeziehung von Tierwohl- und Gesundheitsmerkmalen die wirtschaftliche Effizienz nicht beeinträchtigt und durch flexible Modellierungsinstrumente unterstützt werden kann, die komplexe Merkmalsmuster berücksichtigen können. Diese Arbeit trägt daher zur Entwicklung von Zuchtstrategien bei, die das genetische Potenzial, die wirtschaftliche Rentabilität und die gesellschaftlichen Erwartungen an einen verbesserten Tierschutz in der modernen Schafhaltung in Einklang bringen.

Summary

The aim of this cumulative dissertation is to advance the scientific and practical foundations for sustainable sheep breeding by integrating genetic, phenotypic, and economic perspectives, with a particular focus on health and welfare traits such as tail length. Across three complementary studies, this work investigates (chapter 2) the genetic architecture and trait interrelationships of tail length and growth traits in Merinoland sheep, (chapter 3) the heterogeneity of German sheep production systems and their implications for breeding goal prioritization, and (chapter 4) the development of an enhanced bio-economic modelling framework to derive economic values for a broad spectrum of breeding traits, including novel welfare and disease resistance traits. Together, these studies contribute to a more holistic understanding of how welfare-oriented breeding strategies can be implemented without compromising production efficiency or economic viability.
The first study provides a detailed quantitative-genetic analysis of tail length (TL) and its associations with key growth traits. Using single-trait, multiple-trait, and structural equation models (SEM), the study demonstrates that TL is highly heritable, indicating strong potential for genetic shortening of tails as an alternative to tail docking. Importantly, SEM approaches reveal that phenotypic pathways linking TL to growth performance differ from the underlying genetic correlations. While the genetic correlations between TL and weight traits are positive, suggesting antagonistic relationships from a breeding perspective, the SEM-based time-lagged phenotypic effects are negative. This implies that longer tails may impair growth due to increased susceptibility to contamination and infection. These findings highlight the importance of modelling trait interdependencies not only genetically, but also through causal phenotypic pathways that reflect environmental and health-related risk factors. The study thus establishes a methodological and conceptual foundation for integrating welfare traits into breeding programs while accounting for their complex biological relationships.

Building on this genetic perspective, the second study shifts focus to the diversity of production environments and management systems within the German sheep sector. Through hierarchical clustering of 25 sheep farms, three distinct production system types are identified, differing in herd size, production orientation, and management philosophy (e.g. organic vs. conventional). Using a contingent valuation approach, the study derives cluster-specific economic weights for 12 breeding goal traits based on farmers' willingness to pay for genetic improvement. While most traits show similar valuation across clusters, feed utilization exhibits significant differences, underscoring the influence of production context on economic trait relevance. Notably, all clusters assign substantial importance to the trait category "health and welfare," including tail length, with values ranging from 24% to 29%. In some clusters, welfare traits are prioritized even above performance traits. These results emphasize that modern breeding goals must be tailored to

production system characteristics and increasingly reflect societal and farmer-driven expectations regarding animal welfare and functional robustness.

The third study further deepens the economic evaluation by extending the ECOWEIGHT bio-economic model to incorporate health and welfare traits more explicitly. The enhanced model allows for the integration of disease incidence, treatment costs, and herd-level tail-length status, enabling the derivation of marginal and relative economic values for 15 breeding traits in Merinoland sheep. Fertility and lamb survival traits emerge as the economically most influential, collectively accounting for most of the relative economic value. In contrast, health traits, parasite resistance, tail length, and production traits contribute only marginally to overall economic value in the evaluated research herd, largely due to its exceptionally high health status. Sensitivity analyses altering the proportion of short-tailed animals reveal only minor shifts in economic values, suggesting that welfare-oriented breeding for shorter tails can be implemented without substantial economic trade-offs. The study also highlights the need for broader datasets representing more diverse production environments to ensure generalizable economic evaluations.

Taken together, the three studies provide a comprehensive framework for incorporating welfare traits, particularly tail length, into sheep breeding programs. The genetic analyses demonstrate the feasibility of selecting for shorter tails while revealing the importance of accounting for phenotypic pathways linked to health risks. The characterization of production systems underscores that welfare traits are increasingly valued by farmers and should be reflected in breeding goals. Finally, the bio-economic modelling confirms that incorporating welfare traits does not compromise economic efficiency and can be supported by flexible modelling tools capable of accommodating complex trait patterns. This cumulative work therefore contributes to the development of breeding strategies that align genetic potential, economic viability, and societal expectations for improved animal welfare in modern sheep production.

CHAPTER 1

General Introduction

1 Introduction

1.1 Tail length

1.1.1 Tail anatomy and function

Tail length in sheep is an important breeding trait and an increasingly important animal welfare issue. Sheep have between three and 24 tail vertebrae, which is highly breed dependent (Ellenberger & Baum, 2013). As part of a study on tail length, numerous malformations were found in Merino sheep, especially in the lower tail section, in addition to the number of 19 to 24 tail vertebrae (Haverkamp et al., 2015). The malformations mainly consist of one or more block vertebrae, i.e. a bony fusion of two or more vertebrae, which may involve only the vertebral bodies, the vertebral arches or the entire vertebra (Noden & Lahunta, 1985). Visually easily recognisable deformities, so-called buckling tails, are usually caused by malformed block vertebrae (Herzog, 2001; Hümmelchen et al., 2023).

While the ancestor of domestic sheep, the mouflon, has a naturally short, narrow tail, domestication and targeted breeding for high wool yield has resulted in many sheep breeds with much longer, densely woolly tails (Shelton, 1977). This originally had the advantage of maximizing the woolly body surface area and hence wool yield. However, as the economic importance of wool declined, the disadvantages of long tails, such as contamination and increased risk of disease (e.g. myiasis, dermatitis), became increasingly important (Mereu et al., 2024).

In sheep, the tail is mainly used for insect defense and can be actively moved by the animal. However, a long, woolly and dirty tail impairs mobility. Increased tail movement in the form of raising and lowering as well as wagging, also in combination, is possible (Kiley-Worthington, 1976).

1.1.2 Tail docking and reasons for the practice

The docking of sheep's tails is a practice that goes back centuries, and the main reasons for this procedure have not changed to the present day. The main reason is to prevent the infestation of maggots (myiasis) in the anal, vulva and inner thigh areas. Faeces can accumulate on the tail, which greatly increases the risk of fly infestation, especially in long-tailed, heavily wool-covered breeds of sheep. The flies lay their eggs in the contaminated wool and the eggs hatch into maggots, which cause severe damage to the tissues on which they feed and can cause considerable pain and even death to the animal if left untreated (Shephard et al., 2022). Various methods of docking have been used internationally, including cutting the tail with a knife, squeezing with docking pliers, twisting and cauterizing with hot pliers. However, these methods were often associated with significant blood loss, risk of infection and pain (Graham et al., 1947; French et al., 1994; Gascoigne et al., 2021).

Today, the only approved method in Germany is the rubber ring method, in which an elastic rubber ring is placed between the vertebrae using special forceps. The aim is to cut off the blood supply to the distal part of the tail. The strangulated part of the tail dies and falls off after a few days. This method is considered comparatively gentle but is still associated with acute pain and stress for the lambs, as evidenced by increased cortisol levels and restlessness (Hannemann et al., 2017).

1.1.3 Legal status

In Germany, the docking of sheep tails is regulated by the Animal Welfare Act. According to §5 and §6 of the Animal Welfare Act (TierSchG, 2006), the complete or partial amputation of body parts of vertebrates is generally prohibited. However, there are exceptions that are explicitly listed in the law, e.g. lambs may be docked with an elastic rubber ring until the 8th day of life. In the case of organically reared sheep in accordance with the EU Organic Regulation 889/2008 (Verordnung (EG) Nr. 889/2008, 2008), routine docking is also prohibited, and a special permit is required to justify the reason for this procedure. In addition, an anesthetic or analgesic must be administered after the procedure. There is no general authorization for tail docking in sheep in most countries.

According to the EU, there is no general authorization for tail docking in sheep. The EU leaves the specific formulation of the law to the Member States. For other species, such as pigs, EU Directive 2008/120/EC prohibits routine tail docking (European Union, 2008). Countries such as Finland and Sweden have a complete ban on tail docking for pigs, while there are no similarly strict regulations for sheep. In Switzerland, there are new regulations for the docking of lambs from 2025. These will require a minimum tail length of 15cm to be retained. However, there is also a transition period of 15 years to switch to breeding animals with shorter tails, until which time the docking of lambs under 8 days old is allowed without anaesthesia (Hannemann et al., 2017). Austria has set an age limit of 3 days for lambs. In addition, the personnel performing the procedure must be qualified. For lambs older than 3 days, veterinary anaesthesia is mandatory. The approved method is not the elastic rubber ring as in Germany, but a sharp cut with a knife. As in Switzerland, the length of the tail is also regulated, with a maximum of one third of the tail for fattening lambs and half of the tail for breeding animals. In the Netherlands, there has been a general ban on tail docking since 2008, and the procedure may only be carried out in individual cases if indicated by a veterinarian (Hannemann et al., 2017). Mulesing is a practice that is not permitted in Germany to prevent fly maggot infestation. This animal welfare practice is widespread in Australia, where strips of skin are removed from around the tail of young Merino lambs with little or no anesthetic. The method was developed in the 1920s and is still used today, particularly in Australia, the world's largest wool producer. It is estimated that around 10 million lambs are affected each year. Scientific studies show that Mulesing is associated with considerable pain and stress for the animals (Woodruff et al., 2020; Wilson et al., 2011). The procedure causes a sharp increase in the stress hormone cortisol, and lambs show significant pain behavior and reduced activity for days after the procedure (Bayerische Landesanstalt für Landwirtschaft, 2017-2019). Mulesing has been banned by law in New Zealand since 2018. Violations of the ban are severely punished, and the use of anaesthesia is also prohibited. Experience in New Zealand shows that alternatives such as breeding sheep with fewer skin folds or other management measures can be successfully applied without compromising animal welfare (James, 2006).

1.1.4 Breeding for shorter tails

Tail length is the visible result of complex genetic and developmental processes and can be used to characterize and differentiate sheep breeds. In addition to its mechanical function, such as balancing the body, the tail performs other functions in different breeds, such as thermoregulation, insect defense or the accumulation of energy reserves in the form of fat. These differences are used to classify sheep by tail type (Porter et al., 2016). The group of long-tailed sheep includes most European commercial breeds, such as Merino sheep. Their tails usually extend to or beyond the hock and are narrow and thin. Long-tailed sheep are the most common breed in the world and are known for their wool and meat production. Short-tailed sheep are mainly Nordic breeds such as Finn sheep and Romanov. Their tails are much shorter, less woolly and usually only a few centimeters above the base. These animals are often particularly hardy and adapted to harsh climates. Fat-tailed sheep store a large proportion of their body fat in their tails, which can become conspicuously thick and heavy. Typical examples of this group are the Awassi, Karakul and Damara. These breeds are particularly common in North Africa, Central Asia and the Middle East, where the stored fat serves as an energy reserve in times of scarcity (Mohapatra & Shinde, 2018). The final group are the fat-tailed sheep. In contrast to fat-tailed sheep, fat-tailed sheep store fat mainly on the rump and have a very short tail or no visible tail. These breeds are mainly found in Africa and Central Asia (Halimani et al., 2021). Phenotypically, the tail can be categorized as short, medium or long, either using a tape measure or purely visually based on the hock joint (Eck, 2020; Hümmelchen et al., 2023). However, information on tail length in the literature varies from breed to breed. Tail length is a quantitative trait and is influenced by several genes. The heritability is between 0.38 and 0.77 depending on the breed (Oberpenning et al., 2023; Lagler et al., 2022; Haverkamp et al., 2015; Scobie & O'Connell, 2002).

An important gene that significantly influences tail length is HOXB13. The short-tailed variant of this gene is also present in long-tailed domestic sheep breeds and can be enriched by targeted selection and mating. Animals homozygous for the short-tailed variant are phenotypically short-tailed, while heterozygous animals have tail lengths between the two extremes (Kalds et al., 2022). A genetic test for the HOXB13 variant would allow targeted selection of breeding animals and thus accelerate breeding progress

(Lagler et al., 2022). Crossbreeding experiments, for example with Finn sheep, have confirmed that the offspring of the first generation have significantly shorter tails than the long-tailed parents (Oltenacu & Boyalan, 1974). Targeted crossbreeding of short-tailed breeds, or enrichment of a population with short-tailed alleles, therefore, offers a sustainable way to reduce tail length and eliminate the need for routine docking.

1.1.5 Genetic and environmental effects on tail length

Shortening the length of the tail through breeding means a physiological reduction in the number of vertebrae. The effects on other body traits are considered in this context. There are correlations between tail length and other body traits (James, 2006). For example, body size needs to be corrected in relation to tail length (Greeff et al., 2015). Hümmelchen et al. (2023) go one step further and measure tail circumference in addition to body measurements using ultrasonography and radiology, finding higher accuracy and repeatability. Other trait correlations investigated by Hümmelchen et al. (2025) in relation to tail length are fertility parameters and body traits. They found that tail length had no negative effect on the latter traits.

Structural equation modelling (SEM) is used in animal breeding to record complex relationships between latent (non-measurable) and measurable breeding target traits. It is possible to integrate data from the areas of environment, management and genetics. Los Campos (2006) used SEM in dairy cows to describe the relationship between somatic cell count and milk yield. König et al. (2008) investigated causal relationships between claw diseases and milk yield in Holstein cows using recursive linear and threshold models. A correlation between high milk production and the occurrence of claw diseases is suspected, which may be induced by metabolic stress, pain and restricted feed intake. These innovative models are also used in sheep breeding. Jafaroghli et al. (2022) investigated the usefulness of SEM for the genetic evaluation of lifetime performance traits (e.g. number of lambs born per lambing period) and first lambing age in Moghani sheep. In the study, SEM showed higher predictive accuracy for traits with complex causal relationships (e.g. time lags between first lambing age and later reproductive performance) and demonstrated the potential for analyzing reproductive traits in breeding.

1.1.6 Overall breeding value

The overall breeding value (OBV) for sheep serves as a central instrument for assessing the genetic suitability of breeding animals. In Germany, it has been calculated nationwide for 25 sheep breeds since 2014 and has been updated every six months since 2021, integrating various individual traits such as fertility, fattening performance, carcass quality and conformation into an overall assessment (VIT, 2024). An overall breeding value for organically reared animals has also been established, but not explicitly for sheep. So far, however, no further traits relating to animal health or animal welfare have been added for Germany; the focus is on production traits. In Austria, the OBV has been calculated for 17 sheep and 7 goat breeds since 2017, focusing on functional and production traits.

France has a milk-emphasized weighting with a focus on milk quantity and milk composition (ÖBSZ, 2021). The main breeding goals of African sheep and goat breeding programs are high meat and reproductive performance, supplemented by functional traits such as disease and parasite resistance, fertility, adaptability, and a high survival rate of offspring (Ojango et al., 2025). The French dairy sheep breeding industry is pursuing new breeding goals that combine performance traits with characteristics such as disease resistance, longevity and efficiency, to improve resilience (Astruc et al., 2018).

For a dual-purpose Merino sheep breed in central Chile, meat production traits such as body weight and daily weight gain have the highest economic importance. Wool quantity, wool quality, fertility, and lamb survival are less important but still have economic relevance (Lembeye & Castellaro, 2025).

A study by Welday et al. (2022) was conducted to determine the breeding goals of smallholder sheep farmers for Northern Ethiopia. The key traits for rams were body size, tail shape and libido, while for ewes, the most relevant traits were body size, litter size and maternal ability.

Conrad et al. (2022) examined the suitability of different sheep breeds for use in Central European vineyards during the growing season. The authors emphasise that the most relevant factors are body size and the inability to stand on hind legs, to prevent damage to the vines. Therefore, the animals' characteristics of low mouth and standing height are essential for this form of sheep farming and for preserving particularly endangered breeds.

Animal welfare is an increasingly important issue in the sheep industry. It encompasses aspects such as animal health, behavior and welfare and is directly linked to husbandry systems and meat production. Consumption of sheep meat in Germany is increasing and consumers are becoming more aware of the production of sheep meat. Current welfare issues in sheep production include the non-docking of ewe lambs, the increasing presence of wolves and the need for flock protection measures, and parasite management. To obtain an economic weighting for breeding traits such as tail length, which cannot be measured directly in economic terms, it is helpful to conduct a consumer survey. This survey technique is called the Contingent Valuation Method (CVM) and has been successfully used in agriculture. The CVM asks consumers about their hypothetical willingness to pay for a change in utility. The result is economic weights for target breeding traits, which are needed to design and adjust an overall breeding value.

1.2 Derivation of economic weights in sheep production systems

1.2.1 Economic efficiency of sheep farming

Defining the profitability of sheep farming in Germany is a challenge. In contrast to economic figures for other animal species such as pigs or cattle, there are no reports on sheep farming. Due to the diversity of husbandry systems, breeds and regional aspects, an economic evaluation of pure sheep farms seems inconsistent, but is essential for maintaining competitiveness.

Sheep farming in the European Union is largely supported by the Common Agricultural Policy (CAP), which operates under two pillars. The first pillar comprises direct payments, including coupled premiums for ewes, which vary depending on the member state and region. In Bavaria, for example, the planned premium for 2025 is 39 € per ewe, while Saxony grants additional wolf protection premiums of 55 € per animal per year. Area-based payments, which average around 286 € per hectare in the EU, particularly benefit farms in less-favored areas, where sheep often graze grassland to maintain the landscape. The second pillar of the CAP focusses on agri-environmental measures that promote extensive grazing systems with up to 280 € per hectare for species-rich grassland. These funding instruments are indispensable, as up to 60% of German sheep farmers' income comes from public funds and the sector would not be able to survive without subsidies.

The profitability of sheep farming in Germany was analyzed by von Korn (2020) as part of a project. Over 460 farms and 450,000 ewes were considered. In addition to a high average number of 611 animals per farm, it was recognized that 88% of the land used was leased. The most important source of income for the farms is lamb production, which generates an average of 97.7 € per lamb. However, 60% of the total proceeds are public subsidies, reported here by von Korn at 42 - 225 € per ewe per year. Production costs amount to an average of 246 € per ewe per year. Without public subsidies, a profit of -68 € was recorded, which emphasizes the need for subsidies in sheep farming. Regarding the remuneration of working hours, it can be stated that the remuneration is 5.70 €/hour, whereas in agriculture it is around 17.50 €/hour. To date, no further figures are available on the economic situation of sheep farming in Germany. The precarious working conditions on many farms are pointed out throughout the EU, where average pay is often less than 6 € per hour (Belanche et al., 2020).

In a Brazilian study, the production costs for lamb are mainly determined by variable expenses (64.15%), 63.17% of which are feed costs (Raineri et al., 2015). Fixed costs account for over 20%, mainly due to labour (11.10%) and infrastructure depreciation (5.75%), supplemented by 14.19% return on capital. In order to work more efficiently and profitably, Raineri et al. (2015) calculated that a 1% increase in carcass weight reduces costs by 0.91% and that this can be increased by better utilization of pastures and better feed conversion. Low technical efficiency, e.g. due to low stocking densities or inefficient breeds, is cited as a cost factor. In order to reduce these costs sustainably, farms should invest in breeding programmes and modern pasture management, as well as in more efficient infrastructure and automation in the long term. In relation to more efficient breeding programmes, El Sabry et al. (2023) reported a correlation between space availability and higher performance. Daily weight gain and milk yield increase with more space, which in turn reduces stress and optimizes the animals' feed conversion. There is also an improvement in wool quality when the animals are kept outdoors, and the frequency of skin irritations decreases. According to Lima et al. (2017), feed efficiency has a significant influence on profitability. As feed accounts for 71% of total costs, feed efficiency is essential to remain profitable even with opportunity costs. It is important that feed efficiency does not compromise carcass quality. Practical measures to increase competitiveness include digital feeding systems and genotyping to identify high performing lambs.

Another breeding focus should be on breeding heat-tolerant animals in order to secure sheep farming in the long term (Al-Barakeh et al., 2024; Belanche et al., 2020). Making farms climate-resilient is also a promising aspect for the future. The resilience of farms should be increased through the introduction of regenerative agricultural practices, such as soil-conserving grazing techniques or agroforestry systems. At the same time, markets for ecosystem services can open up new sources of income. These include, for example, certification systems for carbon storage. Sheep farming in arid regions also faces particular challenges such as economic dependencies and sustainability issues (Al-Barakeh et al., 2024). As previously described, extensive grazing preserves semi-natural habitats such as nutrient-poor grasslands and helps to store carbon. However, poorly managed grazing systems also harbor risks such as nutrient surpluses due to overgrazing, which pollute groundwater and soils.

1.2.2 Economic evaluation of sheep farming systems

Sheep farming in Germany is characterized by a duality between traditional landscape management and modern livestock production. As multifunctional production systems, sheep farms combine ecological, cultural and economic tasks. Through grazing, they preserve biotopes worthy of protection, such as juniper heaths and dyke landscapes, and contribute to biodiversity (Müller et al., 2019). An attempt to identify the different farm structures in German sheep farming reveals the following. Around 72% of farms keep a maximum of 49 animals, while only 4.6% manage flocks of more than 500 sheep (Statistisches Bundesamt, 2023). At the same time, hobby farming is becoming increasingly important, often as a sideline to maintain grassland. Migratory flocks with historical herding concepts continue to characterise regions that cannot be maintained or worked with agricultural machinery. However, there is no clear overview of existing livestock systems, e.g. for cattle or pigs (Herold et al., 2021).

Cluster analysis is used in modern animal husbandry to classify heterogeneous farm structures, animal behavior or management strategies into homogeneous groups. When these methods are applied to the German sheep industry, three superordinate husbandry systems can be identified: stable management, paddock management and traditional grazing. These systems are often combined seasonally. During the winter months, for example, lambing is increasingly carried out in stables, but for the rest of the year the animals are kept in paddocks.

Schütte (2023) goes one step further and uses cluster analysis to define nine different farming systems. The husbandry systems are identical throughout Germany for both conventional and organic husbandry. All the husbandry systems mentioned are represented in both systems.

A comparison of German and international sheep production systems shows that extensive grazing is predominant, particularly in Australia, New Zealand, Great Britain and parts of South America. Because of the large areas of land available, sheep are often kept in very large flocks, sometimes with minimal human labour.

Intensive farming systems such as milk sheep are particularly common in southern Europe (e.g. Greece, Italy), the Middle East and parts of North Africa. Here, sheep are kept year-round or predominantly indoors in order to control feeding and achieve high milk yields.

While in Germany the focus is on landscape conservation and meat production, internationally the emphasis is sometimes more on milk (e.g. feta production in Greece) or wool (Australia, New Zealand). Sheep farming in Germany is characterised by extensive, semi-natural grazing and makes an important contribution to landscape conservation. Internationally, there are similar extensive systems (especially in countries with large areas) and intensive systems designed to maximize production. The choice of farming system is highly dependent on regional conditions, economic objectives and regulatory frameworks.

1.2.3 Bio-economic models for derivation of economic values for breeding traits

To quantify the monetary impact of individual breeding target traits on overall farm performance, bio-economic models integrate production and functional parameters (e.g. fertility rates, fattening performance) with economic indicators (cost structures, market prices). In the face of structural challenges, such as high labour costs and subsidy dependency, this approach allows data-driven prioritization of traits that can increase both productivity and profitability. Using bio-economic modelling, it is possible to calculate economic weights for target traits in relation to the production system. Economic weights are generally defined as partial derivatives of the profit function. They describe the relationship between profit and biological, economic and production parameters for each of the evaluated target traits (Wolfová et al., 2011).

The international literature often emphasizes the importance of growth rates and carcass quality as central economic weights in bio-economic models (Conington et al., 2004; Jones et al., 2004; Wolfová et al., 2011). Compared to Germany, they show a stronger focus on market dynamics and economies of scale, often with a more comprehensive data base. They also underline the need to give greater weight to climate resilience and labour productivity in future models. When calculating the economic weights for 14 production and functional traits, milk yield, conception rate of ewes, litter size and lifespan of ewes were identified as the most economically important traits (Krupová et al., 2009).

It is not only breeding traits alone that play a role in bio-economic models, but also the current issue of climate resilience and the carbon footprint. These topics were addressed in an Irish study by Kilcline et al. (2024), which analyses the profitability of sheep farming with regard to the carbon footprint. Technical optimizations such as increasing slaughter weights through targeted flock management or increasing grazing capacity could increase productivity by up to 20% and reduce nitrogen use at the same time. Breeding progress, especially in the area of maternal traits and feed efficiency, plays a key role here - higher litter sizes and survival rates not only reduce costs, but also emissions per kilogram of meat. Emissions from feed production could be offset by the introduction of climate-smart grazing systems, e.g. perennial mixed crops that sequester carbon in the soil. This study again emphasizes the importance and necessity of subsidies, without which sheep farming would be unprofitable. Another bio-economic modelling on the economics of carbon sequestration looks at the possibility of planting marginal land and grazing it with sheep and cattle (Wangui et al., 2021). The planted shrubs not only serve as an additional source of fodder, but also as erosion control and a carbon sink. At the same time, the carbon sequestered in the shrubs can open up new sources of income through the trading of certificates. Here, too, it is emphasized that without state subsidies or higher carbon prices, the measure is hardly profitable due to the high costs of planting and maintaining the shrubs and the currently still low revenues on the carbon market.

The German literature on bio-economic models in sheep production focuses on the dependency on agricultural policy frameworks and cost reduction through breeding optimization. When comparing trait weights, functional traits such as hoof health and longevity are gaining importance in Germany to reduce labour costs (Oberpenning et al., 2025).

1.3 Aims of the study

The first study aimed to clarify the genetic architecture linking tail length and growth traits in Merinoland sheep. Given the increasing importance of breeding for short tails as an alternative to tail docking, the study sought to estimate genetic parameters for tail length, birth weight, weaning weight, and post-weaning weight using single-trait, multiple-trait, and structural equation models. A key objective was to determine whether structural equation models, which incorporate time-lagged causal pathways, provide deeper insights into the biological and environmental mechanisms connecting tail morphology with growth performance. By quantifying direct and maternal genetic effects, as well as recursive relationships among traits, the study intended to evaluate potential antagonistic genetic correlations and identify whether environmental risk factors, such as hygiene-related infections in long-tailed lambs, should be integrated into breeding strategies.

The second study focused on characterizing German sheep production systems and deriving cluster-specific economic weights for breeding goal traits. By applying hierarchical clustering to 25 herds, the study aimed to identify production system types that differ in size, management intensity, and economic orientation. A central objective was to quantify farmers' willingness to pay for improvements in twelve breeding traits and to determine how these preferences vary across production clusters. The study sought to reveal whether health and welfare traits, particularly tail length, are consistently valued across systems and to evaluate whether breeding goals should shift from performance-driven selection toward greater emphasis on functionality, welfare, and system-specific needs.

The third study aimed to extend an existing bio-economic model to incorporate health and welfare traits, with a particular focus on parasite resistance and tail length in Merinoland sheep. By enhancing the ECOWEIGHT software with modules for disease incidence, treatment costs, and herd tail-length composition, the study sought to derive marginal and relative economic values for fifteen breeding traits. A key objective was to assess the economic relevance of health and welfare traits under varying herd tail-length scenarios and to evaluate the robustness of economic values through sensitivity analyses. The study further aimed to determine whether current economic weights are biased by the high health status of research herds and to highlight the need for broader data sources to ensure representative economic evaluations.

References

Al-Barakeh, F., Khashroum, A. O., Tarawneh, R. A., Al-Lataifeh, F. A., Al-Yacoub, A. N., Dayoub, M., & Al-Najjar, K. (2024). Challenges, economics, and sustainability of sheep and goat farming in drylands https://doi.org/10.20944/preprints202403.1478.v1

Astruc, J. M., Buisson, D., Larroque, H., & Lagriffoul, G. (2018, August). New breeding goals and role of genomics on adaptation and resilience traits in French dairy sheep. In 69. Annual Meeting of the European Federation of Animal Science (EAAP) (Vol. 24, No. 1ère Ed., pp. 705-p). Wageningen Academic Publishers.

Bayerische Landesanstalt für Landwirtschaft. (2017–2019). Auswirkungen verschiedener Methoden des Schwanzkupierens bei Lämmern. https://www.lfl.bayern.de/itz/schaf/172856/index.php

Belanche, A., Martín-Collado, D., Rose, G., & Yánez-Ruiz, D. R. (2020). A multi-stakeholder participatory study identifies the priorities for the sustainability of the small ruminants farming sector in Europe. Animal 15, 100131. https://doi.org/10.1016/j.animal.2020.100131

Conington, J., Bishop, S. C., Waterhouse, A., & Simm, G. (2004). A bio-economic approach to derive economic values for pasture-based sheep genetic improvement programs. Journal of Animal Science, 82 (5), 1290–1304. https://doi.org/10.2527/2004.8251290x

Conrad, L., Hörl, J., Henke, M., Luick, R., & Schoof, N. (2022). Sheep in the Vineyard: Suitability of Different Breeds and Potential Breeding Objectives. Animals 2022, 12, 2575.

Eck, K. (2020). Untersuchung der natürlichen Schwanzlängenvariation beim Merinolandschaf als mögliche Zuchtalternative zur tierschutzrelevanten Praktik des Schwanzkupierens (Doctoral dissertation, lmu).

El Sabry, M. I., Motsei, L. E., Abdel-Mageed, I. I., & Almasri, O. (2023). Space allowance impacts behavior, productivity, reproductivity and immunity of sheep—a review. Tropical Animal Health and Production, 55(3), 207. https://doi.org/10.1007/s11250-023-03615-2

Ellenberger, W., & Baum, H. (2013). Handbuch der vergleichenden Anatomie der Haustiere. Springer-Verlag. https://doi.org/10.1007/978-3-642-55550-2

European Union. (2008). Richtlinie 2008/120/EG des Rates vom 18. Dezember 2008 über Mindestanforderungen für den Schutz von Schweinen. https://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:32008L0120

French, N. P., Wall, R., & Morgan, K. L. (1994). Lamb tail docking: a controlled field study of the effects of tail amputation on health and productivity. Veterinary Record, 134, 463-463. https://doi.org/10.1136/vr.134.18.463

Gascoigne, E., Mouland, C., & Lovatt, F. (2021). Considering the 3Rs for castration and tail docking in sheep. In Practice, 43(3), 152-162. https://doi.org/10.1002/inpr.29

Graham, N. P. H., Johnstone, I. L., & Riches, J. H. (1947). Studies on Fly Strike in Merino Sheep. No. 7. The Effect of Tail-length on Susceptibility to Fly Strike in Ewes. https://doi.org/10.1111/j.1751-0813.1947.tb04510.x

Greeff, J. C., Karlsson, L. J. E., & Schlink, A. C. (2015). Inheritance of tail length in Merino sheep. Proceedings of the Association for the Advancement of Animal Breeding and Genetics, 21, 237–240. https://www.aaabg.org/aaabghome/AAABG21papers/Greeff21237.pdf

Halimani, T., Marandure, T., Chikwanha, O. C., Molotsi, A. H., Abiodun, B. J., Dzama, K., & Mapiye, C. (2021). Smallholder sheep farmers' perceived impact of water scarcity in the dry ecozones of South Africa: Determinants and response strategies. Climate Risk Management, 34, 100369. https://doi.org/10.1016/j.crm.2021.100369

Hannemann, R., Bauer, B., Ganter, M. & Strobel, H. (2017). Schmerzhafte Eingriffe beim Schaf – Schwanzkupieren. Eine Übersicht. Tierärztliche Praxis G: Großtiere/Nutztiere 45, 302-311, doi:10.15653/TPG-170354. https://doi.org/10.15653/TPG-170354

Haverkamp, H., Brandt, H., & Erhardt, G. (2015). Variation in der Schwanzlänge beim Merinolandschaf als Basis für züchterische Aktivitäten. In: Vortragstagung der DGfZ/GfT, September 16–17.

Herold, J., Brügemann, K., & König, S. (2021). Herd clustering strategies and corresponding genetic evaluations based on social–ecological characteristics for a local endangered cattle breed. Archives Animal Breeding, 64 (1), 187–198. https://doi.org/10.5194/aab-64-187-2021

Herzog, A. (2001). Pareys Lexikon der Syndrome: Erb- und Zuchtkrankheiten der Haus- und Nutztiere; mit 63 Tabellen. Parey Buchverlag.

Hümmelchen, H., Wagner, H., Brügemann, K., König, S., & Wehrend, A. (2025). Effects of breeding for short-tailedness in sheep on parameters of reproduction and lamb development. Veterinary Medicine and Science, 11 (1), e70138. https://doi.org/10.1002/vms3.701

Hümmelchen, H., Wenisch, S., Brügemann, K., König, S., & Wagner, H. (2023). Phänotypisierung des Schafschwanzes – Darstellung von Methoden zur Charakterisierung im Rahmen der Zucht auf Kurzschwänzigkeit. Tierärztliche Praxis Ausgabe G: Großtiere/Nutztiere, 51 (1), 6–14. https://doi.org/10.1055/a-1983-2083

Jafaroghli, M., Ghafouri-Kesbi, F., Khorami, S. J., Barazandeh, A., & Mokhtari, M. (2022). Application of structural equation models for genetic evaluation of lifetime reproductive traits and age at first lambing in Moghani sheep. Small Ruminant Research, 214, 106761. https://doi.org/10.1016/j.smallrumres.2022.106761

James, P. J. (2006). Genetic alternatives to mulesing and tail docking in sheep: A review. Australian Journal of Experimental Agriculture, 46 (1), 1–18. https://doi.org/10.1071/EA05100

Jones, H. E., Amer, P. R., Lewis, R. M., & Emmans, G. C. (2004). Economic values for changes in carcass lean and fat weights at a fixed age for terminal sire breeds of sheep in the UK. Livestock Production Science, 89 (1), 1–17. https://doi.org/10.1016/j.livprodsci.2004.01.001

Kalds, P., Huang, S., Chen, Y., & Wang, X. (2022). Ovine HOXB13: Expanding the gene repertoire of sheep tail patterning and implications in genetic improvement. Communications Biology, 5, Article 1196. https://doi.org/10.1038/s42003-022-04199-7

Kilcline, K., Hynes, S., & O'Donoghue, C. (2024, March). A nationally representative bio-economic modelling of sheep production systems: Modelling the carbon footprint and economic performance of Irish sheep flocks. AES Annual Conference Paper. https://ageconsearch.umn.edu/record/355331

Kiley-Worthington, M. (1976). The tail movements of ungulates, canids and felids with particular reference to their causation and function as displays. Behaviour, 56 (1–2), 69–114. https://doi.org/10.1163/156853976X00307

König, S., Wu, X. L., Gianola, D., Heringstad, B., & Simianer, H. (2008). Exploration of relationships between claw disorders and milk yield in Holstein cows via recursive linear and threshold models. Journal of Dairy Science, 91 (1), 395–406. https://doi.org/10.3168/jds.2007-0344

Krupová, Z., Wolfová, M., Wolf, J., Oravcová, M., Margetín, M., Peškovičová, D., & Daňo, J. (2009). Economic values for dairy sheep breeds in Slovakia. Asian-Australasian Journal of Animal Sciences, 22 (12), 1693–1702. https://doi.org/10.5713/ajas.2009.90113

Lagler, D. K., Hannemann, E., Eck, K., Klawatsch, J., Seichter, D., Russ, I., Mendel, C., Lühken, G., Krebs, S., Blum, H., Upadhyay, M., & Međugorac, I. (2022). Fine-mapping and identification of candidate causal genes for tail length in the Merinolandschaf breed. bioRxiv. https://doi.org/10.1101/2022.02.27.481613

Lembeye, F., & Castellaro, G. (2025). Developing a Breeding Objective for Dual-Purpose Merino Precoz Breed in Central Chile: Derivation of Economic Weights. Chilean journal of agricultural & animal sciences, 41(2), 209-216.

Lima, N. L. L., Ribeiro, C. R. D. F., Sá, H. C. M. D., Leopoldino-Júnior, I., Cavalcanti, L. F. L., Santana, R. A. V., & Pereira, I. G. (2017). Economic analysis, performance, and feed efficiency in feedlot lambs. Revista Brasileira de Zootecnia, 46, 821–829. https://doi.org/10.1590/s1806-92902017001000003

Los Campos, G. de, D. Gianola, & B. Heringstad (2006). A structural equation model for describing relationships between somatic cell score and milk yield in first-lactation dairy cows. Journal of dairy science 89(11):4445–4455. https://doi.org/10.3168/jds.S00220302(06)72493-6

Mereu, P., Pirastru, M., Sanna, D., Bassu, G., Naitana, S., & Leoni, G. G. (2024). Phenotype transition from wild mouflon to domestic sheep. Genetics Selection Evolution, 56(1), 1.

Mohapatra, A., & Shinde, A. K. (2018). Fat-tailed sheep-an important sheep genetic resource for meat production in tropical countries: an overview. Indian J. Small Rumin, 24(1), 1-17.

Müller, S. M., Peisker, J., Bieling, C., Linnemann, K., Reidl, K., & Schmieder, K. (2019). The importance of cultural ecosystem services and biodiversity for landscape visitors in the biosphere reserve Swabian Alb (Germany). Sustainability, 11(9), 2650.

Noden, D. M., & Lahunta, A. D. (1985). The embryology of domestic animals. Developmental mechanisms and malformations, Williams and Wilkins.

Oberpenning, J., Bohlouli, M., Engel, P., Hümmelchen, H., Wagner, H., Wehrend, A., & König, S. (2023). Multiple-trait and structural equation modelling approaches to infer genetic relationships between tail length and weight traits in Merinoland sheep. Journal of Animal Breeding and Genetics, 140(2), 132-143.

Oberpenning, J., Brügemann, K., & König, S. (2025). Characterization of German sheep production systems and derivation of respective economic values for breeding traits. Veterinary and Animal Science, 27, 100432.

Ojango, J. M., Osei-Amponsah, R., Houaga, I., Gondwe, T., Okpeku, M., & Kugonza, D. R. (2025). Breeding goals and strategies for improving small ruminant productivity in African input systems. In *African Livestock Genetic Resources and Sustainable Breeding Strategies: Unlocking a Treasure Trove and Guide for Improved Productivity* (pp. 759-783). Cham: Springer Nature Switzerland.

Oltenacu, E. B., & Boyalan, W. J. (1974). Inheritance of tail length in crossbred Finnsheep.

Österreichischer Bundesverband für Schafe und Ziegen (ÖBSZ) (2021). Zuchtwerte für Schafe und Ziegen verstehen. https://www.oebsz.at/fileadmin/user_upload/merkblatt_zuchtwerte.pdf

Porter, V., Alderson, L., Hall, S. J., & Sponenberg, D. P. (2016). Mason's world encyclopedia of livestock breeds and breeding, 2 Volume Pack (Vol. 1). Cabi.

Raineri, C., Stivari, T. S. S., & Gameiro, A. H. (2015). Lamb production costs: Analyses of composition and elasticities analysis of lamb production costs. Asian-Australasian Journal of Animal Sciences, 28(8), 1209.

Schütte, J. (2023). Typology of German sheep farms-Differences in structure, characteristics, challenges and the provision of goods and services. Small Ruminant Research, 226, 107022. https://doi.org/10.1016/j.smallrumres.2023.107022

Scobie, D. R., & O Connell, D. (2002, September). Genetic reduction of tail length in New Zealand sheep. In Proceedings-New Zealand Society of Animal Production (Vol. 62, pp. 195-198). New Zealand Society of Animal Production; 1999.

Shelton, M. (1977). Studies on tail length of Rambouillet and Mouflon sheep. The Journal of heredity, 68(2), 128-130.

Shephard, R., Webb Ware, J., Blomfield, B., & Niethe, G. (2022). Priority list of endemic diseases for the red meat industry–2022 update. Final Report, Project B. AHE, 327.

Statistisches Bundesamt. (2023). Land- und Forstwirtschaft, Fischerei, Viehhaltung der Betriebe Viehbestandserhebung: Fachserie 3 Reihe 2.1.3.

TierSchG, 2006. §5 Absatz 3 Satz 4, §6: Tierschutzgesetz in der Fassung der Bekanntmachung vom 18. Mai 2006 (BGBl. I S. 1206, 1313), das zuletzt durch Artikel 105 des Gesetzes vom 10. August 2021 (BGBl. I S. 3436) geändert worden ist. Im Internet: https://www.gesetze-im-internet.de/tierschg/BJNR0 12770 972.html. (Accessed: 19 March 2024)

Verordnung (EG) Nr. 889/2008 der Kommission vom 5. September 2008 mit Durchführungsvorschriften zur Verordnung (EG) Nr. 834/2007 des Rates über die ökologische/biologische Produktion und die Kennzeichnung von ökologischen/biologischen Erzeugnissen hinsichtlich der ökologischen/biologischen Produktion, Kennzeichnung und Kontrolle (ABl. L 250 vom 18.9.2008, S. 1–84)

VIT (2024). https://www.vit.de/vit-fuers-tier/zuchtwertschaetzung/zws-sonstige-tierarten (accessed 19 March 2024).

von Korn, S. (2020). Wirtschaftlichkeit der Schafhaltung in Deutschland – Abschlussbericht. Nutztierhaltung.de. https://www.nutztierhaltung.de/fileadmin/Redaktion/Dokumente/5-Schafe/3-Stallbau/Abschlussbericht_Wirtschaftlichkeit_Schafhaltung.pdf

Wangui, J. C., Kenyon, P. R., Tozer, P. R., Millner, J. P., & Pain, S. J. (2021). Bioeconomic modelling to assess the impacts of using native shrubs on the marginal portions of the sheep and beef hill country farms in New Zealand. Agriculture, 11(10), 1019.

Welday, K., Abegaz, S., Urge, M., Abebe, A., & Mezgebe, G. (2022). Defining smallholders' breeding objectives for common Tigray highland sheep in Northern Ethiopia. Journal of Animal Breeding and Genetics, 139(6), 623-633.

Wilson, S., Jacob, C. J., & Powell, D. (2011). Behavior-change interventions to improve hand-hygiene practice: A review of alternatives to education. Critical Public Health, 21 (1), 119–127. https://doi.org/10.1080/09581596.2010.529421

Wolfová, M., Wolf, J., & Milerski, M. (2011). Economic weights of production and functional traits for Merinolandschaf, Romney, Romanov and Sumavska sheep in the Czech Republic. Small Ruminant Research, 99 (1), 25–33. https://doi.org/10.1016/j.smallrumres.2011.03.001

Woodruff, M. E., Doyle, R., Coleman, G., Hemsworth, L., & Munoz, C. (2020). Knowledge and attitudes are important factors in farmers' choice of lamb tail docking length. Veterinary Record, 186 (10), 319. https://doi.org/10.1136/vr.105631

CHAPTER 2

Multiple-trait and structural equation modelling approaches to infer genetic relationships between tail length and weight traits in Merinoland sheep

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Abstract

Tail docking is routinely conducted in long-tailed sheep breeds to prevent fly-strike infections, but it is not in agreement with legal guidelines and animal welfare issues. Selection on short tails is a sustainable alternative in this regard, but side effects on other breeding goal traits are unclear. In consequence, the present study aimed to estimate genetic parameters for tail length (TL) at birth, birth weight (BW), weaning weight (WW) and postweaning weight (PWW) at the slaughtering date considering single-trait (STM), multiple-trait (MTM) and structural equation models (SEM) with different random effects, and accordingly, different covariance structures. The SEM considered time-lagged recursive relationships among response variables in three different pathways. The first path pertained to the effect of TL on WW and of WW on PWW. The second path reflected the effect of BW on WW and of WW on PWW. The third path was the recursive effect of TL on PWW. The phenotypic data consisted of 2803 records for TL, 13,042 records for BW, 1556 records for WW and 3986 records for PWW from Merinoland lambs. Lambs were born in the period from 1995 to 2021 and kept at the university Gießen research station, Germany, with their naturally long tails. Genetic statistical model evaluation based on Bayesian and Akaike's information criteria suggested models simultaneously considering direct genetic, maternal genetic and maternal permanent environmental effects and respective covariances. For statistical models including the same random effects and covariance structures, SEM were superior over MTM. The direct heritability for TL from the best-fitting STM was 0.60 ± 0.08, indicating the potential for genetic reduction of tail length within a few generations. For growth traits, the direct heritabilities ranged from 0.16 ± 0.03 for BW to 0.31 ± 0.09 for PWW. The maternal heritabilities were 0.03 ± 0.03 for TL, 0.12 ± 0.02 for BW, 0.04 ± 0.03 for WW and 0.07 ± 0.03 for PWW, reflecting small, but the non-significant influence of uterine characteristics on the tail development. The direct genetic correlations between TL and

analyses, we evaluated different MTM and focused on the estimation of genetic covariance components and genetic correlations for all trait combinations. Corresponding SEM including the three pathways as described above aimed at inferring genetic (co)variance components and structural equation coefficients for mutual direct and time-lagged trait associations.

2 | MATERIALS AND METHODS

The committee of animal care and protection as established by University of Giessen officially approved this study. The official number for this study is V 54–19c 20 15 h 01 GI 18/14 Nr. G 44/2021.

2.1 | Animals and traits

The present study considered the experimental purebred Merinoland sheep population from the University Gießen research station "Oberer Hardthof," Germany, with their natural and undocked tails. The flock was kept in grazing (spring to fall) and high-input (fall to spring) production systems. The phenotypic records were collected over a period of 27 years (1995–2021) and included tail length at birth (**TL**) measured in cm, birth weight (**BW**) in kg, weaning weight (**WW**) in kg (average age of 62 days) and postweaning weight (**PWW**) in kg recorded at the slaughtering date (average age of 118 days). Year-month combinations with a small number of records (less than 10 lambs with records for TL, BW, WW or PWW) were discarded, implying the exclusion of records from 11-year-month combinations for the ongoing genetic analyses. In addition, all traits were checked for outliers by excluding records with values lower or higher than the mean ± 3 SD. After editing and discarding 11% of all initial records, the data consisted of 2803 records for TL, 13,042 records for BW, 1556 records for WW and 3986 records for PWW. All lambs with records for TL had records for the weight traits BW and PWW, and all lambs with records for WW had a TL measurement. The descriptive statistics for the traits are given in Table 1.

The pedigree of the lambs with trait records was traced back as many generations as possible and comprised 30,708 animals. In genetic analyses, all lambs with records could be traced back for at least three generations, but most of the lambs even had deeper pedigrees. Lourenco et al. (2014) evaluated the effects of pedigree depth on the accuracy of genetic evaluations, which depended on the data structure and the trait, but for genotyped animals, two or three generations of phenotypic records plus two additional pedigree generations were mostly sufficient in terms of accuracies. The pedigree completeness index was calculated according to MacCluer et al. (1983) and was 96.4%.

TABLE 1 Descriptive statistics of tail length at birth, birth weight, weaning weight and postweaning weight

Trait	No. of records	Mean	SD	Min	Max
Tail length (TL, in cm)	2803	23.42	2.36	16.2	30.4
Birth weight (BW, in kg)	13,042	5.50	1.04	2.4	8.6
Weaning weight (WW, in kg)	1556	29.20	5.58	14.0	53.0
Postweaning weight (PWW, in kg)	3986	43.69	6.56	22.0	73.0

The lambs with phenotypic records were offspring from 169 different rams and different 4689 ewes. The average pedigree-based inbreeding coefficient of the lambs calculated with the CFC software package (Sargolzaei et al., 2006) was 6.5%, and increased from 2.8% in 1995 to 8.3% in 2021.

2.2 | Genetic-statistical analyses

Genetic parameters for all traits were estimated using the software package WOMBAT (Meyer, 2007) and applying restricted maximum likelihood. First, 6 different single-trait models (**STM**) were fitted including different random effects and considering different covariance structures for random effects. The single-trait models 1–6 (i.e., STM-1–STM-6) were defined as follows:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_a\boldsymbol{a} + \boldsymbol{e} \qquad \text{(STM-1)}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_a\boldsymbol{a} + \boldsymbol{Z}_c\boldsymbol{c} + \boldsymbol{e} \qquad \text{(STM-2)}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_a\boldsymbol{a} + \boldsymbol{Z}_m\boldsymbol{m} + \boldsymbol{e} \text{ with } Cov\,(a, m) = 0 \qquad \text{(STM-3)}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_a\boldsymbol{a} + \boldsymbol{Z}_m\boldsymbol{m} + \boldsymbol{e} \text{ with } Cov\,(a, m) = \mathbf{A}\sigma_{am} \qquad \text{(STM-4)}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_a\boldsymbol{a} + \boldsymbol{Z}_m\boldsymbol{m} + \boldsymbol{Z}_c\boldsymbol{c} + \boldsymbol{e} \text{ with } Cov\,(a, m) = 0 \qquad \text{(STM-5)}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z}_a\boldsymbol{a} + \boldsymbol{Z}_m\boldsymbol{m} + \boldsymbol{Z}_c\boldsymbol{c} + \boldsymbol{e} \text{ with } Cov\,(a, m) = \mathbf{A}\sigma_{am} \qquad \text{(STM-6)}$$

where $\boldsymbol{y}$ was the observation vector for the lamb trait (TL, BW, WW or PWW); $\boldsymbol{b}$ was the vector of fixed effects including year-month at recording, litter size, litter number and sex; $\boldsymbol{a}$ was the vector of random direct genetic effects; $\boldsymbol{c}$ was the vector of random maternal permanent environmental effects; $\boldsymbol{m}$ was the vector of random maternal genetic effects and $\boldsymbol{e}$ was the vector of random residual effects. $\boldsymbol{X}$, $\boldsymbol{Z}_a$, $\boldsymbol{Z}_m$ and $\boldsymbol{Z}_c$ were incidence matrices relating the records to fixed, additive direct genetic, maternal genetic and maternal permanent environmental effects, respectively. $\boldsymbol{A}$ was the numerator relationship matrix and σ_{am} was the genetic covariance between direct and maternal genetic effects. It was assumed that the random effects are independent and normally disturbed. The (co)variance structure for random effects in model 6 (and correspondingly reduced in the remaining models with a smaller number of (co) variance components) was

$$\text{var}\begin{bmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{c} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{am} & 0 & 0 \\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma_c^2 & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

where σ_a^2 and σ_m^2 were the direct and maternal genetic variances, respectively; σ_{am} was the covariance between direct and maternal genetic effects; σ_c^2 was the maternal permanent environmental variance; σ_e^2 was the residual variance and $\boldsymbol{I}$ was an identity matrix.

The phenotypic variance (σ_p^2) was computed as the sum of the (co)variance components with $\sigma_p^2 = \sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_c^2 + \sigma_e^2$. The direct heritability (h_d^2), the maternal heritability (h_m^2), the maternal permanent environmental variance as a proportion of the phenotypic variance (c^2) and the direct-maternal genetic correlation ($r_{g_{am}}$) were calculated as $h_d^2 = \sigma_a^2 / \sigma_p^2$, $h_m^2 = \sigma_m^2 / \sigma_p^2$, $c^2 = \sigma_c^2 / \sigma_p^2$ and $r_{g_{am}} = \sigma_{am} / \sqrt{\sigma_a^2 \times \sigma_m^2}$, respectively.The effects from STM-1 to STM-6 were considered in respective MTM by simultaneously including TL, BW, WW and PWW. For the most sophisticated model with all random effects, that is MTM-6, the matrix notation was as follows:

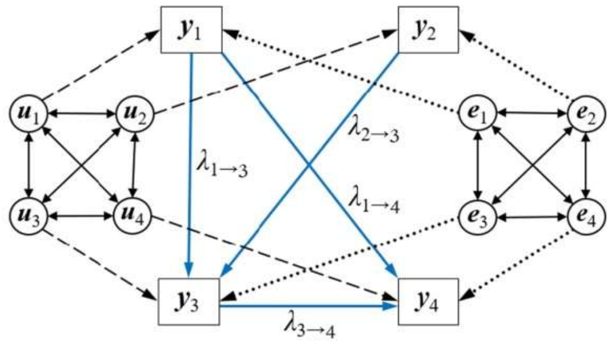

FIGURE 1 Recursive causal structure involving tail length at birth (y_1), birth weight (y_2), weaning weight (y_3) and postweaning weight (y_4) traits influenced by direct genetic effects ($\mathbf{u}_i$) and by residual (e_i) effects. Bidirectional arrows indicate genetic or residual correlations between pairs of traits. Blue arrows represent the direct recursive effect of trait i on trait j ($\lambda_{i\to j}$) [Colour figure can be viewed at wileyonlinelibrary.com]

where $\boldsymbol{y}_1$ to $\boldsymbol{y}_4$ were the observations for BW, TL, WW and PWW, respectively. For the remaining multiple-trait models MTM-1 to MTM-5 with a smaller number of effects and partly ignored covariance structures (see the STM definitions above), effects as defined in MTM-6 were excluded accordingly.

With regard to SEM, we hypothesized three pathways. The first path described the recursive and time-lagged effects of TL (trait 1) on WW (trait 3), and in the same path of WW (trait 3) on PWW (trait 4). A second pathway included the three weight traits simultaneously, that is, a recursive effect of BW (trait 2) on WW (trait 3), and in the ongoing process of ageing the causal recursive effect of WW (trait 3) on PWW (trait 4). The third pathway reflected the effect of TL (trait 1) on PWW (trait 4). From a biological and physiological perspective, such research objectives require a sheep population with undocked tails as kept on the research station of Oberer Hardthof, University of Giessen, Germany. The different recursive pathways are outlined in Figure 1.

Consequently, a matrix of structural equation coefficients (∧) was premultiplied with the observation vector. In analogy to the six STM and MTM, SEM-1 to SEM-6 were defined with the corresponding effects. Thus, SEM-6 was constructed as follows (and correspondingly reduced in the remaining five models with a smaller number of random effects):

$$\begin{bmatrix} \boldsymbol{y}_1 \\ \vdots \\ \boldsymbol{y}_4 \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_1 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \boldsymbol{X}_4 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \vdots \\ \boldsymbol{b}_4 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_{a1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \boldsymbol{Z}_{a4} \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_1 \\ \vdots \\ \boldsymbol{a}_4 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_{m1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \boldsymbol{Z}_{m4} \end{bmatrix} \begin{bmatrix} \boldsymbol{m}_1 \\ \vdots \\ \boldsymbol{m}_4 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_{c1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \boldsymbol{Z}_{c4} \end{bmatrix} \begin{bmatrix} \boldsymbol{c}_1 \\ \vdots \\ \boldsymbol{c}_4 \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_1 \\ \vdots \\ \boldsymbol{e}_4 \end{bmatrix} \text{with } Cov(a, m) = \mathbf{A}\sigma_{am}$$

(MTM-6)

$$\begin{bmatrix} \boldsymbol{y}_1 \\ \vdots \\ \boldsymbol{y}_4 \end{bmatrix} = \wedge \begin{bmatrix} \boldsymbol{y}_1 \\ \vdots \\ \boldsymbol{y}_4 \end{bmatrix} + \begin{bmatrix} \boldsymbol{X}_1 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \boldsymbol{X}_4 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \vdots \\ \boldsymbol{b}_4 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_{a1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \boldsymbol{Z}_{a4} \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_1 \\ \vdots \\ \boldsymbol{a}_4 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_{m1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \boldsymbol{Z}_{m4} \end{bmatrix} \begin{bmatrix} \boldsymbol{m}_1 \\ \vdots \\ \boldsymbol{m}_4 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_{c1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \boldsymbol{Z}_{c4} \end{bmatrix} \begin{bmatrix} \boldsymbol{c}_1 \\ \vdots \\ \boldsymbol{c}_4 \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_1 \\ \vdots \\ \boldsymbol{e}_4 \end{bmatrix} \text{with } Cov\,(a, m) = \mathbf{A}\sigma_{am} \qquad \text{(SEM-6)}$$

and

$$\wedge = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \boldsymbol{I}\lambda_{1\to3} & \boldsymbol{I}\lambda_{2\to3} & 0 & 0 \\ 0 & \boldsymbol{I}\lambda_{2\to4} & \boldsymbol{I}\lambda_{3\to4} & 0 \end{bmatrix}$$

where $\boldsymbol{I}$ was the identity matrix and $\lambda_{i\to j}$ represented direct effects of trait i on trait j. If all elements of the $\wedge$ matrix are equal to 0, then the SEM model is equal to an MTM model. Despite the difference in interpretations of MTM and SEM, the distribution of random effects was assumed to be the same for both models. Thus, the (co)variance structures for random effects using the model with all random effects (model 6) were

$$var\begin{bmatrix} \boldsymbol{a}_1 \\ \vdots \\ \boldsymbol{a}_4 \\ \boldsymbol{m}_1 \\ \vdots \\ \boldsymbol{m}_4 \end{bmatrix} = \boldsymbol{A} \otimes \begin{bmatrix} \sigma^2_{a_1} & \cdots & \sigma_{a_1,m_4} \\ \vdots & \ddots & \vdots \\ \sigma_{m_4,a_1} & \cdots & \sigma^2_{m_4} \end{bmatrix},$$

$$var\begin{bmatrix} \boldsymbol{c}_1 \\ \vdots \\ \boldsymbol{c}_4 \end{bmatrix} = \boldsymbol{I} \otimes \begin{bmatrix} \sigma^2_{c_1} & \cdots & \sigma_{c_1,c_4} \\ \vdots & \ddots & \vdots \\ \sigma_{c_4,c_1} & \cdots & \sigma^2_{c_4} \end{bmatrix},$$

$$var\begin{bmatrix} \boldsymbol{e}_1 \\ \vdots \\ \boldsymbol{e}_4 \end{bmatrix} = \boldsymbol{I} \otimes \begin{bmatrix} \sigma^2_{e_1} & \cdots & \sigma_{e_1,e_4} \\ \vdots & \ddots & \vdots \\ \sigma_{e_4,e_1} & \cdots & \sigma^2_{e_4} \end{bmatrix}$$

where $\sigma^2_{a_i}$ and $\sigma^2_{m_i}$ were direct and maternal genetic variances, respectively, for trait i ($i = 1$ to 4); σ_{a_i,m_j} was the covariance between the direct genetic effect for trait i and the maternal genetic effect for trait j ($j = 1$ and 4); $\sigma^2_{c_i}$ was the maternal permanent environmental variance for trait i; $\sigma_{c_{ij}}$ was the maternal permanent covariance between traits i and j; $\sigma^2_{e_i}$ and $\sigma_{e_{ij}}$ were residual variances and covariances, respectively and $\boldsymbol{A}$ and $\boldsymbol{I}$ were the numerator relationship and identity matrices, respectively.

In both MTM and SEM analyses, direct or maternal genetic correlations between traits i and j ($r_{g_{ij}}$) were $r_{g_{ij}} = \sigma_{g_{ij}} / \sqrt{\sigma^2_{g_i} \times \sigma^2_{g_j}}$, where $\sigma_{g_{ij}}$ was the direct or maternal genetic covariance between traits i and j, and $\sigma^2_{g_i}$ and $\sigma^2_{g_j}$ were the direct or maternal genetic variances for trait i and trait j, respectively. Phenotypic correlations were calculated based on the estimated (co)variance components from the WOMBAT software package (Meyer, 2007). In this regard, the phenotypic correlation is equal to the sum of the additive genetic, maternal genetic, permanent environmental and residual covariances between traits one and two, divided by the product of the square roots of the phenotypic variances for both traits.

The goodness of fit for the 6 models combined with the 3 approaches (i.e., STM, MTM and SEM) was determined based on Akaike's information criterion (**AIC**) and the Bayesian information criterion (**BIC**). The AIC was calculated as $AIC = -2logL + 2p$, and $BIC = -2logL + p\log(N - r(x))$, where $logL$ was the natural logarithm of the likelihood function value, p was the

TABLE 2 Model evaluation of the six single-trait animal models (as described in the materials and methods) for tail length (TL), birth weight (BW), weaning weight (WW) and postweaning weight (PWW) according to the AIC and BIC evaluation criteria

Trait	Model	p[a]	AIC	BIC
TL	STM-1	2	6817.2	6829.0
	STM-2	3	6813.4	6831.2
	STM-3	3	**6813.0**	**6830.7**
	STM-4	4	6815.4	6839.1
	STM-5	4	6813.0	6836.7
	STM-6	5	6814.7	6844.3
BW	STM-1	2	7850.5	7865.4
	STM-2	3	7634.0	7656.4
	STM-3	3	7620.7	7643.1
	STM-4	4	7617.8	7647.6
	STM-5	4	**7600.7**	**7632.6**
	STM-6	5	7601.4	7638.7
WW	STM-1	2	5937.1	5947.8
	STM-2	3	5937.9	5953.8
	STM-3	3	**5928.7**	**5944.6**
	STM-4	4	5938.6	5959.8
	STM-5	4	5930.7	5951.9
	STM-6	5	5929.1	5955.7
PWW	STM-1	2	16,666.0	16,678.6
	STM-2	3	16,659.4	16,678.2
	STM-3	3	16,658.4	16,677.2
	STM-4	4	**16,654.0**	**16,680.0**
	STM-5	4	16,657.4	16,682.5
	STM-6	5	16,654.0	16,685.3

Note: Values for model evaluation criteria (AIC and BIC) from the best model are highlighted in bold.

[a]Number of parameters.

TABLE 3 Model evaluation of multiple-trait (MTM) and structural equation models (SEM) (as described in the materials and methods) considering AIC and BIC

		MTM		SEM		
Model	p[a]	AIC	BIC	AIC	BIC	Diff[b]
1	20	35,691.5	35,850.5	35,678.2	35,837.3	13.2
2	30	35,467.5	35,706.0	35,452.3	35,690.9	15.1
3	30	35,455.7	35,602.3	35,438.2	35,679.8	17.5
4	46	35,448.7	35,814.5	35,431.0	35,796.8	17.8
5	40	35,444.4	35,762.5	35,427.1	35,745.1	17.4
6	56	35,441.3	35,786.6	35,427.3	35,682.6	14.0
Best[c]	33	35,439.2	35,694.6	35,422.3	35,674.7	16.9

[a]Number of parameters.

[b]AIC value from the MTM minus AIC from the respective SEM.

[c]The best MTM and SEM models were constructed using the most appropriate single-trait models (i.e., STM-3 for TL, STM-5 for BW, STM-3 for WW and STM-4 for PWW).

number of parameters in the model, N was the number of observations and $r(x)$ was the rank of the fixed effect incidence matrix. The model with the lowest AIC and BIC values was considered the most appropriate model.

3 | RESULTS

3.1 | Model comparison

AIC and BIC values for STM-1 to STM-6 from the genetic analyses of all four traits are given in Table 2. For TL, the largest AIC value was obtained for STM-1, and no significant differences were identified among models STM-2 to STM-6. For the growth traits, models with maternal genetic effects indicated lower AIC and BIC values compared to STM-1 and STM-2. For BW, the best fitting model was STM-5, considering direct genetic, maternal genetic and permanent environmental effects. Model STM-3 was favourable for WW, and STM-4 for PWW. The same favourable STM were selected based on AIC and on BIC.

Table 3 shows the AIC and BIC values for the different MTM and SEM. In the last row for the "best model," we considered the effects and covariance structure for each trait from the respective superior STM for each trait, that is, STM-3 for TL, STM-5 for BW, STM-3 for WW and STM-4 for PWW. Regarding model comparisons with a focus on the same traits and same effects, SEM displayed lower AIC and BIC values compared to MTM, and thus, SEM improved the goodness of fit. Due to the small differences in AIC and BIC values from the full models 6 compared to the "best" MTM or STM, we chose the results from STM-6, MTM-6 and SEM-6 for the ongoing interpretations and discussions in this manuscript. Such an approach allows the deepest insights into all possible covariances for all random effects and trait combinations.

3.2 | (Co)variance components and heritabilities

The STM-6 generates all possible estimates for variance and covariance components of all random effects and displays almost the same AIC and BIC values for all traits compared to the best-fitting model (see Table 3). Genetic parameter estimates for all traits from the full single-trait model (STM-6) are given in Table 4. Additive genetic variances were 3.15 ± 0.87 for TL, 0.11 ± 0.02 for BW, 5.48 ± 2.21 for BW and 8.43 ± 2.68 for PWW. A quite large direct heritability of 0.60 ± 0.08 was estimated for TL. For body weight traits, direct heritabilities ranged from 0.16 ± 0.03 for BW to 0.31 ± 0.09 for PWW. In comparison to the models STM-3 and STM-5, consideration of the direct-maternal genetic covariances in single-trait models (STM-4 and STM-6) was associated with an increase of maternal heritabilities for the studied traits of 20%–50%. Using STM-6, maternal heritability estimates were 0.03 ± 0.03 for TL, 0.12 ± 0.02 for BW, 0.04 ± 0.03 for WW and 0.07 ± 0.03 for PWW. The maternal permanent environmental variance as the proportion of the phenotypic variance (c^2) ranged from 0.04 ± 0.02 for TL to 0.13 ± 0.04 for WW. For TL, a negative correlation of -0.26 ± 0.20 was estimated between direct and maternal genetic effects. The antagonistic direct-maternal correlations were stronger for the weight traits, that is, -0.33 ± 0.15 for BW, -0.65 ± 0.23 for WW and -0.74 ± 0.13 for PWW.

3.3 | Phenotypic and genetic correlations between tail length and body weight traits

Estimates of phenotypic and genetic correlations between the traits from the models MTM-6 and SEM-6 are shown in Table 5. Using MTM-6, the smallest phenotypic correlation was estimated between TL and PWW (0.16 ± 0.03),

TABLE 4 Genetic parameters (σ_p^2 = phenotypic variance; σ_a^2 = additive genetic variance; σ_m^2 = maternal genetic variance; σ_{am} = covariance between direct and maternal genetic effects; σ_c^2 = maternal permanent environmental variance; σ_e^2 = residual variance; h_d^2 = direct heritability; h_m^2 = maternal heritability; $r_{g_{am}}$ = correlation between direct and maternal genetic effects and c^2 = maternal permanent environmental variance as a proportion of the phenotypic variance) from the full single-trait animal model (STM-6) for tail length at birth (TL), birth weight (BW), weaning weight (WW) and postweaning weight (PWW)

	Genetic parameters									
Trait	σ_p^2	σ_a^2	σ_m^2	σ_{am}	σ_c^2	σ_e^2	h_d^2	h_m^2	$r_{g_{am}}$	c^2
TL	5.24 (0.25)	3.15 (0.87)	0.16 (0.14)	−0.19 (0.02)	0.19 (0.10)	1.92 (0.45)	0.60 (0.08)	0.03 (0.03)	−0.26 (0.11)	0.04 (0.02)
BW	0.70 (0.01)	0.11 (0.02)	0.08 (0.01)	−0.03 (0.02)	0.05 (0.01)	0.49 (0.02)	0.16 (0.03)	0.12 (0.02)	−0.33 (0.15)	0.07 (0.01)
WW	18.32 (0.99)	5.48 (2.21)	0.72 (0.44)	−1.28 (0.58)	2.47 (0.77)	11.64 (1.78)	0.30 (0.11)	0.04 (0.03)	−0.65 (0.23)	0.13 (0.04)
PWW	27.03 (0.83)	8.43 (2.68)	2.02 (1.23)	−3.07 (1.04)	0.97 (0.56)	18.68 (1.53)	0.31 (0.09)	0.07 (0.03)	−0.74 (0.13)	0.04 (0.02)

Note: Corresponding standard errors of estimates as generated by the WOMBAT software package (Meyer, 2007) are given in brackets.

TABLE 5 Phenotypic, direct genetic and maternal genetic covariances (above the diagonal) and respective correlations (below the diagonal) between traits from the full multiple-trait (MTM-6) and full structural equation model (SEM-6)

		Phenotypic				Direct genetic				Maternal genetic			
Model	Trait	TL	BW	WW	PWW	TL	BW	WW	PWW	TL	BW	WW	PWW
MTM	TL		0.78 (0.04)	2.01 (0.38)	1.89 (0.34)		0.16 (0.08)	0.62 (0.17)	1.07 (0.65)		0.12 (0.03)	0.25 (0.20)	0.10 (0.15)
	BW	0.41 (0.02)		1.56 (0.09)	1.29 (0.07)	0. 33 (0.14)		0.33 (0.10)	0.22 (0.11)	0.70 (0.16)		0.30 (0.07)	0.23 (0.05)
	WW	0.20 (0.04)	0.42 (0.02)		17.88 (0.64)	0.23 (0.12)	0.67 (0.18)		1.82 (1.05)	0.25 (0.15)	0.72 (0.13)		2.31 (0.46)
	PWW	0.16 (0.03)	0.31 (0.02)	0.78 (0.01)		0.38 (0.22)	0.43 (0.10)	0.66 (0.19)		0.10 (0.04)	0.58 (0.11)	0.98 (0.07)	
SEM	TL		0.77 (0.04)	1.37 (0.39)	4.24 (0.40)		0.16 (0.08)	0.47 (0.27)	1.89 (0.68)		0.12 (0.03)	0.12 (0.20)	0.26 (0.15)
	BW	0.43 (0.02)		0.52 (0.09)	1.51 (0.08)	0.34 (0.15)		0.20 (0.10)	0.28 (0.12)	0.67 (0.15)		0.18 (0.07)	0.26 (0.05)
	WW	0.15 (0.04)	0.17 (0.03)		16.84 (0.61)	0.23 (0.13)	0.50 (0.24)		1.67 (0.94)	0.14 (0.15)	0.55 (0.19)		1.95 (0.46)
	PWW	0.34 (0.03)	0.35 (0.02)	0.78 (0.01)		0.62 (0.18)	0.48 (0.07)	0.66 (0.19)		0.25 (0.19)	0.62 (0.11)	0.99 (0.10)	

Note: Corresponding standard errors of estimates as generated by the WOMBAT software package (Meyer, 2007) are given in brackets.

TABLE 6 Structural coefficients λ estimated with different structural equation models (SEM-1 to SEM-6)

	Model[b]						
Path[a]	SEM-1	SEM-2	SEM-3	SEM-4	SEM-5	SEM-6	Best[c]
$\lambda_{1\to3}$	−0.07	−0.08	−0.12	−0.11	−0.12	−0.08	−0.13
$\lambda_{1\to4}$	−0.39	−0.41	−0.49	−0.49	−0.47	−0.24	−0.47
$\lambda_{2\to3}$	1.21	1.25	0.98	0.66	1.51	1.37	1.49
$\lambda_{3\to4}$	−0.18	−0.19	−0.19	−0.18	−0.19	−0.14	−0.19

[a]$\lambda_{i\to j}$ represents the change in trait j per 1-unit increase of trait i. Traits are TL (trait 1), BW (trait 2), WW (trait 3) and PWW (trait 4).

[b]Effects of the different models are specified in the materials and methods.

[c]The best SEM was constructed using the effects from the most appropriate single-trait models (i.e., STM-3 for TL, STM-5 for BW, STM-3 for WW and STM-4 for PWW).

and the largest phenotypic correlation was between WW and PWW (0.78 ± 0.01). Similarly, phenotypic correlations among all traits were positive when fitting SEM-6. Direct genetic correlations from MTM-6 ranged from 0.23 ± 0.12 between TL and WW to 0.67 ± 0.19 between BW and WW. With regard to SEM-6, the direct genetic correlations ranged from 0.23 ± 0.13 between TL and WW to 0.66 ± 0.19 between WW and PWW. Maternal genetic correlations were strong and positive among body weight traits with the largest estimates of 0.98 ± 0.07 and 0.99 ± 0.10 between WW and PWW from MTM-6 and from SEM-6, respectively. Strong positive maternal genetic correlations (0.70 ± 0.16 from MTM-6 and 0.67 ± 0.15 from SEM-6) were estimated between TL and BW, but the correlations were smaller between TL and the weight traits WW and PWW recorded at later ages.

3.4 | Structural equation coefficients

Estimated structural coefficients for the effects of TL on WW ($\lambda_{1\to3}$) and on PWW ($\lambda_{1\to4}$) were negative (Table 6). The negative effect of TL on weight traits increased with ageing. In SEM-6, for instance, structural coefficients of −0.08 ($\lambda_{1\to3}$) and of −0.24 ($\lambda_{1\to4}$) indicate that 1 cm increase in TL was associated with a decline of 0.08 kg for WW and 0.24 kg for PWW. With regard to the different SEM, positive structural coefficients were estimated for the effect of BW on WW in the range from 0.66 to 1.49. In contrast, structural coefficients for the effect of WW on PWW ($\lambda_{3\to4}$) were negative in the range from −0.14 to −0.19.

4 | DISCUSSION

4.1 | Genetic parameters and heritabilities for tail length and body weight traits

The quite large direct heritability (0.60) for TL reflects estimates as previously reported for different sheep breeds (e.g., Gizaw et al., 2008; Greeff et al., 2015). Especially the direct heritability of 0.58 for TL in another Merino population (Greeff et al., 2015) is very similar to the estimate of 0.60 from the present study. An even larger heritability of 0.82 was reported for crosses of short-tailed Finnish Landrace and long-tailed Cheviot sheep (Scobie & O'Connell, 2002). In the context of this study, Scobie and O'Connell (2002) addressed the favourable allele frequencies of major genes for TL in this specific population. A crossing focus only on TL might be associated with indirect losses in genetic gain for other breeding goal traits, which have been improved in purebred Merino sheep based on additive-genetic effects during the past decades. Nevertheless, the large heritability for TL in our study indicates the possibility to generate a short-tailed sheep population within a few generations also for intra-breed selection strategies. In a recent study conducted in Merino sheep, Lagler et al. (2022) proved a strong quantitative-genetic background for TL, because a large number of genome-wide markers explained a large proportion of TL variation. Nevertheless, in ongoing gene annotations, Lagler et al. (2022) identified *HOXB13* on chromosome 11 as a potential candidate gene and suggested gene-assisted selection on shorter tails. From a physiological perspective, Fowden et al. (2006) addressed the effects of uterus characteristics of the dam on morphological traits in offspring, possibly explaining the maternal heritability for TL of 0.03. However, the maternal heritability for TL was quite small in the range of the respective standard error, and non-significantly different from zero.

The direct heritability for BW of 0.16 in the present study for Merino is very similar compared to estimates reported for Baluchi sheep (Abbasi et al., 2012), Chinese Merino (Di et al., 2011), Dorper (Kariuki et al., 2010) and the Horro sheep breed (Gowane et al., 2015). In various sheep breeds, the direct heritability for weight traits tended to increase with ageing and ranged from 0.09 to 0.39 for WW and from 0.14 to 0.55 for PWW (Di et al., 2011; Gowane et al., 2015; Jafaroghli et al., 2010), confirming the results from the present study. Especially from the most complex model STM-6, the maternal heritabilities for body weight traits were in agreement with estimates reported by several authors (e.g., Abbasi et al., 2012; Di et al., 2011). Even larger maternal heritabilities were estimated by El Fadili et al. (2000) for BW (0.59) in Moroccan Timahdit breeds and by Areb et al. (2021) for BW (0.34) and WW (0.20) in Bonga sheep. In agreement with our findings, several studies (e.g., Areb et al., 2021; El Fadili et al., 2000) estimated negative direct-maternal genetic covariances for body weight traits. The negative covariances implied increased maternal heritabilities as outlined by Areb et al. (2021), in comparison to maternal heritabilities from models ignoring a direct-maternal covariance structure. From a statistical modelling perspective, Solanes et al. (2004) assumed biased genetic evaluations when ignoring maternal genetic effects and maternal-direct genetic covariances. The antagonism between direct and maternal genetic effects for TL and body weight traits might be due to natural selection for an intermediate optimum (Tosh & Kemp, 1994). From an evolutionary point of view, the genetic background of the physiological and uterine capacities of ewes may prevent oversized body proportions of lambs.

The estimate of c^2 for BW (0.07 from both STM-5 and STM-6) was in accordance with ratios for permanent environmental variances in studies by Abbasi et al. (2012) in Baluchi sheep (0.08), by Areb et al. (2021) in Bonga sheep (0.15), by Gowane et al. (2015) in Malpura sheep (0.09) and by Mandal et al. (2015) in Muzaffarnagari sheep (0.09). For the weight traits WW and PWW recorded later in life, the inclusion of the maternal permanent environmental effect in STM-5 and STM-6 did not improve the goodness of fit when compared to AIC and BIC for STM-3 and STM-4. The significant effect of the maternal permanent environment on BW is mainly due to the uterine capacity and nutritional quality, especially during late gestation. The permanent maternal environmental variance consistently decreased with lamb ageing, especially when altering the feeding behaviour from milk to roughage (Mandal et al., 2012; Zishiri et al., 2013).

4.2 | Genetic correlations between tail length and body weight traits

Direct genetic and maternal genetic correlations between TL and body weight traits from both modelling approaches MTM and SEM were positive, genetically indicating that heavier lambs have longer tails. However, the direct genetic correlations between TL and weight traits were only low to moderate. Thus, selection on shorter tails will not significantly impair body weight development, especially with regard to only small detrimental effects on WW. Genetic correlations among body weight traits decreased with increasing age distances, which is in agreement with estimates in other sheep breeds (Abbasi et al., 2012; Areb et al., 2021; Mohammadi et al., 2015). The positive genetic correlations among the weight traits are evidence for common genetic and physiological mechanisms. Hence, selection for increased WW implies associated calving difficulties due to the positive correlation with BW. Weaning weight can be used as an indicator trait for PWW, especially in the context of the quite large maternal genetic correlations (i.e., 0.98 and 0.99 from MTM-6 and SEM-6, respectively).

4.3 | Structural equation coefficients

We found negative recursive relationships from TL on WW, and from TL on PWW ($\lambda_{1\to3}$ and $\lambda_{1\to4}$, respectively). Lambs with longer tails are more susceptible to breech and tail strikes, which in turn can impair their body weight development. The long and woolly tails imply an increased risk for contamination with dirt and dust, and in causality, causing infections with fly larvae, the so-called myiasis (Pijpers et al., 2006). Physiologically, the contamination caused by excrement residues provides space for the accumulation of fly larvae in the host's skin and subcutaneous membrane. The fly larvae grow inside the host while feeding on its tissue, causing considerable tissue destruction and potential losses of appetite and associated weight losses (Wall, 2012). The different signs in structural equation coefficients and genetic correlations for the same trait combinations impressively demonstrate the advantage of SEM to infer phenotypic trait causalities from genetic mechanisms. The positive genetic correlations between TL and body weight traits indicate that lambs with longer tails may carry the favourable genes for body weight development and would be heavier later in life when ignoring negative recursive relationships at the phenotypic level. Such recursive effects might be induced by additional external risk factors such as tail infections hampering animal performance.

Interestingly, the pure phenotypic correlations between TL and body weight traits were positive, indicating biased estimates when ignoring recursive relationships and feedback mechanisms among traits as outlined by König et al. (2008) in the case of claw health and milk yield. Thus, the magnitude and sign of selection response in trait A by indirect selection on trait B strongly depend on the level of recursiveness and genetic covariances between both traits. In agreement with our results, Razmkabir et al. (2020) and Jafaroghli et al. (2021) reported positive structural equation coefficients of 1.24 and 1.19 for the recursive effect of BW on WW in Markhoz goats and in Moghani sheep, respectively. In the present study, both the recursive relationship and the genetic covariance between BW and WW were positive, indicating correlated genetic gain in WW for an early selection strategy on BW. In contrast to our results for the recursive effect of WW on PWW, positive structural equation coefficients of 0.79 were reported by Razmkabir et al. (2020) and of 0.67 by Jafaroghli et al. (2021). A negative recursive effect of WW on PWW indicates that heavy lambs until weaning (due to the favourable milk supply of their mother) may face difficulties when switching the feeding strategy to own roughage intake, especially for sheep kept in harsh grazing systems (Gernand et al., 2008). Vice versa, lambs with low WW may respond with compensatory growth after weaning (Homem et al., 2007), implying a stronger growth rate increase after weaning compared to heavy lambs with high WW. Furthermore, Valente et al. (2013) pointed out that environmental conditions may determine the sign and magnitude of recursive relationships among phenotypes. In merino sheep, for instance, Dakhlan et al. (2018) and Kelman et al. (2022) reported stronger compensatory growth after weaning for multiple-born lambs compared to single-born lambs, especially in the case of nutritional restrictions.

In contrast to MTM, a great advantage of SEM is the ability to discriminate genetic correlations and recursive relationships among traits (e.g., König et al., 2008; Rosa et al., 2011). From a practical breeding perspective, genetic correlations classically determine the success of breeding goal definitions and genetic gain in single traits. However, it should be kept in mind that recursive relationships between traits of interest can affect selection response. For instance, the sign and magnitude of the response to selection for WW depend on two pathways of relationships: one representing an antagonistic path (i.e., a negative recursive relationship and positive genetic covariance between TL and WW), and another pathway including positive recursive and genetic relationships between BW and WW. As mentioned above, a large heritability for TL and small direct and maternal correlations between TL and WW indicate successful genetic selection on short tails without unfavourable effects on WW. Furthermore, the negative recursive effect of TL on WW indicates short tails in the context of improved body weight development. Especially in the ongoing postweaning period, long-tailed lambs have a greater risk to suffer due to the unfavourable side effects of long tails including breech, tail strikes and infections. Thus, ignoring recursive effects can hamper selection efficiency in a long-term perspective.

5 | CONCLUSION

Different modelling approaches favoured models considering both direct-genetic and maternal-genetic effects plus respective covariance components for the genetic evaluation of TL and body weight traits in Merinoland sheep. The direct heritability for TL from the best-fitting STM was 0.60 ± 0.08, indicating the potential for genetic reduction of tail length within a few generations. For TL, also a small maternal heritability of 0.03 ± 0.03 was estimated, maybe due to intrauterine effects determining the embryonic development. As expected, the maternal heritabilities for body weight traits decreased with ageing. The direct genetic correlations between TL and body weight traits from MTM were positive, indicating unfavourable relationships from a breeding perspective. Genetic correlations between the same traits were very similar when applying SEM. Nevertheless, the structural equation coefficients reflecting trait associations phenotypically were negative (favourable) for the time-lagged effects of TL on WW and on PWW. As an explanation, lambs with long and woolly tails have an increased risk for tail contaminations with dirt and dust causing infections, which in turn impairs the body weight development. The mutual relationships depicted via structural equation coefficients differed in sign and magnitude from the pure phenotypic and genetic correlations. Hence, optimized breeding strategies imply consideration of environmental risk factors, that is, alterations in disease susceptibility when breeding short-tailed Merinoland sheep.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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REFERENCES

Abbasi, M. A., Abdollahi-Arpanahi, R., Maghsoudi, A., Torshizi, R. V., & Nejati-Javaremi, A. (2012). Evaluation of models for estimation of genetic parameters and maternal effects for early growth traits of Iranian Baluchi sheep. *Small Ruminant Research*, *104*(1–3), 62–69.

Aikins-Wilson, S., Bohlouli, M., & König, S. (2021). Maternal and direct genetic parameters for tail length, tail lesions, and growth traits in pigs. *Journal of Animal Science*, *99*(1), skaa398. https://doi.org/10.1093/jas/skaa398

Areb, E., Getachew, T., Kirmani, M. A., Abate, Z., & Haile, A. (2021). Estimation of (co)variance components, genetic parameters, and genetic trends of growth traits in community-based breeding programs of Bonga sheep. *Animal*, *15*(5), 100202.

Dakhlan, A., Moghaddar, N., & van der Werf, J. H. J. (2018). Genotype × birth type or rearing-type interactions for growth and ultrasound scanning traits in merino sheep. *Animal Production Science*, *59*(6), 1016.

Di, J., Zhang, Y., Tian, K. C., Lazate, J. F., Liu, X. M., Xu, Y. J. Z., & Zhang, T. H. (2011). Estimation of (co)variance components and genetic parameters for growth and wool traits of Chinese superfine merino sheep with the use of a multi-trait animal model. *Livestock Science*, *138*(1–3), 278–288.

El Fadili, M., Michaux, C., Detilleux, J., & Leroy, P. L. (2000). Genetic parameters for growth traits of the Moroccan Timahdit breed of sheep. *Small Ruminant Research*, *37*(3), 203–208.

European Union. (2008). Richtlinie 2008/120/EG des Rates vom 18. Dezember 2008 über Mindestanforderungen für den Schutz von Schweinen. https://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX%3A32008L0120 Accessed July 14, 2020.

Fowden, A. L., Ward, J. W., Wooding, F. P. B., Fordhead, A. J., & Christensen, O. F. (2006). Programming placental nutrient transport capacity. *The Journal of Physiology*, *572*(1), 5–15.

French, N. P., Wall, R., & Morgan, K. L. (1994). Lamb tail docking: A controlled field study of the effects of tail amputation on health and productivity. *The Veterinary Record*, *134*(18), 463–467.

Gernand, E., Wassmuth, R., Lenz, H., von Borstel, U. U., Gauly, M., & König, S. (2008). Impact of energy supply of ewes on genetic parameters for fertility and carcass traits in merino long wool sheep. *Small Ruminant Research*, *75*, 80–89.

Gianola, D., & Sorensen, D. (2004). Quantitative genetic models for describing simultaneous and recursive relationships between phenotypes. *Genetics*, *167*(3), 1407–1424.

Gizaw, S., Komen, H., & van Arendonk, J. A. M. (2008). Selection on linear size traits to improve live weight in Menz sheep under nucleus and village breeding programs. *Livestock Science*, *118*(1–2), 92–98.

Gowane, G. R., Prince, L. L. L., Lopes, F. B., Paswan, C., & Sharma, R. C. (2015). Genetic and phenotypic parameter estimates of live weight and daily gain traits in Malpura sheep using Bayesian approach. *Small Ruminant Research*, *128*, 10–18.

Greeff, J. C., Karlsson, L. J. E., & Schlink, A. C. (2015). *Inheritance of tail length in merino sheep* (pp. 237–240). Association for the Advancement of Animal Breeding and Genetics, University of New England.

Haverkamp, H., Brandt, H., & Erhardt, G. (2015). *Variation in der Schwanzlänge beim Merinolandschaf als Basis für züchterische Aktivitäten*. Vortragstagung der DGfZ/GfT September 16–17.

Homem, A. R., da Silva Sobrinho, A. G., Yamamo, S. M., Pinheiro, R. S. B., Buzzulini, C., & Alves de Lima, C. S. (2007). Compensatory body weight gain in growing lambs: Performance and biometrical measurements. *Revista Brasileira de Zootecnia*, *36*(1), 111–119.

Hümmelchen, H., Wagner, H., König, S., & Wehrend, A. (2022). Importance of tail length in sheep and the breeding for short tails. *Tierarztl Prax Grosstiere*, *50*(3), 187–194. https://doi.org/10.1055/a-1851-9402

Jafaroghli, M., Rashidi, A., Mokhtari, M. S., & Shadparvar, A. A. (2010). (Co)variance components and genetic parameter estimates for growth traits in Moghani sheep. *Small Ruminant Research*, *91*(2–3), 170–177.

Jafaroghli, M., Soflaee Sharbabak, M., Ghafouri Kesbi, F., & Mokhtari, M. (2021). Estimation of the autosomal and sex-linked genetic parameters for growth rate and efficiency related traits in Moghani sheep. *Journal of Livestock Science and Technologies*, *9*(1), 69–75.

Kariuki, C. M., Ilatsia, E. D., Kosgey, I. S., & Kahi, A. K. (2010). Direct and maternal (co)variance components, genetic parameters and annual trends for growth traits of dorper sheep in semi-arid Kenya. *Tropical Animal Health and Production*, *42*(3), 473–481.

Kelman, K. R., Alston-Knox, C., Pethick, D. W., & Gardner, G. E. (2022). Sire breed, litter size, and environment influence genetic potential for lamb growth when using sire breeding values. *Animals an open access journal from MDPI*, *12*(4), 501.

König, S., Wu, X. L., Gianola, D., Heringstad, B., & Simianer, H. (2008). Exploration of relationships between claw disorders and milk yield in Holstein cows via recursive linear and threshold models. *Journal of Dairy Science*, *91*(1), 395–406.

Lagler, D. K., Hannemann, E., Eck, K., Klawatsch, J., Seichter, D., Russ, I., Mendel, C., Lühken, G., Krebs, S., Blum, H., Upadhyay, M., & Međugorac, I. (2022). Fine-mapping and identification of candidate causal genes for tail length in the Merinolandschaf breed. *bioRxiv Preprint*. https://doi.org/10.1101/2022.02.27.481613

Lourenco, D. A., Misztal, I., Tsuruta, S., Aguilar, I., Lawlor, T. J., Forni, S., & Weller, J. I. (2014). Are evaluations on young genotyped animals benefiting from the past generations? *Journal of Dairy Science*, *97*(6), 3930–3942. https://doi.org/10.3168/jds.2013-7769

MacCluer, J. W., Boyce, A. J., Dyke, B., Weitkamp, L. R., Pfennig, D. W., & Parson, C. J. (1983). Inbreeding and pedigree structure in standardbred horses. *Journal of Heredity*, *74*, 394–399.

Mandal, A., Dass, G., & Rout, P. K. (2012). Model comparisons for estimation of genetic parameters of pre-weaning daily weight gains in Muzaffarnagari sheep. *Small Ruminant Research*, *106*(2–3), 118–124.

Mandal, A., Karunakaran, M., Sharma, D. K., Baneh, H., & Rout, P. K. (2015). Variance components and genetic parameters of growth traits and Kleiber ratio in Muzaffarnagari sheep. *Small Ruminant Research*, *132*, 79–85.

Meyer, K. (2007). WOMBAT—A tool for mixed model analyses in quantitative genetics by restricted maximum likelihood (REML). *Journal of Zhejiang University Science*, *8*, 815–821.

Mohammadi, K., Abdollahi-Arpanahi, R., Amraei, F., Mohamadi, E. M., & Rashidi, A. (2015). Genetic parameter estimates for growth and reproductive traits in Lori sheep. *Small Ruminant Research*, *131*, 35–42.

Pijpers, A., A. Stegemann, H. Hopster. 2006. Het is in de Nederlandse situatie mogelijk om met goed management verantwoord schapen te houden zonder het couperen van staarten. library.wur.nl/ebooks/minlnv/rapporten/1883153.pdf. Accessed October 12, 2021.

Posht-e Masari, H. A., Hafezian, S. H., Abdollahi-Arpanahi, R., Mokhtari, M. S., Mianji, G. R., & Yeganeh, A. T. (2019). The comparison of alternative models for genetic evaluation of growth traits in Lori-Bakhtiari sheep: Implications on predictive ability and ranking of animals. *Small Ruminant Research*, *173*, 59–64.

Razmkabir, M., Mokhtari, M., Mahmoudi, P., & Rashidi, A. (2020). The comparison of standard and fully recursive multivariate models for genetic evaluation of growth traits in Markhoz goat: Predictive ability of models and ranking of animals. *The Journal of Agricultural Science*, *158*(6), 511–517.

Rosa, G. J. M., Valente, B. D., de los Campos, G., Wu, X. L., Gianola, D., & Silva, M. A. (2011). Inferring causal phenotype networks using structural equation models. *Genetics Selection Evolution GSE*, *43*, 6.

Sambraus, H. H. (2011). Sheep. In *Color atlas of livestock breeds* (7th ed., pp. 160–181). Eugen Ulmer KG.

Sargolzaei, M., Iwaisaki, H., & Colleau, J. J. (2006). CFC: A tool for monitoring genetic diversity. Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, Belo Horizonte, Brazil, CD-Rom comm. No. 27-28.

Schiller, K. F., Grams, V., & Bennewitz, J. (2015). Analysis of growth and feed conversion in purebred and crossbred German Merinolandschaf lambs. *Acronym Animal Breed*, *58*(1), 177–183.

Scobie, D., & O'Connell, D. (2002). Genetic reduction of tail length in New Zealand sheep. *Proceedings of the New Zealand Society of Animal Production.*, *62*, 195–198.

Solanes, F. X., Grandinson, K., Rydhmer, L., Stern, S., Andersson, K., & Lundeheim, N. (2004). Direct and maternal influences on the early growth, fattening performance, and carcass traits of pigs. *Livestock Production Science*, *88*(3), 199–212. https://doi.org/10.1016/j.livprodsci.2003.12.002

Strittmatter, K. (2005). Development, situation and perspectives of the sheep production in Germany. *Züchtungskunde*, *77*, 496–501.

Sutherland, M. A., & Tucker, C. B. (2011). The long and short of it: A review of tail docking in farm animals. *Applied Animal Behaviour Science*, *135*(3), 179–191.

TierSchG. 2006. §5 Absatz 3 Satz 4, §6: Tierschutzgesetz in der Fassung der Bekanntmachung vom 18. Mai 2006 (BGBl. I S. 1206, 1313), das zuletzt durch Artikel 105 des Gesetzes vom 10. August 2021 (BGBl. I S. 3436) geändert worden ist. Im Internet: https://www.gesetze-im-internet.de/tierschg/BJNR012770972.html. Accessed: 02.12.2021

Tosh, J. J., & Kemp, R. A. (1994). Estimation of variance components for lamb weights in three sheep populations. *Journal of Animal Science*, *72*(5), 1184–1190.

Valente, B. D., Rosa, G. J. M., Gianola, D., Wu, X. L., & Weigel, K. (2013). Is structural equation modeling advantageous for the genetic improvement of multiple traits? *Genetics*, *194*(3), 561–572.

Wall, R. (2012). Ovine cutaneous myiasis: Effects on production and control. *Veterinary Parasitology*, *189*(1), 44–51.

Zishiri, O. T., Cloete, S. W. P., Olivier, J. J., & Dzama, K. (2013). Genetic parameters for growth, reproduction and fitness traits in the south African dorper sheep breed. *Small Ruminant Research*, *112*(1–3), 39–48.

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CHAPTER 3

Characterization of German sheep production systems and derivation of respective economic values for breeding traits.

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Characterization of German sheep production systems and derivation of respective economic values for breeding traits

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ABSTRACT

The aim of this study was to derive economic weights for sheep breeding goal traits for specific cluster types. The herd clustering approach considered 25 German sheep herds including descriptors related to area-based factors, management factors, herd information and socio-economic characteristics. The evaluation criterion suggested the application of agglomerative hierarchical clustering with the respective allocation of 25 herds to 3 different clusters. The clusters mainly differed with regard to herd size, production focus, and organic versus conventional management practices. The ongoing contingent valuation approach to derive cluster specific economic weights for 12 breeding goal traits based on the willingness to pay (WTP) considering 25 German sheep farmers, a hypothetical budget of 1000 € for the improvement of a trait per 1 genetic SD, and linear mixed model applications. Significant cluster differences for the WTP ($P < 0.01$) were only identified for the trait feed utilisation with regard to clusters 2 (least-squares mean = 101.65 €) and 3 (least-squares mean = 9.46 €). Least-squares means for individual breeding goal traits were summed up into four overall breeding goal categories. The highest trait importance was expressed for "functional", but displaying a variation among cluster. All clusters rated the trait category "health and welfare" including tail length very similar (range from 24 % to 29 %), with even stronger emphasize on "health and welfare" over "performance" in clusters 1 and 3. In consequence, we suggest to modify sheep breeding goals with a shift from production towards health, welfare and functionality, by consideration of production system particularities.

1. Introduction

Recently, Wiedemann et al. (2023) outlined the economic challenges of sheep production in Germany. In this regard, they highlighted the increasing importance of compensatory payments for agri-environmental service including landscape conservation. From a production perspective, most of the farm income is due to quality lamb meat production in niche markets (Mandolesi et al., 2020). In a comprehensive economic evaluation for the German ministry, von Korn (2020) indicated a profit of 55 € per ewe and year when considering the compensatory payments, but financial losses of 68 € per ewe and year without financial support.

Nevertheless, despite the economic challenges, sheep farming in Germany plays an important role in the German livestock sector. In total 1559,100 sheep from 35 different breeds (count in 2023) are kept in 9560 different farms (Schütte, 2023). A quite large number of 4310 small-sized farms keep less than 49 sheep, mostly in extensive or organic production systems. In contrast, only 850 large-scale herds with more than 500 sheep are listed in official statistics (Statistisches Bundesamt, 2023). Generally, especially with regard to production system characteristics and utilized breeds, sheep farming in Germany is very heterogeneous. Schütte (2023) highlighted nine different major husbandry systems for German sheep farming which were defined as follows: 1. "site-independent herding", 2. "full-time site-bound herding farms", 3. "full-time combined herding and paddock farms", 4. "full-time sheep meat mixed farms", 5. "full-time farms with focus on extensive meat production and landscape management", 6. "part-time landscape managing farms", 7. "part-time direct marketers", 8. "small-scale breeders and self-suppliers, and 9. "small-scale lifestyle sheep farms". The nine identified systems mainly differed with regard to herd size, the grazing area in hectares, the production focus (wool, meat or landscape conservation) and the overall breeding approach (pure breeding versus crossbreeding). The diversity of sheep farm types and sheep farming systems was outlined on the basis of within-country evaluations in

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Tunisia (Ibidhi et al., 2018), but also on a broader Mediterranean scale (Caballero, 2001).

Cluster analyses enables the identification and grouping of herds with similar production system characteristics, as applied for breeding objectives in cattle and pigs (Herold et al., 2021). The most relevant cluster approaches in the context of animal breeding include agglomerative hierarchical clustering (AHC), fuzzy clustering (FZC) and partition around medoids (PAM). A detailed description of the methodological aspects with regard to AHC, FZC and PAM applications is given by Herold et al. (2021). For all cluster approaches, the silhouette width is the mostly used standard evaluation criterion to assess the quality of clustering and to determine the optimal number of clusters. Gorgulu (2010) applied FZC clustering to classify dairy cow herds according to milk yield characteristics. Milán et al. (2003) focused on AHC and used economic data to group sheep herds in an international context. In an international breeding context, Weigel and Rekaya (1999) suggested so-called "borderless clustering", i.e., basing breeding value estimations and breeding goal definitions on production system characteristics rather than on country borders.

Ideally and theoretically, economic weights for breeding goal traits should consider production system particularities and respective farm economy, as well as demands raised by consumers and the society (Amer, 1999; Conington et al., 2004). From a practical perspective, it is not feasible to derive economic weights for breeding goal traits for all specific farm types, but for overall production systems, as determined, e.g., via cluster analyses. So-called objective methods to derive economic weights require detailed information including revenues, costs, herd parameters and biological coefficients related to animal traits (Groen, 1989). However, for novel functional traits without market values (tail length, temperament or sheep behaviour), it might be challenging to set up appropriate profit functions. Especially organic farming aims on alternative functional breeding goal traits, encouraging the development of specific breeding indices. In this regard, Simianer et al. (2007) suggested to broadening existing organic breeding goals by including novel functional traits, but they also noticed the difficulties in deriving economic weights by applying objective approaches. An alternative method to derive economic weights for breeding goal traits is the so called "contingent valuation (CV) method". The CV estimates reflect the respondent́s "willingness to pay" (WTP) using survey technique (Venkatachalam, 2004), taking into account non-market values of traits and products as well as optional values reflecting, e.g., the beauty or elegance of breeding animals for specific conformation traits (Schierenbeck et al., 2009). However, also in the context of breeding goal definitions based on CV and WTP, the expression "economic weight" have been applied widely for many species (e.g., Biermann et al., 2016). The main focus in such context is the WTP for a change per trait unit, e.g., with regard to alterations of productivity or the health status (Olesen et al., 1999). Modified CV methods have been applied to derive economic weights for pig and horse breeding goal traits (Bennett & Blaney, 2003; Edel & Dempfle, 2004; Rohr et al., 1999; Teegen et al., 2008).

Existing sheep breeding goals include performance traits (focus on daily gain, muscling score and back fat thickness), but ignore animal health and welfare indicators (Schäler et al., 2018). Legal regulations will affect future sheep breeding goal definitions, especially the need to breed sheep with short tails, i.e., to avoid tail docking of lambs. Connor and Cowan (2020) conducted a consumer survey addressing the topic of body part mutilations in pigs, calves, lambs, poultry and chicken. The consumer acceptance for such practice was quite low, stimulating the reformulation of breeding objectives and breeding goals. In New Zealand, Kongara et al. (2023) analysed data from a sheep farmer survey. In contrast to consumer opinions, tail docking and castration is considered as a common management practice. The practical breeders highlighted the importance of other breeding goal traits, indicating the need for a compromise, e.g., the development of sustainable breeding goals considering both productivity and novel welfare related traits.

In the context of the above-mentioned challenges, the objectives of this study were twofold. First, we focused on sheep herd-clustering approaches to allocate the herds to specific groups, which can be used for ongoing breeding objectives, e.g., production system specific genetic evaluations. Aiming on production system genetic evaluations, respective economic weights for breeding goal traits are imperative when setting up novel breeding indices. Hence, the second objective addressed the derivation of economic weights for sheep breeding goal traits, taking into account cluster particularities.

2. Material and methods

The present study incorporates two scientific parts. In a first part, cluster analyses was applied for the herd allocation into sheep production systems. In a second part, ongoing CV and WTP approaches were used to derive production system specific economic weights for breeding goal traits. The general database for both parts based on data recorded in 25 participating German sheep farms.

2.1. Herd and farm characterizations

The recorded major farm characteristics (MFC) used as input parameters for the cluster and WTP analyses are presented in Table 1. The MFC can be sub-grouped into A) area-based factors, B) management factors, C) herd information and D) socio-economic characteristics of the farmer. The area-based factors included the total cultivated land area in hectares, distinguished in meadows and pasture used for sheep grazing and the hectares used for crop production (arable land), as well as the number of farm sites. The farm management factors include the subsistence strategy (conventional versus organic), and the distinction in full-time or part-time farming. Further criteria to describe the farm management addressed the farm animal composition (only sheep or mixed farming with other species), the sheep husbandry system (herding without fencing, outside paddock husbandry or permanently keeping the sheep in the stable), and the number of farm employees. Herd

Table 1
Description of the major farm characteristics (MFC) from the 25 sheep farms (area-based factors, management factors, herd information and social -economic characteristics of the farmers).

Main category	Variable	Categories
A) Area-based factors	Farm sites	No. of farm sites
	Grassland	Yes
		No
	Arable land	Yes
		No
	Total area	ha
B) Management factors	Farming method	Conventional
		Organic
	Subsistence strategy	Full-time
		Part-time
	Other animals than sheep	Yes
		No
	Husbandry system	Stable husbandry
		Herding
		Paddock husbandry
	Employees	No. of employees
C) Herd information	Herd size	No. of sheep
	Production type	Meat production
		Landscape management
	Lambings per year	No. of lambings
	Lambing seasons	Spring
		Summer
		Autumn
		Winter
D) Social-economic characteristics of the farmer	Age of the farmer	Years
	Agricultural or veterinary education	Yes
		No

information comprised the herd size, the production focus (meat production or landscape conservation), the number of lambings per year and the primary lambing season. Socio-economic characterizations focused on a direct description of the farmer including age and education in veterinary medicine or agriculture.

2.2. Herd clustering approaches

We applied and evaluated the following three herd clustering approaches AHC, PAM and FZC. All cluster analyses were conducted in R version 2023.09.1 (R Core Team, 2021), and applying the packages “cluster” (Maechler et al., 2023) and “ClustOfVar” (Chavent et al., 2022). In order to identify the best clustering method and to determine the optimal number of clusters, the overall evaluation criterion was the average silhouette width.

2.3. Contingent valuation method

2.3.1. Survey to determine the willingness to pay for 12 breeding goal traits

The general structure of the questionnaire followed the approach as applied by Teegen et al. (2008) and Edel and Dempfle (2004) for horse breeding objectives, supplemented with criteria specific to sheep farming. The WTP for 12 breeding goal traits was assessed by identifying economic preferences of the 25 German sheep farmers. In this regard, each farmer had to allocate a fixed budget of 1000 Euro to the 12 possible breeding goal traits, following the question “which amount of money from the fixed 1000 Euro budget should be used to improve the respective breeding goal trait by 1 genetic standard deviation?” The genetic standard deviation per trait for the respective trait unit was communicated with the farmers, so that they experienced a practical impression for neutral trait comparisons. Overall, the breeding goal traits comprised the 4 categories production, functionality, health and welfare, and exterior traits. Performance traits included 1. Muscle and fat thickness (measured in cm, with a genetic standard deviation of 5.5 cm), 2. Daily weight gain (measured in g, with a genetic standard deviation of 265 g) and 3. Feed utilization (measured as feed conversion ration with a genetic standard deviation of 0.25). The functional trait category considered 4. Maternity (measured as weight gain in lambs (in kg) until day 42 with a genetic standard deviation of 3.5 kg), 5. Longevity (measured in ewes (in years) with a genetic standard deviation of 0.83 years), 6. female fertility (measured as litter size with a genetic standard deviation of 0.20) and 7. Landscape suitability (measured as daily basic activity for grazing and rumination (in hours) with a genetic standard deviation of 2.4 h). The category for health and welfare considered 8. Tail length (measured in cm with a genetic standard deviation of 2.05 cm) , 9. Claw health (measured as an incidence (in %) with a genetic standard deviation of 0.30 %) and 10. endoparasite resistance (measured in eggs per g faeces (a count) with a genetic standard deviation of 280 eggs). Exterior included 11. wool quality (measured as fibre diameter in cm with a genetic standard deviation of 0.5 cm) and 12. Conformation (subjectively scored in points with a genetic standard deviation of 0.4 points)

2.3.2. Derivation of cluster specific economic weights for breeding goal traits

A linear mixed model applying the least square means procedure from the software package “lsmeans” (Lenth, 2016) was used to determine economic weights for breeding goal traits in the previously identified production systems (= clusters). All calculations were performed with R version 2023.09.1 (R Core Team, 2021).

The dependent variable y in this approach was the WTP per trait and respondent, implying 12 consecutive runs considering each breeding goal trait separately. The respective statistical model 1 was defined as follows:

$$y_{ijklmn} = \mu + Breedtype_i + Numberofewes_j + Cluster_k + Farmerage_l + Farmereducation_m + e_{ijklmn} \quad (1)$$

where y = the WTP for the respective breeding goal trait; Breed type$_i$= the fixed effect for meat- or land sheep (i= 1: meat production, i= 2 land sheep), Number of ewes$_j$= the fixed effect for the number of ewes of considering 3 herd size classes (j= 1: < 100 ewes, j= 2: ≥ 100 and < 500 ewes, j= 3: ≥ 500 ewes), Cluster$_k$ = the fixed effect of the respective cluster of the respondent (k= 1, 2 or 3), Farmer age$_l$ = the fixed effect of the age class of the respondent (l= 1: ≤ 35 years, l= 2: 36–55 years, l= 3: ≥ 56 years), Farmer education$_m$= the fixed effect for the agricultural or veterinary education of the respondent (m= 1: veterinarian/agriculture education, m= 2: no veterinarian/agriculture education), and e_{ijklmn}= random residual effect.

In a final step, cluster-specific sheep breeding goals were constructed. In this regard, the lsmeans for the WTP per trait were summed up per cluster, and expressed in percentage in relation to the total WTP (= sum of all lsmeans for all traits within the respective cluster).

3. Results

3.1. Cluster approach comparisons

With regard to the evaluation criterion “silhouette width”, the higher the value, the better the chosen method. Fig. 1 indicates the average silhouette width for the three methods AHC, PAM and FZC. Accordingly, the most suitable method indicating best fit to our data was AHC (black solid line). The first local maximum of the line indicates the optimal number of clusters, i.e., 3 clusters for AHC. Consequently, all ongoing analyses base on the results from the AHC method with 3 clusters. The dendrogram (Fig. 2) shows the allocation of the 25 sheep herds to the 3 clusters. The 25 farms are marked on the x-axis with their respective farm number, while the y-axis reflects the distances with regard to the silhouette width for farm comparisons. Six herds were allocated to cluster 1, 10 herds to cluster 2, and 9 herds to cluster 3.

3.2. Cluster description

A detailed description of the clusters with regard to the farm characterizations is given in Table 2. Cluster 1 includes the smallest number of farms (n= 6) and represents the medium-sized farms with only one farm site. The number of sheep kept in cluster 1 herds is very similar with cluster 3 (median of 103 ewes in cluster 1 herds (range from 50 to 200 ewes), and of 100 ewes in cluster 3 herds), but the total land area per farm comprising with a median of 280 ha is quite large in cluster 1. The cultivated agricultural area ranged from 45 ha to 912 ha. The majority of these farms focus on conventional management strategies, but with regard to between-cluster comparisons, cluster 1 includes the largest percentage of organic farms. All the farms from cluster 1 keep other animal species in addition to sheep, with predominant focus on one specific sheep breed. The majority of these farms use their sheep for meat production and keep them exclusively in stable- or paddock husbandry systems, with one lambing season per year. These farms allocated to cluster 1 have a medium number of employees (at average 5.3 persons) when compared to the cluster 3 farming system (at average 16.6 persons).

Cluster 2 includes the largest number of farms (n= 10), and all of them are full-time conventional farms. With regard to sheep breed diversity, 70 % of the farms allocated to cluster 2 keep more than one sheep breed. A further characteristic of a quite large fraction of farms in cluster 2 is “mixed farming”, i.e., to utilize the sheep for meat production and for landscape conservation. The sheep are kept in stable- or paddock husbandry systems. The farm and herd sizes in cluster 2 are quite large, with at least 65 ha of land under cultivation and at average 525 ewes per herd (range: 255 to 2500 ewes per herd).

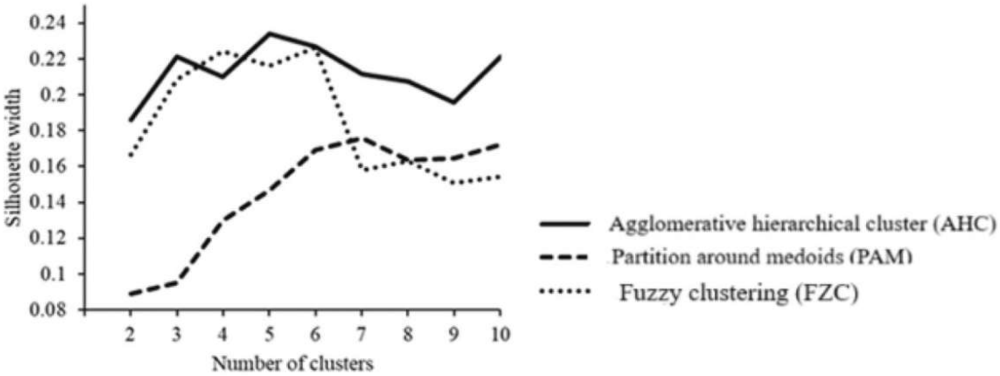

Fig. 1. Average silhouette width for the three clustering methods agglomerative hierarchical cluster (AHC), partition around medoids (PAM) and fuzzy clustering (FZC) and the defined number of clusters.

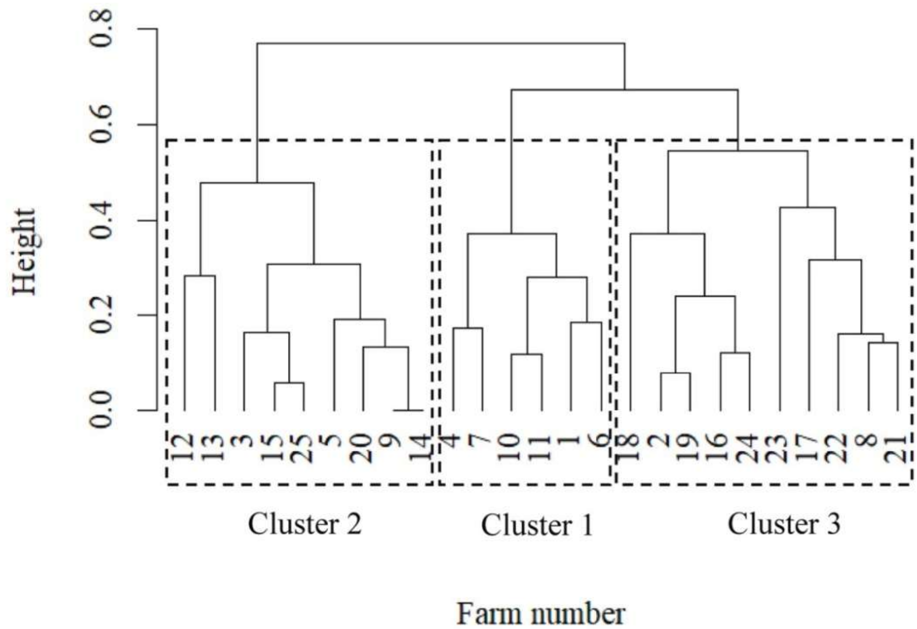

Fig. 2. Dendrogram for the farm allocation via agglomerative hierarchical clustering.

Cluster 3 exclusively includes the 9 part-time and hobby farms. The majority of these farms practice conventional farm management. The main production focus is landscape management, by completely ignoring herding. All of the herds practice a paddock husbandry system, keep at least 56 ewes, and cultivate maximal 88 ha of arable land.

3.3. Willingness to pay for breeding goal traits

The breed type which strongly reflects the production focus significantly affected ($P < 0.05$) the WTP for wool quality. The breeders focussing on meat production valued wool quality with 52.3 € ± 10.8 €, and the farmers keeping land sheep with 82.5 € ± 10.3 €. The lsmeans for the trait "suitability for landscaping" significantly differed ($P < 0.05$) between both breed types, i.e., with 64.1 € ± 17.5 € for the farms with focus on meat production, and with 117.4 € ± 18.2 € for the landscape maintenance production focus. The breed type (i.e., the production focus) also significantly affected the WTP for daily gain ($P < 0.05$). The respective lsmeans was 117.4 € ± € 18.2 € for the farms with focus on meat production, and 64.1 € ± 17.5 € for the landscape maintenance production focus. The age of the farmers significantly affected the WTP for endoparasite resistance ($P < 0.05$), with lsmeans of 84.7 € ± 23 € for the youngest age group, but 134.8 € ± 15 € for the older farmers. In this regard, also the education of the farmer significantly ($P < 0.05$) affected the WTP for endoparasite resistance. Interestingly, farmers without agricultural or veterinary education rated this trait significantly higher (124 € ± 13 €) than the farmer group with education (76 € ± 13 €). Hence, the older farmers without proved qualification in animal or veterinary science stronger emphasis breeding on endoparasite resistance than the younger farmers experiencing a modern education in agricultural or veterinary sciences. The other factors as included in model 1 were not significant ($P > 0.05$) with regard to WTP differences of the breeding goal traits. The number of ewes kept in the herds indicated very similar lsmeans for the respective breeding goal trait WTP, suggesting same breeding objectives for different herd size classes.

The lsmeans for the WTP of the 12 breeding goal traits for the respective cluster are shown in Fig. 3. Among the 12 breeding goal traits, the cluster effect was only significant for the trait feed utilization ($P = 0.008$), with the highest WTP for feed efficiency in cluster 2. In cluster 1, the three breeding goal traits representing the highest values for WTP

Table 2
Distribution of major farm characteristics in clusters 1, 2 and 3.

	Cluster 1	Cluster 2	Cluster 3
Number of farms	6	10	9
A) Area-based factors			
Farm sites			
Single	100 %	70.0 %	77.8 %
Multiple	0 %	30.0 %	22.2 %
Use of grassland	100 %	100 %	100 %
Use of arable land	83.3 %	60.0 %	22.2 %
Total area			
Median (ha)	280	189	20
Range (ha)	45 to 912	65 to 2380	10 to 88
B) Management factors			
Farming method			
Conventional	66.7 %	100 %	77.8 %
Organic	33.3 %	0 %	22.2 %
Subsistence strategy			
Full-time	100 %	100 %	0 %
Part-time	0 %	0 %	100 %
Other animals than sheep	100 %	70.0 %	11.1 %
Number of sheep breeds			
One sheep breed	66.7 %	30.0 %	44.4 %
Several sheep breeds	33.3 %	70.0 %	55.5 %
Husbandry system			
Stable husbandry	100 %	80.0 %	66.7 %
Herding	0 %	50.0 %	0 %
Paddock husbandry	100 %	80.0 %	100 %
No. of employees (average)	5.3	16.6	1.5
C) Herd information			
Number of sheep			
Median	103	525	100
Range	50 to 200	255 to 2500	56 to 350
Production focus on			
Meat production	66.7 %	50.0 %	33.3 %
Landscape management	33.3 %	50.0 %	66.7 %
Lambing seasons			
One lambing season	100 %	80.0 %	100 %
Several per year	0 %	20.0 %	0 %

The variables from category D) are not shown, because they were treated as extra effects in the model for the WTP and not included in the cluster analysis.

were endoparasite resistance with 114.2 € ± 17.6 €, claw health with 106 € ± 29.5 € and female fertility with 104.2 € ± € 22.8 €. The traits with lowest lsmeans for the WTP were landscape suitability (14.9 € ± 30.2 €), tail length (63.5 € ± 19.7 €) and feed utilization (65.39 € ± 19 €). The most important breeding goal traits in cluster 2 included maternity (134 € ± € 40.3), daily gain (116.8 € ± € 21.8 €) and female fertility (112.8 € ± 20.1 €). In contrast, of minor importance were wool quality (40.4 € ± 12.9 €), exterior (47.7 € ± 24.9 €) and muscle- fat thickness (54.4 € ± 19.4 €). With regard to cluster 3, the breeding goal traits reflecting highest lsmeans for the WTP included maternity (180 € ± 43.1 €), endoparasite resistance (96.1 € ± 16.6 €) and female fertility (90.5 € ± 21.5 €). The three traits with minor breeding goal importance in cluster 3 were feed utilization (9.46 € ± 17.9 €), daily gain (65.1 € ± 23.3 €) and longevity (67.5 € ± 30.2 €).

The relative emphasize for the WTP of the breeding goal traits per cluster is expressed in terms of the four overall categories production, functionality, health and welfare, and exterior in Fig. 4. In this regard, the general highest trait importance was expressed for "functional", but displaying a variation across the three cluster (32 % economic weighting in cluster 1, 40 % economic weighting in cluster 2, 43 % economic weighting in cluster 3). All clusters rated the trait category "health and welfare" including the novel traits such as tail length very similar (range from 24 % to 29 %), with even stronger emphasize on "health and welfare" over "performance" in clusters 1 and 3. The classical "exterior" category including wool quality and conformation was of minor importance in cluster 2 (9 %). Accordingly, in clusters 1 and 3, the relative weights of exterior in the overall breeding goal were lower compared to "functional" and "health and welfare". "Performance" displayed a moderate importance in the breeding goal of cluster 2 (27 %), but a relative economic weight of only 15 % in cluster 3.

4. Discussion

This study combines characterizations of sheep farms with a cluster analysis, contributing to a deeper understanding of sheep production particularities in Germany. The ongoing WTP approach for breeding goal traits based a contingent survey technique, aiming on the implementation of production system (= cluster) specific breeding strategies. The respective implications are discussed and contextualized in the following sections.

4.1. Cluster approach comparisons

Most of the clustering approaches addressing animal science topics focused one specific method, i.e., either AHC, PAM or FZC (Gorgulu, 2010; Köbrich et al, 2003; Schütte, 2023). The optimal cluster number generally depends on three major influential factors, i.e., a) the applied cluster method, b) the number of herd characteristics, and c) the number of farms considered in the study (Herold et al., 2021). In the present study, one focus was the evaluation of the different cluster approaches with regard to sheep production system classifications. The overall evaluation criterion was the average silhouette width, allowing the optimal consideration and combination of different farm characteristics with different measurements units such as count data, yield measurements or pure herd descriptions. Fig. 1 shows the comparison of the clustering methods based on the silhouette width, indicating superiority of AHC. Consequently, as suggested by Kaufmann and Rousseeuw (1990) for similar number of clustering elements (i.e., sheep herds in the

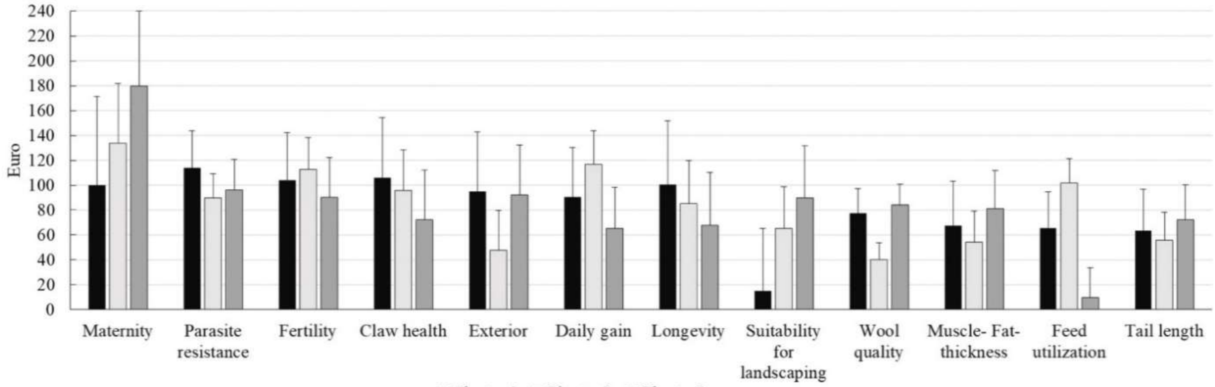

Fig. 3. Least square means for the WTP of breeding goal traits in different clusters with respective standard errors.

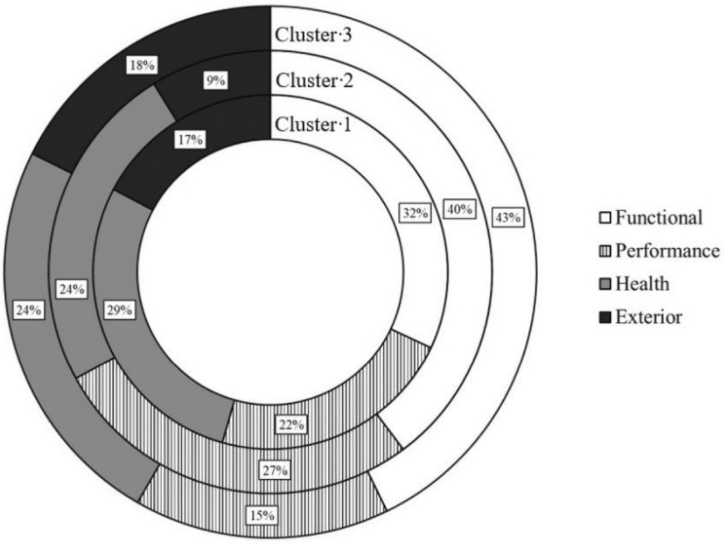

Fig. 4. Relative weighs for the overall trait categories functionality, performance, health and welfare, and exterior in breeding goals of the three different clusters.

present study), we chose the clusters generated via AHC for the ongoing breeding approaches. Although PAM and FZC enable the simultaneous consideration of different input data types (e.g., binary data, Gaussian distributed data, count data, etc.), the number of farms is the most relevant parameter contributing to the average silhouette width (Maione et al., 2019). Herd allocations to the different clusters indicated some differences, depending on the applied clustering approach FZC, PAM or AHC. Especially when comparing herd allocations from FZC and PAM, cluster compositions differed. With the AHC application, a clear distinction between the three clusters was possible, indicated through the obvious vertical distances in the dendrogram (Fig. 2). Distance calculations in AHC base on the "gower"-distance (Gower, 1971) as modified by Struyf et al. (1997), optimally taking into account the different scale levels and measurement units (Pavoine et al., 2009). Consequently, the AHC superiority in the present study might be due to the heterogeneity of input parameters (area-based factors plus management factors plus herd information plus social characteristics). To our knowledge, FZC was applied in other species with focus on only one or two types of input parameters, but not in sheep. Gorgulu (2010) used FZC to allocate 136 dairy cows into 4 clusters according to 6 cow characteristics including only "individual cow variables", i.e., lactation number, 305-day milk yield, age at first insemination, age at first calving, the length of the dry period and calving interval. In our study, the average silhouette width for FZC was smaller compared to the average silhouette from the AHC application. A possible explanation addresses the chosen herd characteristics. Gorgulu (2010) solely focused on individual cow variables, by completely ignoring environmental or average herd characteristics. For such objective, FZC might be the most suitable approach (Herold et al., 2021).

Schütte (2023) applied the PAM herd clustering approach, and allocated 359 German sheep herds to 9 different clusters reflecting distinct production system characteristics. In contrast to our approach with only 2 or maximal 3 possible options per question, the survey by Schütte (2023) implied a broader range of possible answers per characterization parameter. For example, with regard to the input parameter "utilization", we considered the options "meat production" and "suitability for landscaping", but Schütte (2023) additionally included herds with focus on "wool production" and on "milk production". However, a larger number of herds included in the survey enables a larger variety of possible answers per questions, ultimately contributing to the preference of a specific clustering approach.

In Tunisia and on the basis of 1025 sheep farms, Ibidhi et al. (2018) identified 5 sheep production systems and 4 distinct feeding systems using principal components analysis (PCA) and multivariate *k*-means classification. The identified cluster characteristics differed from the results in our study, because most of the considered herd input parameters were related to feed supply, feed resources and feed availability. Milán et al. (2003) used a 2-step approach considering PCA for a first categorization of farm types, and afterwards, on the basis of an overall categorisation, they applied AHC clustering. Input data from 52 sheep farms in Spain considered characteristics being related to our MFC: total surface (ha), arable land (ha), production focus, herd size and age of the farmer. In their clustering approach, 4 cluster groups were formed on the basis of 41 variables. Toro-Mujica et al. (2015) characterized sheep production systems in Chile by applying AHC. In analogy with our AHC results, 3 major production systems (cluster) were identified, mainly differing with regard to herd size, sheep / cattle ratio and agricultural particularities. Similar to our study, 14 variables were used for the analysis.

The four main farm characteristics used for sheep farm clustering in the present study were also considered by Riveiro et al. (2013) to categorize 44 Spanish dairy sheep herds, but the number of questions was much larger (in total 190 herd variables). Riveiro et al. (2013) defined 6 distinct clusters: large traditional farms, small traditional farms, farms with complementary agricultural activities, emerging small farms, modernized medium-sized farms and dairy sheep farms without arable land. Osorio-Avalos et al. (2015) used the Ward clustering approach (Ward, 1963) to allocate Merino sheep herds with similar environmental conditions into distinct groups to improve the reliability of genetic evaluations through the consideration of larger contemporary groups. For clustering, they considered 4 climatic variables, 10 variables related to managing systems and 6 variables reflecting the productivity of the herd. In analogy to our study, Osorio-Avalos et al. (2015) considered 25 sheep herds. However, in contrast to the quite homogeneous herds included in their dataset, the heterogeneity of herd characteristics contributed to a clearer separation of clusters in our present study. An alternative for simultaneous consideration of classical environmental and animal characteristics might be the application of a 2-step cluster analysis. In this regard, for the classification of 2024 organic dairy cattle herds, Ivemeyer et al. (2018) considered topographic and structural herd characteristics in a first step, and afterwards in step 2, the cow-related factors such as productivity.

4.2. Interpretation of cluster characteristics

The cluster analysis clearly indicated 3 production systems for sheep husbandry in Germany, with a main separation criterion according to herd size. Cluster 1 is comprised of medium-sized family farms, cluster 2 of large-scale farms, and cluster 3 of small farms with focus on sheep husbandry from a leisure time perspective. Nevertheless, a substantially larger percentage of farms is represented in clusters 2 and 3, supporting the classification by Schütte (2023), i.e., a fraction of 65 % of small and medium sized herds versus 35 % large-scale sheep herds in Germany. In all clusters, utilization of grasslands for the sheep played a dominant role, but differences in the utilization of arable land are obvious. Arable land as an additional source for forage production comprised more than 60 % of all herds in clusters 1 and 3, but only 22.3 % in cluster 2. Grazing of sheep on pasture still is a common farming practice in Germany as outlined in a comprehensive survey almost 20 years ago (Statistisches Bundesamt, 2010). Cluster particularities are due to the utilization of arable land in a feeding context. Especially the small and medium-sized herds as allocated to clusters 1 and 3 are seeking for alternative food resources due to the scarcity of areas for pasturing. The different clusters generally focus on different management practices. The large-scale herds from cluster 2 with access to large grazing areas have an exclusive focus on conventional farming practices, while the percentage of organic farming is increasing in the small and medium-sized sheep herds in Germany. In cluster 3 (representing the type of "hobby farming"), organic agriculture is accompanied with part-time sheep farming as an additional source to increase farm income. The herds allocated to clusters 1 and 2 are exclusively managed in full-time. Furthermore, there are notable differences with regard to the distribution of housing systems across the three clusters. Herding is a common practice exclusively used in large-scale herds (cluster 2), which are typically suited to accommodate large flocks. Accordingly, the herd management characteristics were emphasized by Schütte (2023) with regard to sheep herd classifications. Herd management differences were intensively addressed for sheep herd characterization in Spain (Riveiro et al., 2013), but with focus on other factors including the type of buildings and facilities, status of mechanization and digitalization. In consequence, due to the country specific particularities describing sheep farming, there are limitations for a borderless clustering approach in an international context as suggested for dairy cattle (Jaeger et al., 2019). In Germany, the obvious distinction between full-time (herds in clusters 1 and 2) and hobby sheep farming explains the different production focus, i.e., the priority in landscape management (cluster 3) versus meat production (clusters 1 and 2). Nevertheless, there is an increasing trend in Germany to utilize sheep farming for landscape conservation, especially in regions with declining cattle populations and poor yields from crop production, indicating the growing importance of adaption and female fertility instead of productivity (Gernand et al., 2008).

4.3. Willingness to pay for breeding goal traits

The significant cluster effect differences for the WTP for feed utilization between cluster 2 (101.65 € ± 16.7 €) and cluster 3 (9.46 € ± 17.9 €) supports the above mentioned breeding goal particularities with regard to the production focus. Cluster 2 only includes full-time farms with a strong focus on profit maximization through lamb meat production, explaining the strong importance of feed utilization. In such context, i.e., increasing the income through improved meat production, Barros de Freitas et al. (2021) suggested the new breeding traits residual water intake and residual feed intake in addition to feed utilization. A further classical production trait is daily gain. Consequently, the WTP for daily gain was larger in cluster 2 than in cluster 3, because daily gain plays an inferior role for landscape conservation. The WTP for the production trait muscle and fat thickness was on a similar level across clusters. Clelland et al. (2014) suggested to focus on sheep meat quality (especially on intramuscular fat content) instead of pure muscle content, to accelerate income from meat production on specific niche markets. The importance of meat quality traits when producing for nice markers was highlighted for local pig breeds in the WTP study by Biermann et al. (2016). Among all the traits considered in the present sheep WTP approach, production traits displayed the largest heritabilities (Justinksi et al., 2023). Hence, a large economic weight for large heritability traits implies large genetic gain, and vice versa, only small or moderate WTP for low heritability functional traits only marginal selection response, especially in the case of genetic antagonistic trait relationships (König et al., 2013).

The WTP for tail length as a novel breeding goal trait from the category "health and welfare" was of moderate and similar importance in all clusters (55.9 € to 72.2 €). The necessity for breeding on short tails due to direct and indirect effects on sheep wellbeing was highlighted in several recent studies (e.g., Johnson et al., 2023). From an animal health and welfare perspective, clear causalities in this regard were shown, i.e., detrimental effects of long and wooly traits on uterus infections, tail lesions and fractures, and further injuries. In the context of animal health and welfare, similar to tail length, the WTP for parasite resistance and claw disorders were in a range from 89.7 € to 114.2 €, displaying non-significant differences across clusters. Interestingly, we found a significant effect of the farmers' age and education on the WTP for the trait parasite resistance. One explanation for the stronger breeding goal importance of parasite resistance in the older farmer age class might be related to the practical experiences by the shepherds and their motivations for the continuous improvement of pasture management strategies without utilization of anthelmintics (Häring et al., 2008). In an international context, e.g. in Uruguay, parasite resistance is already included in overall breeding objectives (Ciappesoni et al., 2023). In addition to endoparasite resistance, phenotypic and genetic selection on improved ecoparasite resistance, e.g., symptoms related to breech wrinkles, breech wool coverage and wool characteristics, have been suggested in the context of cutaneous myiasis (Bishop & Morris, 2007). However, the challenge to include a large number of novel functional traits into breeding objectives is related to the logistics, financial efforts and objectivity of phenotyping and trait recording (König & May, 2019). With regard to claw health in sheep, Lambertz et al. (2013) introduced new measurable characteristics, which were strongly related with footrot. Hence, there might be potential to modify existing breeding goals towards more health and animal welfare. Especially for the hobby farmers allocated to cluster 3, social aspects in the context of local and endangered breeds might have an economic value. For Washera sheep in West Gojam, Ethiopia, Hundie et al. (2022) applied a WTP approach in an across-breed perspective, and they identified that the WTP for conservation was related with the level of education and financial farm characteristics. Social-cultural aspects were also highlighted by Gizaw et al. (2009) for sheep breeding in an African context.

4.4. Setting up new breeding goals

The overall breeding value definition for sheep in Germany indicates a strong focus on performance traits (50 %) and conformation traits (35 %) (VIT, 2024). Nevertheless, according to our results for the WTP of the four overall trait categories, highest priority was assigned to the "classical" functional traits in the range from 32 % to 43 % across the three clusters. Also the novel functional traits including the trait category "health and welfare" indicate economic weightings similar to performance. Accordingly, Tabbaa et al. (2019) favored functional traits over morphological or exterior characteristics for local sheep breeds located in the Far East. Morphological body measurements or exterior traits only showed weak correlations with adaptive traits (Vanvanhossou et al., 2020), justifying their minor importance for the breeding goal definition in the present study. In sheep, in addition to morphological body traits, wool quality is considered as an exterior trait, but nowadays, wool quality only marginally contributes to the farm income (Krupová et al., 2014). However, some country or breed specific particularities are related with breeding trait preferences. For example in Greece, relative economic weights were larger for production than for functional traits (Theodoridis et al., (2018). In the present study, the complex of novel health and welfare traits is of highest importance in cluster 3, comprising the "hobby farmers" with small sheep herds. Without focus on a specific product (meat), the health and welfare component mainly determines the farm profit for landscape conservation. Nevertheless, the category health and welfare played also a dominant role for meat sheep breeding in Ireland (Byrne et al., 2010), because of the indirect effect of health on productivity. In several studies, resistance to endoparasite or claw disease infections were associated with inefficiency of feed utilization, reduction in growth, and losses in daily gain or weights at different ages (Piedrafita et al., 2010). In agreement with the results from our study, the female fertility trait component (lambing difficulty, litter size) only had moderate importance for sheep breeding in Ireland (Byrne et al., 2010). As a novelty, our study is a first approach considering tail length in the health and welfare category, and aiming on the derivation of economic weights for tail length in sheep. In the context of the future legal aspects related to the routine of tail docking, breeding on short tails will be a major breeding focus, especially in European countries. Trait associations between tail length and other functional or production traits have been evaluated in several studies and sheep populations (e.g., Zhu et al., 2024; Teubes et al. 2023), but without addressing tail length in a breeding goals context. Nevertheless, in contrast to Germany, some other countries already defined overall sheep breeding goals and included an animal health and welfare component. For example in New Zealand, the overall breeding goal considers endoparasite resistance in addition to the "classical traits" lamb growth, meat yield, wooly quality and lamb survival rate till weaning (Sheep Improvement Limited, 2022). In Greece (Ragkos & Abas, 2015), health and welfare traits of the breeding index are the grazing ability and disease resistance. In Ireland, in agreement with the results from our study, the highest breeding goal weight is assigned to functionality, and sheep health is indirectly considered via the entries for medical treatments (Byrne et al., 2012).

5. Conclusion

The AHC clustering approach was superior in terms of the evaluation criterion "average silhouette width" compared to the PAM and FZC methods, and clearly allocated 25 German sheep herds into 3 distinct clusters. Main cluster differences were related to herd size, to the production focus (meat production or landscape conservation) and to organic or conventional herd management practices. Also social characteristics (education and age of the herd manager) played a role in this regard. Economic weights for breeding goal traits basing on the CV approach and the WTP, displayed the increasing importance of the trait categories functionality and health and welfare over classical production and exterior traits. Nevertheless, variations of economic weights for trait categories (e.g., a range from 32 % to 40 % for "functionality" across clusters) or of single trait importance (least-squares mean of 101.65€ for feed utilisation in cluster 2, but only 9.46 € in cluster 3) suggest specific breeding strategies for specific sheep production systems. Accordingly, genetic evaluations should be evaluated in ongoing studies in the context of possible genotype x production system interactions.

Ethical statement

This breeding study is based on general farm information and costs and prices to derive economic weights. Hence, no specific animal care statement is required.

CRediT authorship contribution statement

J. Oberpenning: Methodology, Investigation, Formal analysis. **K. Brügemann:** Software, Methodology, Investigation. **S. König:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

Herewith we declare that we have no conflicts of interest.

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References

Amer, P. R. (1999). Economic accounting of numbers of expressions and delays in sheep genetic improvement. *New Zealand Journal of Agricultural Research, 42*, 325–336. https://doi.org/10.1080/00288233.1999.9513382

Barros de Freitas, A. C. B., Junior, A. B., Quirino, C. R., & da Costa, R. L. D. (2021). Water and food utilization efficiencies in sheep and their relationship with some production traits. *Small Ruminant Research, 197*, Article 106334.

Bennett, R. M., & Blaney, R. J. (2003). Estimating the benefits of farm animal welfare legislation using the contingent valuation method. *Agricultural Economics, 29*, 85–98. https://doi.org/10.1111/j.1574-0862.2003.tb00149.x

Biermann, A. D. M., Rommelfanger, E., Anthe, H., Frevert, H., & König, S. (2016). Economic values and evaluation of breeding schemes for non-market traits with applications to an endangered pig breed. *Livestock Science, 183*, 63–71.

Bishop, S. C., & Morris, C. A. (2007). Genetics of disease resistance in sheep and goats. *Small Ruminant Res, 70*(1), 48–59. https://doi.org/10.1016/j.smallrumres.2007.01.006

Byrne, T. J., Amer, P. R., Fennessy, P. F., Hansen, P., & Wickham, B. W. (2012). A preference-based approach to deriving breeding objectives: applied to sheep breeding. *Animal : an international journal of animal bioscience, 6*(5), 778–788.

Byrne, T. J., Amer, P. R., Fennessy, P. F., Cromie, A. R., Keady, T. W. J., Hanrahan, J. P., McHugh, M. P., & Wickham, B. W. (2010). Breeding objectives for sheep in Ireland: a bio-economic approach. *Livestock Science, 132*(1-3), 135–144.

Caballero, R. (2001). Typology of cereal-sheep farming systems in Castile-La Mancha (south central Spain). *Agricultural Systems, 68*, 215–232.

Chavent, M., Kuentz, V., Liquet, B., & Saracco, J. (2022). *ClustOfVar: Clustering of Variables*, 21.

Ciappesoni, G., Marques, C., Navajas, E., Peraza, P., Carracelas, B., Vera, B., & Monzalvo, C. (2023). Breeding for sheep parasite resistance in extensive production systems in Uruguay: From phenotype to genotype. In *, 28. Proceedings of the International Symposium on Sustainable Animal Production and Health: Current Status and Way Forward* (pp. 224–235).

Clelland, N., Bunger, L., McLean, K. A., Conington, J., Maltin, C., Knott, S., & Lambe, N. R. (2014). Prediction of intramuscular fat levels in Texel lamb loins using X-ray computed tomography scanning. *Meat Science, 98*(2), 263–271.

Conington, J., Bishop, S. C., Waterhouse, A., & Simm, G. (2004). A bioeconomic approach to derive economic values for pasture-based sheep genetic improvement programs. *Journal of Animal Science*, 1290–1304.

Connor, M., & Cowan, S. L. (2020). Consumer evaluation of farm animal mutilations. *Research in Veterinary Science, 128*, 35–42.

Edel, C., & Dempfle, L. (2004). Ergebnisse einer contingent valuation studie zur bestimmung eines. *Zuchtziels beim Süddeutschen Kaltblut. Züchtungskunde, 2*, 108–116.

Gernand, E., Wassmuth, R., Lenz, H., von Borstel, U. U., Gauly, M., & König, S. (2008). Impact of energy supply of ewes on genetic parameters for fertility and carcass traits in Merino Long Wool sheep. *Small Ruminant Research, 75*(1), 80–89.

Gizaw, S., Komen, H., & van Arendonk, J. A. (2009). Participatory definition of breeding objectives and selection indexes for sheep breeding in traditional systems. *Livestock Science, 128*(1-3), 67–74.

Gorgulu, O. (2010). Classification of dairy cattle Connin terms of some milk yield characteristics using by fuzzy clustering. *Journal of Animal and Veterinary Advances, 9*, 1947–1951.

Groen, A. F. (1989). *Cattle breeding goals and production circumstances*. Wageningen University and Research.

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics, 27*, 857–871.

Häring, D. A., Scharenberg, A., Heckendorn, F., Dohme, F., Lüscher, A., Maurer, V., & Hertzberg, H. (2008). Tanniferous forage plants: agronomic performance, palatability and efficacy against parasitic nematodes in sheep. *Renewable Agriculture and Food Systems, 23*(1), 19–29.

Herold, J., Brügemann, K., & König, S. (2021). Herd clustering strategies and corresponding genetic evaluations based on social-ecological characteristics for a local endangered cattle breed. *Archives Animal Breeding, 64*, 187–198. https://doi.org/10.5194/aab-64-187-2021

Hundie, K., Melak, A., Aseged, T., Hunduma, T., Hailu, A., Tujuba, & Fekensa, T. (2022). Estimating and identifying factors influencing households' willingness to pay for conservation of washera sheep breed in selected areas of West Gojjam Zone, Ethiopia. *Turkish Journal of Agriculture-Food Science and Technology, 10*(12), 2477–2483.

Ibidhi, R., Frija, A., Jaouad, M., & Ben Salem, H. (2018). Typology analysis of sheep production, feeding systems and farmers strategies for livestock watering in Tunisia. *Small Ruminant Research, 160*, 44–53. https://doi.org/10.1016/j.smallrumres.2018.01.010

Ivemeyer, S., Brinkmann, J., March, S., Simantke, C., Winckler, C., & Knierim, U. (2018). Major organic dairy farm types in Germany and their farm, herd, and management characteristics. *Organic Agriculture, 8*, 231–247.

Jaeger, M., Brügemann, K., Naderi, S., Brandt, H., & König, S. (2019). Variance heterogeneity and genotype by environment interactions in native black and white dual-purpose cattle for different herd allocation schemes. *Animal : An International Journal of Animal Bioscience, 13*(10), 2146–2155. https://doi.org/10.1017/s1751731119000144

Johnson, P. L., Scobie, D. R., Dodds, K. G., Powdrell, S. H., Rowe, S. J., & McRae, K. M. (2023). Genetic parameter analysis of bareness and tail traits in New Zealand sheep. *Journal of Animal Science, 101*, skad161. https://doi.org/10.1093/jas/skad161

Kaufman, L., & Rousseeuw, P. J. (1990). *Finding groups in data: an introduction to cluster analysis* (1st ed., p. 355). Wiley- Interscience.

Kongara, K., Corner-Thomas, R., Bruere, S., Lawrence, K., & Gates, M. (2023). Practices and opinions of New Zealand sheep farmers towards pain management in lambs during castration and/or tail docking. *New Zealand Veterinary Journal, 71*(1), 8–17. https://doi.org/10.1080/00480169.2022.2135626

Köbrich, C., Rehman, T., & Khan, M. (2003). Typification of farming systems for constructing representative farm models: two illustrations of the application of multi-variate analyses in Chile and Pakistan. *Agricultural Systems, 76*(1), 141–157.

König, S., Brügemann, K., & Pimentel, E. C. G. (2013). Züchterische Strategien für Tier- und Klimaschutz: was ist möglich und was brauchen wir? *Züchtungskunde, 85*(1), 22–33.

König, S., & May, K. (2019). Invited review: Phenotyping strategies and quantitative-genetic background of resistance, tolerance and resilience associated traits in dairy cattle. *Animal : An International Journal of Animal Bioscience*. https://doi.org/10.1017/S1751731118003208

Krupová, Z., Krupa, E., Wolfová, M., & Michalicková, M. (2014). Impact of variation in production traits, inputs costs and product prices on profitability in multi-purpose sheep. *Spanish Journal of Agricultural Research, 12*(4), 902–912.

Lambertz, C., Friedrich, C., Moors, E., Brandt, H., Erhardt, G., & Gauly, M. (2013). A comparison of claw conformation and claw horn structure of two sheep breeds, and their relationship to footrot incidence. *Small Ruminant Research, 117*(1), 103–107.

Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software, 69*. https://doi.org/10.18637/jss.v069.i01

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2023. Cluster: cluster analysis basics and extensions.

Maione, C., Nelson, D. R., & Barbosa, R. M. (2019). Research on social data by means of cluster analysis. *Applied Computing and Informations, 15*(2), 153–162.

Mandolesi, S., Naspetti, S., Arsenos, G., Caramelle-Holtz, E., Latvala, T., Martin-Collado, D., Orsini, S., Ozturk, E., & Zanoli, R. (2020). Motivations and barriers for sheep and goat meat consumption in Europe: a means–end chain study. *Animals, 10*, 1105.

Milán, M. J., Arnalte, E., & Caja, G. (2003). Economic profitability and typology of Ripollesa breed sheep farms in Spain. *Small Ruminant Research, 49*, 97–105.

Olesen, I., Gjerde, B., & Groen, F. (1999). Methodology for deriving non-market trait values in animal breeding goals for sustainable production systems. *Interbull Bulletin*, 13–21.

Osorio-Avalos, J., Menéndez-Buxadera, A., Serradilla, J. M., & Molina, A. (2015). Use of descriptors to define clusters of herds under similar environmental conditions to improve the level of connection among contemporary groups of mutton type merino sheep under an extensive production system. *Livestock Science, 176*, 54–60.

Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., & Daniel, H. (2009). On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos (Copenhagen, Denmark), 118*, 391–402. https://doi.org/10.1111/j.1600-0706.2009.16668.x

Piedrafita, D., Raadsma, H. W., Gonzalez, J., & Meeusen, E. (2010). Increased production through parasite control: can ancient breeds of sheep teach us new lessons? *Trends in Parasitology, 26*(12), 568–573.

Ragkos, A., & Abas, Z. (2015). Using the choice experiment method in the design of breeding goals in dairy sheep. *Animal : an international journal of animal bioscience, 9*(2), 208–217.

R Core Team. (2021). *R: a language and environment for statistical computing*. Austria: Vienna.

Riveiro, J. A., Mantecón, A. R., Álvarez, C. J., & Lavín, P. (2013). A typological characterization of dairy Assaf breed sheep farms at NW of Spain based on structural factor. *Agricultural Systems, 120*, 27–37.

Rohr, P. V., Hofer, A., & Künzi, N. (1999). Economic values for meat quality traits in pigs. *Journal of Animal Science*, 2633–2640.

Schäler, J., Thaller, G., & Hinrichs, D. (2018). Implementation of breed-specific traits for a local sheep breed. *Agricultural Sciences, 9*, 958–973. https://doi.org/10.4236/as.2018.98067

Schierenbeck, S., König, S., & Simianer, H. (2009). Genetic and environmental impact on auction prices for Holstein cows. *Livestock Science, 121*, 327–334.

Schütte, J. (2023). Typology of German sheep farms - differences in structure, characteristics, challenges and the provision of goods and services. *Small Ruminant Research, 226*, Article 107022. https://doi.org/10.1016/j.smallrumres.2023.107022

Sheep Improvement Limited, 2022. Sheep industry breeding objectives. SIL technical note. Retrieved from https://www.sil.co.nz/files/1661310874929.pdf.

Simianer, H., Augsten, F., Bapst, B., Franke, E., Maschka, R., Rein-Hardt, F., Schmidtko, J., & Stricker, C. (2007). Ökologische milchviehzucht: entwicklung und bewertung züchterischer ansätze unter berücksichtigung der genotyp x umwelt-interaktion und schaffung eines informationssystems für nachhaltige zuchtstrategien. ***Abschlussbericht des BMELV-Projektes***. http://www.orgprints.org/11222/.

Statistisches Bundesamt, 2010. Land- und Forstwirtschaft, Fischerei, Landwirtschaftszählung/Agrarstrukturerhebung, Fachserie 3, Heft 6.

Statistisches Bundesamt, 2023. Land- und Forstwirtschaft, Fischerei, Viehhaltung der Betriebe Viehbestandserhebung: Fachserie 3 Reihe 2.1.3.

Struyf, A., Hubert, M., & Rousseeuw, P. J. (1997). *Clustering in an object-oriented environment*. Department of Mathematics and Computer Science, U.I.A.

Tabbaa, M. J., Barakeh, F. S., & Baker, M. M. (2019). Factors influencing farmers decision on breeding objectives and selection criteria for sheep breeds in Abu Dhabi Emirate, UAE. *Bulgarian Journal of Agricultural Science, 25*(1), 141–152.

Teegen, R., Edel, C., & Thaller, G. (2008). Bewertung der Zuchtzielmerkmale des Trakehner Verbandes mit hilfe der contingent valuation Methode. *Züchtungskunde, 2*, 99–113.

Teubes, M., Cloete, S. W. P., Dzama, K., & Scholtz, A. J. (2023). Is there sufficient genetic variation to breed Elsenburg Merino sheep with shorter tails? *Animal Production Science, 63*(11), 1043–1051.

Theodoridis, A., Ragkos, A., Rose, G., Roustemis, D., & Arsenos, G. (2018). Defining the breeding goal for a sheep breed including production and functional traits using market data. *Animal: An International Journal of Animal Bioscience, 12*(7), 1508–1515.

Toro-Mujica, P., Aguilar, C., Vera, R., Rivas, J., & García, A. (2015). Sheep production systems in the semi-arid zone: changes and simulated bio-economic performances in a case study in Central Chile. *Livestock Science, 180*, 209–219. https://doi.org/10.1016/j.livsci.2015.07.001

Vanvanhossou, S. F. U., Scheper, C., Dossa, L. H., Yin, T., Brügemann, K., & König, S. (2020). A multi-breed GWAS for morphometric traits in four Beninese indigenous cattle breeds reveals loci associated with conformation, carcass and adaptive traits. *BMC genomics, 21*, 1–16. https://doi.org/10.1186/s12864-020-07170-0

Venkatachalam, L. (2004). The contingent valuation method: a review. *Environmental Impact Assessment Review, 24*, 89–124. https://doi.org/10.1016/S0195-9255(03)00138-0

von Korn, S., 2020. Wirtschaftlichkeit der Schafhaltung in Deutschland. Final report. https://www.nutztierhaltung.de/fileadmin/Redaktion/Dokumente/5-Schafe/3-Stallbau/Abschlussbericht_Wirtschaftlichkeit_Schafhaltung.pdf. Accessed 18-02-2025.

VIT, 2024. https://www.vit.de/vit-fuers-tier/zuchtwertschaetzung/zws-sonstige-tierarten (accessed 19 March 2024).

Ward, J. H. (1963). Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association, 58*, 236. https://doi.org/10.2307/2282967

Weigel, K. A., & Rekaya, R. (1999). Clustering herds across country borders for international genetic evaluation. *Interbull Bulletin*.

Wiedemann, A., Lauterbach, J., & Häring, A. M. (2023). In search of the niche - targeting lamb meat consumers in north-east Germany to communicate the ecosystem services of extensive sheep farming systems. *Sustainability, 15*, 10849. https://doi.org/10.3390/su151410849

Zhu, Q., Liu, P., Zhang, M., Kang, Y., Lv, L., Xu, H., & Lan, X. (2024). The detection of a functional 168 bp deletion of the HOXB13 gene determining short tail and its association with senior growth traits in sheep breeds worldwide. *Animals, 14*(11), 1617.

CHAPTER 4

Extension of bio-economic models towards the derivation of economic values of health and welfare traits in Merinoland sheep

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ABSTRACT

The aim of the present study was to derive economic weights for 15 breeding goal traits of a Merinoland sheep population. The specific focus on novel traits including health (endo- and ectoparasite resistances) and welfare (tail length) implied the enhancement of a bio-economic modelling approach as implemented in the ECO-WEIGHT software package. The newly developed subroutine enabled the consideration of disease incidences and treatment costs for health traits and consideration of the herd tail-length status. Economic evaluation criteria from the breeding goal perspective were marginal economic values (MEVs) expressed in Euro per trait unit per ewe and year, and relative economic values (REVs) standardizing the MEV to the respective genetic standard deviation and related to the sum in Euro of all 15 breeding goal traits. Highest MEVs and REVs were derived for ewe fertility traits and survival rates of lambs. In a scenario assuming 100 % sheep with long tails (sheep tail below the hock), REVs comprised 27 % for litter size, 24 % for the survival rate of lambs until weaning, 18 % for the survival rate of lambs till 24 h after birth, and 18 % for ewe conception rate. The REVs of health traits including endo- and ectoparasite resistance traits, tail length and production traits (lamb weights, wool weight) were close to zero in a range from 0 % to 2 %. In sensitivity analyses, we increased the percentage of short-tailed sheep in the flock by increments of 25 % up to a 100 % short-tailed population, but only minor effects on MEVs and REVs of all breeding goal traits were observed. The MEVs and REVs for disease resistance traits were low due to the very high health status in the research herd considered for input data generation. The newly developed software to derive economic weights for sheep breeding goal traits revealed great flexibility regarding trait pattern and sensitivity analyses in the context of environmental particularities and market conditions.

1. Introduction

Recently, Oberpenning et al. (2025) conducted a survey among German sheep breeders, and they clearly identified a breeding focus towards more health and welfare parameters. In such context, and to sustainably improve the profitability of sheep farming, it is imperative to develop an overall sheep breeding goal considering proper economic values (**EVs**) for all breeding goal traits. However, current approaches to derive EVs only include traditional production and functional traits (vit, 2024), because scientific approaches additionally considering welfare and animal health traits imply methodological enhancements of currently available software packages (Wolfova et al., 2009a).

Economic values for breeding goal traits are partial derivatives of the profit function, describing the relationship between profit and biological, economic and production parameters for each of the evaluated breed goal traits (Wolfová et al., 2011). Regarding available methodological approaches to derive EVs, the overall classification differentiates between subjective and objective methods (Böbner, 1994). Objective methods are portioned into either positive (data evaluation) or normative approaches (data simulation). The positive approach involves a regression analysis, evaluating the relationship between the profit of the system and the breeding values of the animals for the trait of interest (Krupová et al., 2008). In contrast, normative methods use profit functions or bio-economic models yielding a simulation of data. A profit function consists of a single equation, designed to represent the relationship between animal performances in economically important traits on the one hand and farm-level profit or some other measure of economic outcome on the other hand (Bourdon, 1998).

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A profit function, however, is not precise or flexible enough to depict specific production system characteristics and economic conditions (Krupová et al., 2008). Alternatively, bio-economic models derive marginal EVs and can apply gene flow methodology to calculate economic weight for specific animal and trait groups (breeding rams and ewes, direct and maternal components of traits). Respective algorithms are reported in the studies by Wolfová et al. (2009a), Wolfová et al. (2009b) and Wolfová et al. (2011), and are implemented in the ECOWEIGHT software package (Wolf et al., 2025). The special feature of the bio-economic modelling approach in ECOWEIGHT is the combination of deterministic and stochastic methods. In dairy sheep, a bio-economic model was applied by Krupová et al. (2009) to determine the impact of functional and production trait alterations on profit. In this study, highest economic priority was identified for the traits milk yield, conception rate, productive lifetime of ewes and litter size.

In meat sheep and considering different farm types, Conington et al. (2004) reported largest EVs for the traits litter size, number of reared lambs, lamb survival and especially for lamb weight before sale by using a bio-economic model. With a specific focus on fertility traits in meat sheep, Afshar and Aboozari (2018) highlighted the importance of litter size, survival rate of lambs and maternity. In addition to fertility, survival and production traits, health traits were considered in an Irish sheep study by Bohan et al. (2019). They derived EVs for the traits lameness and mastitis for national breeding objects by considering several breeds simultaneously. In this regard, Bohan et al. (2019) applied a bio-economic "Teagasc Lamb Production Model (TLPM)", that included physical, financial and economic information. To our knowledge, this is the first economic study in sheep additionally considering health traits in overall breeding goal definitions.

In addition to animal health, welfare traits play an increasing role in modern sheep breeding programs (Oberpenning et al., 2025). In a welfare context and the critical discussion of tail docking to prevent infections (e.g., myiasis) due to fecal contaminations of the long and wooly tail (Hümmelchen et al., 2023), breeding on short tails is the only sustainable approach. Oberpenning et al. (2023) estimated a quite large heritability of 0.60 for tail length in the German Merinoland sheep population, and in consequence, they suggested the inclusion of tail length into overall sheep breeding goals. However, in addition to sufficient genetic trait variation, successful and sustainable breeding goal definitions imply the availability of EVs for all breeding goal traits. Furthermore, infections with endo-parasites (nematodes) strongly affected farm economy (Forbes et al., 2024) and displayed a moderate genetic component or even major gene effects (Gray, 1997), but respective EVs are missing. Consequently, it is imperative to re-calculate EVs for sheep breeding goal traits simultaneously considering "traditional" primary and functional traits, and additionally the novel health and welfare indicators, especially tail length and endoparasite resistance (Slavova, 2022). For these reasons, Wolf et al. (2024) developed a new version of the ECOWEIGHT software package (version 6.0.5). The expanded program for sheep, EWSH1, version 1.1.7, is customized to the new conditions and characteristics of sheep husbandry systems.

The aim of this study was to apply the recently developed EWSH1 software to derive EVs for breeding goal traits in the German Merinoland sheep population, with specific focus on the new breeding goal traits, namely tail length and endoparasite resistance. The study was enhanced through sensitivity analyses to evaluate the effects of future input parameter constellations regarding alterations of product prices, costs and biological coefficients in various scenarios.

2. Material and methods

For the derivation of EVs of breeding goal traits, the recently expanded program for sheep (EWSH1 version 1.1.7 of the software package ECOWEIGHT version 6.0.5) was applied (Wolf et al., 2024). The respective software includes novel features, allowing the consideration of the new health and welfare traits, such as tail length, and infections with endo-parasites, coccidiosis, myiasis and footrot. The expanded EWSH1 version for sheep is a stand-alone program comprising a full reproduction cycle with one lambing per year. In EWSH1, a bio-economic model is implemented, to mimic effects of genetic changes on production and functional traits under alternative sheep management scenarios. The overall evaluation criterion for economic efficiency is on-farm profit, calculated as the difference between total revenue and total costs per ewe per reproductive cycle. In this regard in the present study, marginal economic values (**MEVs**, in € per trait unit) were derived considering 15 breeding goal traits from three breeding goal trait groups (functional traits, production traits and health traits). The set of input files was filled with biological and economic data from a representative Merinoland sheep research farm reflecting modern production system characteristics.

2.1. Basic characteristics of the production system, ewe flock structure and lambing parameters

Data input for this study considered records of the last five production years from a purebred Merinoland sheep population kept at the University Giessen research station "Oberer Hardthof". The herd size comprised ~300 ewes with 100 % own replacement of breeding lambs with undocked tails. Intra-herd selection criteria for females based on phenotypic values for body conformation traits and body condition score (**BCS**), and in the past five years additionally on estimated breeding values for tail length (Oberpenning et al., 2023). New rams are bought at auctions with selection focus on exterior and BCS, and afterwards, the rams are used in a rotational mating system in different flocks over three years to minimize inbreeding. The implemented farming system on "Oberer Hardthof" includes a variety of modern sheep husbandry and feeding characteristics, being representative for meat sheep production in Germany in the next years. Especially the farming practice of keeping undocked sheep and the implementation of respective selection strategies justifies the role of "Oberer Hardthof" as a model operational unit in the current study.

The typical management practices include lambing indoors in winter, grazing in landscaped pastures in summer, a single breeding season each year from July to August, and natural mating. At the age between 18 and 24 months, replacement ewes are mated for the first time. The peak of the lambing season is mid-January. The lambs are reared with the ewes until April and are sold afterwards (apart from the female replacements) in the fattening period with an average weight of 40 kg. The intensive fattening scheme is based on an ad-libitum feeding scheme for roughage (hay and silage), supplemented with commercially available concentrates and with minerals. Lamb sales for slaughtering from late spring until early summer are the predominant income sources. Ewes with more than nine reproduction cycles are excluded from breeding. For the mating of approximately 100 ewes, up to five rams are used (depending on the season), implying an average ram to ewe ratio of 1:30. For keeping a constant herd size, the replacement rate of ewes is 15 %. After the natural mating period of 36 months, the old rams are sold on auction.

Ewe litter size, defined as the number of total lambs born per parity, and lamb losses from birth until weaning, are the most important parameters to define the offspring population structure as input

Table 1
Means for reproductive and longevity characteristics in the sheep flock in scenario 1.

Reproductive and longevity characteristic	
Average lifetime of ewes (years)	6.58
Ewe conception rate (%)	82.80
Culling rate (%)	3.89
Litter size at birth per ewe lambing and per reproductive cycle averaged over all parities	1.74

parameters in the program EWSH1. Table 1 displays the biological coefficients for reproductive and longevity characteristics of ewes in the flock, including averages for litter size, lifetime periods of ewes, conception rate and culling rate. Input parameters for main biological coefficients of the lambs included birth weights and survival rates until weaning for males and females (Table 2). Defined farm objectives regarding productivity in the fattening period were daily weight gains of 300 g for female lambs and of 350 g for male lambs, lamb survival rates of 90 % until first mating, mature weights of 80 kg for ewes in the flock and mature weights of 100 kg for rams. Animals from the flock are sheared once per year, with average fleece weights of 3.5 kg for ewes and 4.5 kg for rams.

2.2. Costs, revenues and subsidies

For the economic calculations, we distinguished between two feeding seasons. The first season covered the period after lamb weaning from summer to autumn where ewes are kept in pasture paddocks for landscaping. The second season comprised the lambing months in winter and spring. During the lambing season, ewes were fed with hay, concentrates and minerals. No extra costs for roughage were assumed, because of the utilization of marginal grazing areas representing common German sheep farming practices (Gernand et al., 2008). The respective area subsidies per hectare usually cover hay or silage production costs. Feeding costs were calculated considering the daily net energy, mineral and water requirements and the respective prices for the feed components. The feed concentrates had an energy content of 10.8 MJ ME/kg, with respective costs of 0.62 €/kg. The energy content of molasses-based mineral feed supplement was 16 MJ ME/kg and the price was 2.20 €/kg. During the period of stable husbandry, the fixed cost component was increased by 10 % due to feed losses for hay and silage. For the product wool, a small price of 0.80 € per kg was considered. After slaughter, the raw hides are not processed into skins, and in consequence, these by-products have no market value. The government subsidies consisted of two types of funding: a subsidy for grazing livestock and a breed premium. In total, subsidies amounted to 159.00 € per ewe per year. The price and cost components used in the present study as ESWH1 program input parameters are listed in Table 3.

2.3. Economic parameters and derivation of economic values for breeding goal traits

Profit (**P**) per ewe and year considered the total revenues (see Table 3) plus governmental subsidies per ewe and year minus the total costs per ewe per year considering for following "animal categories" in relation to the ewe: the ewe itself, the ram for matings, weaned lambs as offspring, female and male flock replacements as offspring (Wolfová et al., 2009a). The respective formula for the profit calculation was:

$$P = (rev - cost) \quad \times n + sub$$

where *rev* and *cost* were the row vectors for the sums of discounted revenues and costs, respectively, per animal from the different "animal categories", *n* was the column vector for the numbers of allocated animals per ewe and reproduction cycle in the "animal categories", and *sub* was the row vector for subsidies.

As a further economic evaluation criterion, the profitability ratio (**PR**) was calculated relating the overall profit P to the total costs (as defined in Table 3) as follows:

$$PR = \frac{100 \times P}{total\ costs}$$

All revenues and costs in all "animal categories" were discounted to the respective birth dates considering an annual discount rate of 0.05. For the derivation of EVs, realization factors for costs and revenues were considered, i.e., reflecting the possible multiple times for their occurrences during an animal's lifespan.

Economic values were derived considering 15 breeding goal traits simultaneously. The traits were categorized into i) functional traits, ii) production traits and iii) health and welfare traits. The functional trait category included the conception rate of the female lamb replacements for first lambing (in €/%), conception rate of adult ewes (in €/%), litter size of lambing ewes (in €/0.01 lambs), survival rate of lambs with the first 24 h after birth (in €/%), survival rate of lambs from 24 h after birth till weaning (in €/%) and productive lifetime of ewes (in €/year). The production trait category included birth weight (in €/kg), weaning weight (in €/kg), mature weight (in €/kg) and fleece weight (in €/kg). The health trait category included the incidences for footrot and myasis in ewes, for endoparasite infections with nematodes in ewes, and the incidence for coccidiosis in lambs (all EVs of health traits are expressed in € per disease case per ewe and year). These EVs represent the increase in disease costs when increasing the number of infections and consider the length of infection. The welfare trait of interest was tail length, considering the fraction of sheep with short tails above the hocks (in € per % increase of the short tailed weaned lambs).

The MEV of trait *i* (MEV_i) in € per unit of the trait per ewe and year was defined as the partial derivative of the profit function with respect to the trait T_i of interest:

$$MEV_i = \frac{\partial profit}{\partial T_i}$$

For the calculation of relative economic value of breeding goal trait *i* (**REV_i**, in %), the MEV_i where standardized, i.e. multiplied by the respective genetic standard deviation (σ_i), and afterwards expressed as a percentage in relation to the sum of the standardized MEVs for all breeding goal traits. The following formula was applied:

$$REV_i = \frac{abs \quad (MEV_i \times \sigma_i)}{\sum abs \quad (MEV_j \times \sigma_j)} x100$$

The genetic standard deviations for the breeding goal traits (Table 4) based on recent own genetic parameter estimations in the German Merinoland population for endoparasites and coccidiosis (unpublished), and for tail length and weight traits (Oberpenning et al. (2023). For the remaining traits, we referred to genetic standard deviations from the studies by Safari and Fogarty (2003) and Safari et al. (2005).

Table 2
Birth weights and survival traits for different litter sizes (singles, twins or triplets) in the scenario 1.

Traits	Singles	Twins	Triplets
% of lambs stillborn or died until 24 h from birth	0.04	0.05	0.02
% of lambs died until 24 h from birth to weaning	0	0.04	0.008
Birth weight for females (kg)	5.1	4.5	4.1
Birth weight of males (kg)	6.5	5.9	4.8

Table 3
Input parameters (value in Euro) for the calculation of veterinary costs, husbandry costs, slaughter costs, revenues and subsidies in all scenarios.

Parameters (unit)	Value
Price for water (€/kg)	0.00183
Costs for drugs against endo- and ectoparasites (euro per kg live weight and drenching)	0.08
Costs for veterinary service and drugs, excluding parasite treatment (€/animal/year)	1.6
Cost for shearing animals (€/animal/shearing)	3.5
Fixed costs per ewe including lambs till weaning (€/year)	19.95
Fixed costs per ram (€/year)	25.96
Wool price (€/kg)	0.8
Price for lambs at weaning (€/kg live weight)	4.50
Price for adult sheep (€/kg live weight)	3.50
Annual discount rate (%)	5.00
Governmental subsidy including subsidies for farm land (€/ewe/year)	159
Cost of labor (€/man-hour)	13.00

Table 4
Breeding goal traits and their respective genetic standard deviations (σ_g) in the Merinoland sheep breed.

Traits (unit)	σ_g
Birth weight (kg)	0.33
Weaning weight (kg)	0.28
Mature weight (kg)	1.42
Fleece weight (kg)	0.19
Conception rate of ewe lambs (%)	8.0
Conception rate of ewes (%)	7.76
Litter size at lambing (0.01 lambs)	17.7
Survival rate of lambs till 24 h of age (%)	5.8
Survival rate of lambs weaning (%)	7.77
Productive lifetime of ewes (years)	0.82
Incidence for footrot	0.08
Incidence for myiasis	0.24
Incidence for coccidiosis in lambs	0.13
Incidence for endo-parasite infections (nematode)	0.12
Fraction of short-tailed weaned lambs (%)	1.77

2.4. Sensitivity analyses

Economic values were derived in the context of five different tail length mating and selection scenarios, reflecting the current sheep tail length status of the herd (see Table 5). The objective was to compare the REVs of 15 breeding traits among the five scenarios reflecting different proportions of short-tailed animals in the herd. Scenario 1 assumed that 100 % of the animals in the herd are long-tailed. A phenotypically short tail was a tail ending above the hocks, while tails below this threshold were categorized as long. In subsequent scenarios, the proportion of ewes with short tails increased incrementally by 25 %. Simultaneously, with increasing proportions of short-tailed animals in the flock, we assumed favorable effects on labor time (see Table 5). The declining person-hours are because short tails need less shearing and health care prevention as outlined by Hümmelchen et al. (2022). In scenario 5, all animals in the flock are 100 % short-tailed.

Sensitivity analyses additionally considered the antagonistic relationships between tail length and weaning weight of lambs as phenotypically and genetically outlined by Oberpenning et al. (2023) and Greeff et al., (2015). In both studies, the genetic correlation estimates indicated unfavorable effects on weight developments at different ages with increasing selection intensity on short tails. The antagonistic correlations were mimicked through the decline of lamb weights in the scenarios with increasing short-tail sheep in the flock (Table 6).

The following assumptions related to the cost components applied universally across all scenarios:

- Independent from tail length: no tail docking applications
- Tail length of rams was assumed to be unknown and no specific mating strategies in this regard were applied, implying that the effect on EVs is determined through the tail length status of the flock (i.e., percentage of animals above or below the hock threshold)
- Negative correlations between conception rates of ewes and tail length (according to the results by Hümmelchen et al. (2023), the short-tailed ewes had on average a 12 % higher conception rate than the long-tailed ewes)
- Negative correlations between conception rates of F1 female breeding lambs and tail length (according to the results by Hümmelchen et al. (2023))
- Consideration of the following intra-herd disease trait incidences based on "Oberer Hardthof" data analyses: incidence of 10 % for endo-parasite infections, incidence of 10 % for coccidiosis in lambs between the ages of 14 days until weaning, incidence of 5 % for myiasis, and an incidence of 5 % for footrot. Preventive treatments of sheep against myiasis and footrot were considered in regular intervals, implying a quite small number of infected sheep (two cases per year), but moderate costs due to the preventative activities.

Table 5
Working hours per ewe and per year for five breeding scenarios according to the proportion of short-tailed ewes in the flock.

Scenario	Fraction of female breeding lambs with short tails	Number of man-hours per lamb and year	Fraction of ewes with short tails	Number of man-hours per ewe and year
1	0 %	3.00	0 %	12.00
2	25 %	2.88	25 %	11.55
3	50 %	2.77	50 %	11.10
4	75 %	2.66	75 %	10.65
5	100 %	2.55	100 %	10.20

3. Results

3.1. Reproduction cycles

The ewe flock structure and litter sizes per reproduction cycle resulting from the input parameter constellations are shown in Fig. 1. The average productive lifetime of ewes comprised 6.58 years. No triplets were born within the first reproductive cycle. Up to the 4-th cycle, the percentage of single lambings was larger than for twins. From the fifth cycle onwards, twins predominated, and in the ninth cycle (as a particularity of the research station flock), only triplets were born.

3.2. Economic evaluations

Costs, revenues and profits as well as the PR from the five tail length scenarios (0 % short tails to 100 % short tails) are shown in Table 7. The government subsidy allocated per ewe was fixed with 159 €, but the different age structures in the flock implied minor alterations in this regard across scenarios. In scenario 1, the annual revenue per ewe was 283.76 €, implying a profit of 175.40 € per ewe and year, a PR of 65.59 % with subsidies and a PR of 6.12 % without subsidies. Scenarios 2 (25 % short tailed-sheep in the flock) to 4 (75 % short tailed-sheep in the flock) indicated declined revenues compared to scenario 1. The costs decreased steadily from scenario 1 (267.41 €) to scenario 5 (236.71 €), because of reduced labor time for the management of short-tailed sheep. The profit gradually increased with increasing proportions of short-tailed sheep in the flock, i.e. from 175.40 € per ewe and year in scenario 1–200.63 € per ewe and year in scenario 5. The most profitable scenario was scenario 5 (100 % short tails), also regarding PR in both evaluations with consideration of governmental subsidies (PR = 84.76 %) and without consideration of governmental subsidies (PR = 17.23 %).

3.3. Economic values

Marginal economic values for the 15 breeding goal traits for all scenarios are displayed in Table 8. In this regard, the three most important traits in scenario 1 (0 % short-tailed) were birth weight (MEV = 4.97 € per kg), weaning weight (MEV = 4.99 € per kg), average survival rate of lambs at lambing until 24 h after birth (MEV = 2.40 € per 1 %), and average survival rate of lambs from 24 h after birth until weaning (MEV = 2.36 € per 1 %). The lowest rated traits with even negative MEV included productive lifetime (MEV = −3.25 € per year), endoparasite infestation with nematodes (MEV = −1.30 € per case and ewe and year) and myiasis (MEV = −1.65 € per case and ewe and year). The already optimized breeding management for productive lifetime in the research herd and the already old ewe age structure might be the explanation for the negative MEV for productive lifetime. Further improvements in this regard are only possible based on inflating breeding costs. An increase in the number of disease cases is associated with higher costs, but not with higher revenues. Hence, a negative change in MEV for disease traits was identified. Alterations in proportions of short-

Table 6
Change in weaning weights (in kg) by increasing the proportion of short-tailed animals in the five scenarios.

Scenario	Fraction of short-tailed animals in the flock	Weaning weight for females (kg)			Weaning weight for males (kg)		
		Singles	Twins	Triplets	Singles	Twins	Triplets
1	0 %	30.2	28.5	26.7	32.0	30.5	28.6
2	25 %	29.7	28.0	26.2	31.5	30.0	28.1
3	50 %	29.2	27.5	25.7	31.0	29.5	27.6
4	75 %	28.7	27.0	25.5	30.5	29.0	27.1
5	100 %	28.2	26.5	24.7	30.0	28.5	26.6

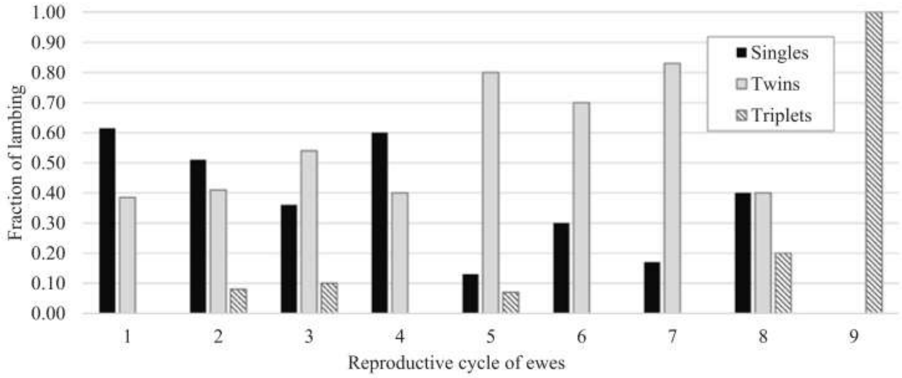

Fig. 1. Fraction of lambings with singles, twins or triplets in different reproduction cycles of the ewe.

Table 7
Revenues, subsidies, costs and profits (in € per ewe and year) and profitability rates (in %) with and without subsidies from five tail length scenarios with increasing proportion of short-tailed animals.

Parameters	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
Revenues (€)	283.76	282.65	281.46	279.27	277.49
Governmental subsidies (€)	159.04	159.27	159.49	159.63	159.85
Costs (€)	267.41	264.49	261.54	259.45	236.71
Profit (€)	175.4	177.42	179.41	179.45	200.63
Profitability rate incl. governmental subsidies (in %)	65.59	67.08	68.6	69.17	84.76
Profitability rate without governmental subsidies % (in %)	6.12	6.86	7.62	7.64	17.23

tailed sheep implied changes in MEVs for production traits. Consequently, MEVs for the breeding goal traits 'birth weight' and 'weaning weight' increased step wisely. The positive (unfavorable) correlation between tail length and weights implied a higher fraction of light sheep in the flock, justifying the stronger economic importance to improve weight traits. The alterations in the proportions of short-tailed sheep in the flocks implied alterations on MEVs for functional traits reflecting female fertility and survival. The MEV for litter size was largest in scenario 1 without short-tailed sheep in the flock with 1.19 € per 0.01 lamb, and steadily declined with increasing short-tailed sheep in the flock up to 1.15 € per 0.01 lamb in scenario 5. Accordingly, the MEV for conception rate of ewes was larger in scenario 1 compared to the other scenarios, and consistently lowest MEVs for litter size and conception rate were derived in scenario 5. This is due to the generally higher female fertility status in short-tailed herds, which explains the marginal economic gain trough further breeding efforts. As expected, the desired herd status for tail length (i.e., a high fraction of short-tailed sheep) was associated with smaller MEVs for tail length, indicated through declining MEVs from scenarios 1–5. Specifically, the MEV for tail length was 0.76 € per % short-tailed weaned lamb per ewe and year in scenario 1, but quite small in scenario 4 (75 % short-tailed sheep in the flock) with 0.1 € per % short-tailed weaned lambs per ewe and year. In scenario 5, with 100 % short-tailed sheep in the herd, further breeding efforts to reduce tail length have no economic value. Marginal economic values for all health and disease resistance traits were very small across all scenarios, due to the high herd health status and assumed genetic correlations of zero between tail length and endoparasite infections.

The REVs are based on the standardized MEVs and enable therefore neutral comparisons of the economic importance of all breeding goal traits (Fig. 2). For all production traits, REVs were smaller in scenario 1 compared to all other scenarios additionally considering tail length. Accordingly, REVs for weaning weight and birth weight increased with increasing percentages of short-tailed sheep in the flock, and were largest in scenario 5. The REVs for the production traits mature weight and for fleece weight were close to zero. Generally, the most important breeding goal traits displaying largest REVs comprised the category for female fertility and longevity, including the survival rate of lambs in the different periods, litter size and conception rate of ewes. The largest REV was 28.24 % for litter size in scenario 5. The small REVs of health traits (incidence of endo-parasite infections, coccidiosis, myiasis, footrot) are due to the low MEVs and small genetic variations of these traits.

4. Discussion

4.1. Modelling approaches for the derivation of economic values

For the derivation of EVs in farm animals, simple profit functions (e.g., Ponzoni, 1988) were applied in the past, while more recently, there is a focus on complex bio-economic modelling approaches (e.g., Conington et al., 2004). Bio-economic model applications imply a higher degree of flexibility, meaning that a quite large number of variables, parameters and breeding traits can be considered simultaneously (Slavova, 2022). In consequence, bio-economic models enable the depiction of specific herd production environments, e.g., as done in the present study for a

Table 8
Marginal economic values (MEV) for the 15 breeding goal traits.

Parameters	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
Birth weight (€ per kg)	4.97	5.15	5.32	5.43	5.58
Weaning weight (€ per kg)	4.99	5.17	5.35	5.46	5.62
Mature weight (€ per kg)	-0.03	-0.07	-0.11	-0.13	-0.15
Fleece weight (€ per kg)	0.89	0.88	0.87	0.87	0.86
Conception rate of ewe lambs (€ per 1 %)	0.06	0.05	0.04	0.03	0.02
Average conception rate of ewes (€ per 1 %)	1.81	1.77	1.73	1.70	1.61
Average litter size for lambing ewes (€ per 0.01 lamb)	1.19	1.17	1.17	1.15	1.15
Average survival rate of lambs at lambing until 24 h after birth (€ per 1 %)	2.40	2.40	2.37	2.34	2.31
Average survival rate of lambs from 24 h after birth till weaning (€ per 1 %)	2.36	2.37	2.38	2.37	2.39
Productive lifetime of ewes in years (€ per year)	-3.25	-2.69	-2.20	-2.00	-1.50
Incidence of footrot in ewes (€ per case per ewe per year)	-0.24	-0.23	-0.22	-0.23	-0.24
Incidence of ecto-parasite infection, myiasis (€ per case per ewe per year)	-1.65	-1.66	-1.67	-1.68	-1.69
Incidence of coccidioses of lambs weaned (€ per case per ewe per year)	-0.15	-0.16	-0.16	-0.16	-0.17
Incidence of endo-parasite infection, nematode (€ per case per ewe per year)	-1.30	-1.29	-1.28	-1.27	-1.27
Fraction of short-tailed weaned lambs (€ per % per ewe and year)	0.77	0.47	0.25	0.10	-

modern Merinoland sheep farming system, and economic evaluations for a broad grid of input parameter pattern and novel trait reflecting health and welfare. Hence, in addition to the sensitivity analyses for the tail length status in the flock, further alternative scenarios can be evaluated in bio-economic modeling approaches. In this regard, important economic evaluations address sheep feeding strategies (e.g., considering feeding intensities or the composition of feeding rations), housing conditions (e.g., considering locations, grassland characteristics or climate), variations of animal-related biological functions (e.g., considering specific lamb growth curves or reproduction cycles), or biological coefficients related to the flock such as varying flock litter sizes (Farell et al., 2022). Such specific features related to, e.g., feed ration particularities, labor time or veterinary costs, are implemented in all programs of the new ECOWEIGHT package for different farm animal species. Furthermore, the detailed consideration and analyses of housing, management and feeding characteristics enable in-depth evaluations and recommendations from a farming system perspective regarding profits, revenues and cost components (Kuchimanchi et al., 2022). Model flexibility in such context of changing input parameter constellations and production system characteristics are of increasing relevance. For sheep farming, Pickering et al. (2015) highlighted the adaptation to new breeding target traits, and emphasized the varying economic importance of health traits with respect to production system characteristics. Furthermore, Pickering et al. (2015) emphasized the consequences of legal regulations and associated effects on sheep breeding issues, e.g., the prohibition of tail docking and correlated impact on myiasis infestations. Standard mixed model applications cannot consider such political or environmental particularities, again favoring the more flexible and comprehensive bio-economic modelling approaches.

A further attempt in this regard, i.e., to derive production system specific EWs of sheep breeding goal traits, was introduced by Oberpenning et al. (2025) by combining contingent valuation technique for sheep breeder survey answers with cluster analyses. The aim of the contingent valuation technique is to create a hypothetical market scenario to infer the 'willingness to pay' of the respondent for specific animal-related traits (Venkatachalam, 2004), enabling consideration of health and welfare traits without direct product prices (Herold et al., 2021). Contingent valuations recently were also applied for economic evaluations of meat quality traits, considering the willingness to pay of consumers (Giannetto et al., 2023). The advantage of such survey-based methodology is the methodological flexibility, but willingness to pay answers mostly reflect spontaneous intentions, which might differ from real household expenses or on-farm cost and revenue components. Cicia et al. (2001) applied a combination of both techniques of bio-economic modelling and contingent valuations to derive EWs for horse breeding traits. In the context of animal exhibitions and show competitions, Schierenbeck et al. (2009) derived EVs for conformation traits by relating animal auction prices to scores for conformation traits in linear regression analyses. This might be a further option to derive EVs for exterior traits in sheep. However, such estimates might be biased, because of the consideration of only pre-selected animals from specific breeding herds instead of a random sample of the population.

4.2. Profitability and economic values in the context of production system and political particularities

For the derivation of EVs of breeding goal traits in sheep, most of the previous studies focused on breeds used for meat production (Wolfová et al., 2011). In the present study, we considered the Merinoland sheep as a dual-purpose breed, i.e., a breed used for landscape conservation and for meat production. The sheep farming system from the research station "Ober Hardthof" represented an environment, which is representative for the future dual-purpose sheep farming sector in Germany (Schütte, 2023). Other authors in other countries derived EVs for dual-purpose sheep reared under extremely challenging environments, or with regard to production system alterations. Amer et al. (1999) derived EVs for sheep breeding goal traits considering different farm types located in New Zealand. On a production intensity scale, Amer et al. (1999) found smallest EVs for litter size in harsh hill regions characterized by low-input production (intensive system:16.45 $ per lamb per ewe and year, hill country: 12.57 $ per lamb per ewe and year, harsh hill country: 11.55 $ per lamb per ewe and year). Accordingly, in UK, Conington et al. (2004) reported differing EVs for ewe fertility, also strongly depending on the production system intensity (intensive, semi-intensive, extensive).

Subsidies for sheep farming in Germany are part of an agricultural

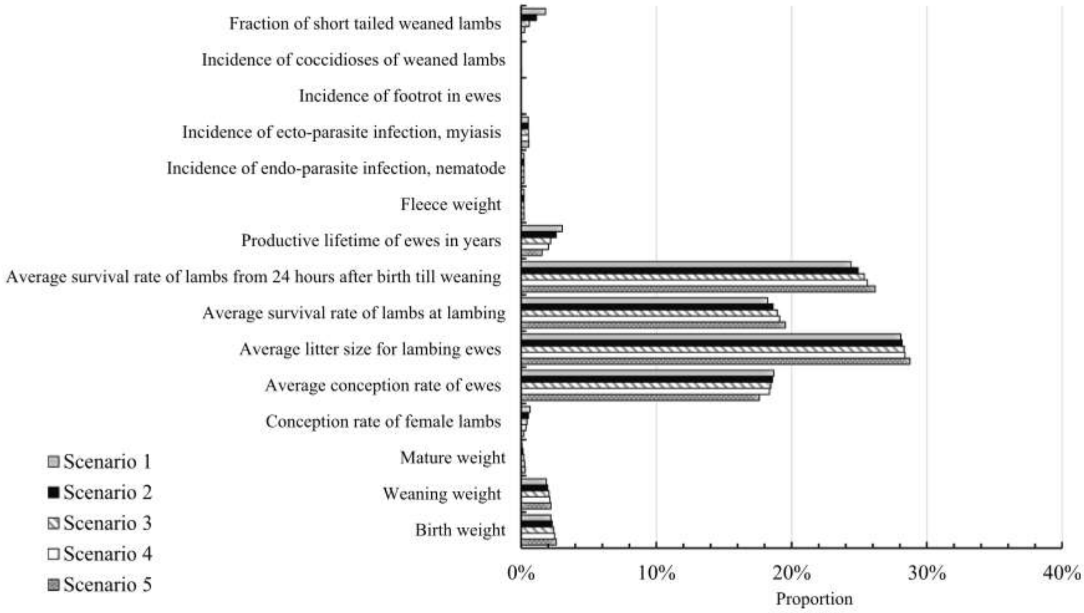

Fig. 2. Relative economic weights (%) for the 15 breeding goal traits for five tail length scenarios (scenario 1–5).

support system (Schütte, 2023). Subsidies are crucial to maintain the profitability of sheep farming in regions with challenging market conditions and environmental factors (Wolfová et al., 2009a). In the modeling approach from the present study, governmental subsidies of 159 € per ewe and year were considered, including payments for landscape conservation. Consideration of subsidies in approaches to derive EVs of breeding goal traits is imperative, because subsidies are a major source of income in sheep farming systems, especially in harsh environments (de Arriba Bueno, 2016). O'Neill et al., (2020) supported the findings from the present study, and strongly emphasized the effect of financial support on sheep-farming profit. For studies conducted in the Czech Republic, Wolfová et al. (2011, 2009b) assumed subsidies of only 15.3 € per ewe for all sheep breeds, indicating the major subsidy differences per ewe and year from an across-country perspective Czech Republic versus Germany. However, also within Germany, differences in governmental payment systems exist due to the structure of German federal states with specific regulations. Krupová et al. (2009) assumed EU subsidies in the range from 70.64 € and 84.63 € per ewe and year for dairy sheep breeds kept in Slovakia. In the study by Conington et al. (2004), subsidies were divided into three categories: compensatory allowance, annual premium, and less favored area supplement. In summary, governmental financial supporting systems differ with respect to country and production system particularities, also explaining differing EW for same traits in different regions or systems.

4.3. Economic values for functional traits, production traits and health and welfare traits

4.3.1. Functional traits

As outlined above, EVs of breeding goal traits strongly depend on the political constraints and production system characteristics. Merinoland sheep are intensively reared and mainly used for lamb meat production in combination with landscaping, explaining the quite large REVs for the functional traits litter size, lamb survival rate from 24 h until weaning and lamb survival rate until 24 h from birth in all scenarios. Especially the litter size trait is given high economic priority in the present study, because larger litters imply more lambs, which can be slaughtered for meat production. On the other hand, farmer surveys indicated that rearing triplets causes significantly more costs than rearing twins, because lamb triplets require more labour time (Oberpenning et al., 2025). Furthermore, lower birth weights in larger litters usually imply higher feeding costs in the fattening period to achieve desired slaughter weights in acceptable time as indicated in breeding goal evaluations for swine (Klein et al., 2018). Nevertheless, in agreement with our study, Slavova and Stancheva (2023) reported large REV for litter size in dairy sheep of 28.74 %. Among all breeding goal traits, largest REVs were also reported for litter size and for lamb survival until weaning for the Merinoland breed by Wolfová et al. (2011). Krupová et al. (2009) reported a large REV for conception rate (15.93 %) in dairy sheep, substantially exceeding the REVs for conception rate in all our "tail-length scenarios" with REV lower than 2 %. An explanation might be the general higher economic importance of conception and fertility in dairy than in meat sheep breeds (Liagka et al., 2025) and the already high level for conception rate in Merinoland sheep in our study. In the present study, the REVs for both lamb survival rates (24 h after birth and from 24 h after birth until weaning) increased almost linearly from scenario 1–5. Such high REVs for lamb survival traits are typical for meat breeds, and were confirmed in the study by Wolfová et al. (2011) considering the Suffolk meat sheep breed. In the present study, the REVs for productive life were comparably small (range 2–3 % for the different scenarios). The already high proportion of ewes can explain the small REVs and MEVs in advanced (high) reproductive cycles, being a major characteristic of the "Oberer Hardthof" research station. Wolfová et al. (2011) reported a younger age structure for ewes in Merino, Romney and Suffolk sheep compared to the average ewe age comprising 6.58 years in our dataset. Accordingly, Meier et al. (2021) found larger REV for cow functional herd life in Holstein than in the local dual-purpose *German Black Pied Cattle* breed, due to the younger age structure in Holstein.

4.3.2. Production traits

The two production traits with highest EVs across all scenarios were birth weight and weaning weight, but both displaying REVs below 3 % across all scenarios. We observed a slight increase in REVs for birth weight from 2 % in scenario 1 to scenarios 2–4, and a REV of 3 % in scenario 5. Accordingly, in economic approaches ignoring tail length as a breeding goal trait, REVs for birth and weaning weights were comparably small with 1.5 % in Merino sheep and 1.2 % Romanov sheep

(Wolfová et al., 2011). The smaller REVs for weight traits than for functional traits reflect the results from the contingent valuation report in other sheep breeds by Oberpenning et al. (2025), and in sheep populations from other countries. In agreement with our study, negative MEVs close to zero and accordingly very small REVs for weight traits until lamb slaughtering were reported by Krupová et al. (2009) in Slovakia and by Conington et al. (2004) in UK.

4.3.3. Health and welfare traits

This is a first study deriving EVs for tail length using a bio-economic modelling approach. In contingent valuations and considering the willingness to pay for novel breeding traits, Oberpenning et al. (2025) reported REVs for health and welfare traits including tail length in a range from 24 % to 29 %. Hümmelchen et al. (2025) and Mainzer et al. (2025) reported neutral phenotypic and genetic relationships between tail length and female fertility in Merinoland sheep. The non-existing impact of the tail length status on ewe fertility might explain the consistently high REV for conception rate in all scenarios 1–5 from the present study.

The health traits including claw health and endoparasite resistance also displayed small REVs. König et al. (2013) applied selection index methodology to assess genetic gain for a variety of breeding strategies and input parameter constellations. For health traits with small heritabilities combined with small EVs, selection response was close to zero or even negative in case of strong antagonistic relationships with production traits. In the present study, the REVs for nematode infections, footrot and coccidiosis were very close to 0 %. The disease trait with a slightly larger REV of 1 % was the infection due to myiasis. Again, the generally high health status in the research herd reflected though the very small number of infection cases per reproduction cycle might explain the small REVs in the overall breeding goal. However, interviews with German shepherds, contingent valuations and willingness to pay approaches indicated an increasing importance of disease resistance in overall sheep breeding goals, especially among the group of younger farmers with university education in agriculture or veterinary sciences (Oberpenning et al., 2025). Farmers are aware of the economic impact of improved disease resistance in sheep, due to the favourable effects on treatment costs and weight gains of lambs (Forbes et al., 2024). Furthermore, the present study indicated the unfavorable effects of endoparasite infections on overall farm profit.

Breeding on improved endoparasite resistance is of increasing economic importance in the near future, due to the concerns of anthelmintic treatments (Cunha et al., 2024). Increasing costs of antibiotic applications are expected (Picot et al., 2022), probably contributing to higher REVs for disease resistance traits in overall breeding goals. In such context, the increasing veterinary costs in the past decade might be an explanation for the increasing weighting factors of health traits in overall breeding goals for dairy cattle (Schmidtmann et al., 2021). Furthermore, expected increasing feeding costs will foster the shift of breeding goal traits from productivity towards functionality and health as shown for dairy cattle kept in tropic Sri Lanka (Samaweera et al., 2022).

The infections with flystrike, named myiasis, were related with health problems and economic losses in several sheep farming systems (Pickering et al., 2015, Shephard et al., 2022). In contrast, in a study conducted over a period of 6 years with Merino sheep, De Barros et al., (2024) reported non-significant associations between tail length and infections with myiasis. In the present study, the respective REVs were close to 1 % in all tail-length scenarios. Again, the currently high health status in a superior research herd environment might explain the comparably small REVs for myiasis. Pickering et al. (2015) also addressed the effect of disease incidences on EWs in a seasonal context. Warmer climates and extensive sheep farming systems will favor fly strike infections, ultimately affecting the economic value and breeding strategies to milden ectoparasite infections (Alahmed, 2004). An indicator trait associated with flystrike infections is the dagginess (**DAG**) score (Sutherland and Tucker, 2011). The MEV for the DAG score was negative in the study by Bohan et al. (2019), because a small value in the scoring system indicates a higher health status.

The incidence of footrot was considered as a novel health trait in our economic evaluations via bio-economic modelling approaches. Byrne et al. (2010) reported REVs for footrot for both animal categories lambs and ewes, reflecting the REV for the footrot incidence of ewes in the present study. Conington et al. (2004) and Green et al. (2012) already considered footrot resistance in breeding objectives, while ignoring bio-economic modelling approaches with simultaneous consideration of the completely breeding trait pattern and biological, revenue and cost input parameters for the derivation of EVs.

In the present study, a bio-economic framework enabling the derivation of EVs additionally for health and welfare traits in sheep, has been developed. However, the current evaluation only represented one specific research herd, and input data recording was restricted to a specific period of the year. In addition to alterations of animal related biological parameters (especially disease incidences), EVs are dynamic due to changing market conditions. Furthermore, sheep production systems are obviously heterogenous (Schütte, 2023), encouraging the derivation of EVs for specific farm types as suggested by Oberpenning et al. (2025).

5. Conclusions

The REVs of breeding goal traits (calculated based on MEVs and genetic standard deviation of traits) in the Merinoland dual-purpose sheep breed indicated strong priority for the female fertility traits litter size and conception rate, and for the lamb survival rates within the first 24 h after birth and from 24 h after birth till weaning. The REVs for production traits of the lambs including weights and weight developments were smaller than 5 %. REVs close to zero were also derived for the health traits reflecting endo- and ectoparasite infections, probably due to the high health status in the research herd evaluated in the present study. In sensitivity analyses with respect to altering fractions of short-tailed sheep in the flock, REV for tail length were smaller than 2 % in all scenarios. The expanded program EWSH1 to derive EWs for sheep breeding goal traits indicated a great flexibility regarding breeding goal trait pattern in sheep and sensitivity analyses, stimulating applications for economic evaluations in other species and breeding scenarios.

Declaration of Competing Interest

Herewith we declare that we have no conflicts of interest.

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References

Afshar, K.P., Aboozari, M., 2018. Estimation of the economic values for the important traits of zel sheep in the intensive production system using a bio-economic model. Veterinary Science. Development 8 (1).

Amer, P.R., McEwan, J.C., Dodds, K.G., Davis, G.H., 1999. Econ. Values ewe prolificacy lamb Surviv. N. Z. sheep. Liv. Prod. Sci. 58, 75–90.

Alahmed, A.M., 2004. Myiasis in sheep farms in Riyadh Region, Saudi Arabia. J. Egypt. Soc. Parasitol. 34 (1), 153–160.

Böbner, C., 1994. Schätzung wirtschaftlicher Gewichte für sekundäre Leistungsmerkmale bei Schweizerischen Zweinutzungsrindern unter Anwendung der dynamischen Optimierung. Diss. ETH Z. üRich. 1994, 127.

Bohan, A., Shalloo, L., Creighton, P., Berry, D.P., Boland, T.M., O'Brien, A.C., Pabiou, T., Wall, E., McDermott, K., McHugh, N., 2019. Deriving economic values for national sheep breeding objectives using a bio-economic model. Livest. Sci. 227, 44–54.

Bourdon, R.M., 1998. Shortcomings of current genetic evaluation systems. J. Anim. Sci. 76 (9), 2308–2323. https://doi.org/10.2527/1998.7692308x.
Byrne, T.J., Amer, P.R., Fennessy, P.F., Cromie, A.R., Keady, T.W.J., Hanrahan, J.P., McHugh, M.P., Wickham, B.W., 2010. Breeding objectives for sheep in Ireland: A bio-economic approach. Livest. Sciene 132, 135–144.
Cicia, G., D'Ercole, E., Marino, D., 2001. Valuing farm animal genetic resources by means of contingent valuation and a bio-economic model: The case of the Pentro horse (No. 108.2001). Nota di Lavoro.
Conington, J., Bishop, S.C., Waterhouse, A., Simm, G., 2004. A bio-economic approach to derive economic values for pasture-based sheep genetic improvement programs. J. Anim. Sci. 82 (5), 1290–1304. https://doi.org/10.2527/2004.8251290x.
Cunha, S.M.F., Lam, S., Mallard, B., Karrow, N.A., Cánovas, Á., 2024. Genomic regions associated with resistance to gastrointestinal nematode parasites in sheep - a review. Genes 15, 187. https://doi.org/10.3390/genes15020187.
de Arriba Bueno, R., 2016. Estimating the importance of subsidies in European sheep farming. Rev. Bras. De. Gest. ão e Desenvolv. Reg. 12 (1), 220–233.
De Barros, G.P., Hötzel, M.J., da Silva, M.C., Avilés, L.L.A., Bricarello, P.A., 2024. Does tail docking prevent Cochliomyia hominivorax myiasis in sheep? A six-year retrospective cohort study. Anim. Welf. 33, e26. https://doi.org/10.1017/awf.2024.26.
Farell, L., Creighton, P., Bohan, A., McGovern, F., McHugh, N., 2022. Bio-economic modelling of sheep meat production systems with varying flock litter size using field data. Animal 16, 100640. https://doi.org/10.1016/j.animal.2022.100640.
Forbes, R.M., Murphy, T.W., Burke, J.M., Lewis, R.M., 2024. Adding parasite resistance to the breeding objective in hair sheep. Journal Animal Science 102 (Supplement_2) 32–33. https://doi.org/10.1093/jas/skae098.
Gernand, E., Wassmuth, R., Lenz, H., von Borstel, U.U., Gauly, M., König, S., 2008. Impact of energy supply of ewes on genetic parameters for fertility and carcass traits in Merino Long Wool sheep. Small Rumin. Res. 75 (1), 80–89.
Giannetto, C., Biondi, V., Previti, A., De Pascale, A., Monti, S., Alibrandi, A., Zirilli, A., Lanfranchi, M., Pugliese, M., Passantino, A., 2023. Willingness to pay a higher price for pork obtained using animal-friendly raising techniques: A consumers' opinion survey. Foods 12 (23), 4201. https://doi.org/10.3390/foods12234201.
Gray, G.D., 1997. The use of genetically resistant sheep to control nematode parasitism. Vet. Parasitol. 72 (3-4), 345–366. https://doi.org/10.1016/S0304-4017(97)00105-2.
Greeff, J.C., Karlsson, L.J.E., Schlink, A.C., 2015. Inheritance of tail length in Merino sheep. Proc. Assoc. Advmt Breed. Genet 21, 237–240.
Green, L.E., Kaler, J., Wassink, G.J., King, E.M., Thomas, R.G., 2012. Impact of rapid treatment of sheep lame with footrot on welfare and economics and farmer attitudes to lameness in sheep. Anim. Welf. 21 (S1), 65–71. https://doi.org/10.7120/096272812X13345905674228.
Herold, J., Brügemann, K., König, S., 2021. Herd clustering strategies and corresponding genetic evaluations based on social-ecological characteristics for a local endangered cattle breed. Arch. Anim. Breed. 64, 187–198. https://doi.org/10.5194/aab-64-187-2021.
Hümmelchen, H., Wagner, H., König, S., Wehrend, A., 2022. Importance of tail length in sheep and the breeding for short tails. Tierarzt Prax. Ausg. G Gross Nutztier 50, 187–194.
Hümmelchen, H., Wagner, H., Brügemann, K., Wenisch, S., König, S., Wehrend, A., 2023. Frequency and characterisation of anomalies and fractures of the caudal spine in sheep with undocked tails. Animals 13 (8), 1419. https://doi.org/10.3390/ani13081419.
Hümmelchen, H., Wagner, H., Brügemann, K., König, S., Wehrend, A., 2025. Effects of breeding for short-tailedness in sheep on parameters of reproduction and lamb development. Vet. Med. Sci. 11 (1), e70138. https://doi.org/10.1002/vms3.70138.
Klein, S., Brandt, H., König, S., 2018. Genetic parameters and selection strategies for female fertility and litter quality traits in organic weaner production systems with closed breeding systems. Livest. Sci. 217, 1–7. https://doi.org/10.1016/j.livsci.2018.08.008.
König, S., Brügemann, K., Pimentel, E.C.G., 2013. Züchterische Strategien für Tier- und Klimaschutz: Was ist möglich und was brauchen wir? Z. üchtungskunde 85, 22–33.
Krupová, Z., Oravcováravcová, M., Krupapa, E., Peškovičová, D., 2008. Methods for calculating economic weights of important traits in sheep. Slovak J. Anim. Sci. 41 (1), 24–29.
Krupová, Z., Wolfová, M., Wolf, J., Oravcová, M., Margetín, M., Peškovičová, D., Daňo, J., 2009. Economic values for dairy sheep breeds in Slovakia. AsianAustralas. J. Anim. Sci. 22 (12), 1693–1702. https://doi.org/10.5713/ajas.2009.90054.
Kuchimanchi, B.R., Bosch, R.R., De Boer, I.J.M., Oosting, S.J., 2022. Understanding farming systems and their economic performance in Telangana, India: Not all that glitters is gold. Curr. Res. Environ. Sustain. 4, 100120. https://doi.org/10.1016/j.crsust.2021.100120.
Liagka, D.V., Politis, A.P., Spilioti, M., Nellas, E., Simitzis, P., Tsiboukas, K., 2025. A comparative economic analysis of different reproductive management strategies in two dairy sheep farms in Greece. Agriculture 15, 719. https://doi.org/10.3390/agriculture15070719.
Mainzer, J., Yin, T., Giambra, I., Hümmelchen, H., Engel, P., Wagner, H., Wehrend, A., König, S., 2025. Parameters, genome-wide associations and potential candidate genes for additive and dominance effects of tail characteristics in Merinoland sheep based on genome sequences in a selection experiment. Anim. Genet. 56, e70041. https://doi.org/10.1111/age.70041.
Meier, S., Arends, D., Korkuc, P., Kipp, S., Segelke, D., Filler, G., Brockmann, G.A., 2021. Implementation of an economic lifetime net merit for the dual-purpose German Black Pied cattle breed. Agriculture 11, 41. https://doi.org/10.3390/agriculture11010041.
Oberpenning, J., Bohlouli, M., Engel, P., Hümmelchen, H., Wagner, H., Wehrend, A., König, S., 2023. Multiple-trait and structural equation modelling approaches to infer genetic relationships between tail length and weight traits in Merinoland sheep. J. Anim. Breed. Genet. 140 (2), 132–143. https://doi.org/10.1111/jbg.12752.
Oberpenning, J., Brügemann, K., König, S., 2025. Characterization of German Sheep Production Systems and Derivation of Respective Economic Values for Breeding Traits. Vet. Anim. Sci. 27, 100432. https://doi.org/10.1016/j.vas.2025.100432.
O'Neill, C., Lim, F.K., Edwards, D.P., Osborne, C.P., 2020. Forest regeneration on European sheep pasture is an economically viable climate change mitigation strategy. Environ. Res. Lett. 15 (10), 104090. https://doi.org/10.1088/1748-9326/abaf87.
Pickering, N.K., Blair, H.T., Hickson, R.E., Johnson, P.L., Dodds, K.G., McEwan, J.C., 2015. Estimates of genetic parameters for breech strike and potential indirect indicators in sheep. N. Z. Vet. J. https://doi.org/10.1080/00480169.2014.961582.
Picot, S., Beugnet, F., Leboucher, G., Bienvenu, A.L., 2022. Drug resistant parasites and fungi from a one-health perspective: A global concern that needs transdisciplinary stewardship programs. One Health 14, 100368. https://doi.org/10.1016/j.onehlt.2021.100368.
Ponzoni, R.W., 1988. The derivation of economic values combining income and expense in different ways - an example with Australian Merino Sheep. J. Anim. Breed. Genet. 105, 143–153. https://doi.org/10.1111/j.1439-0388.1988.tb00260.x.
Safari, A., Fogarty, N.M., 2003. Genetic Parameters for Sheep Production Trait. Estimates from the Literature. Technical Bulletin 49, NSW. Agric. Orange Aust. S 93–100. ISBN 0734715498.
Safari, E., Fogarty, N.M., Gilmour, A.R., 2005. A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. Livest. Prod. Sci. 92, 271–289. https://doi.org/10.1016/j.livprodsci.2004.09.003.
Samaweera, A.M., van der Werf, J.H.J., Boerner, V., Hermesch, S., 2022. Economic values for production, fertility and mastitis traits for temperate dairy cattle breeds in tropical Sri Lanka. J. Anim. Breed. Genet 139, 330–341. https://doi.org/10.1111/jbg.12667.
Schierenbeck, S., König, S., Simianer, H., 2009. Genetic and environmental impact on auction prices for Holstein cows. Livest. Sci. 121, 327–334. https://doi.org/10.1016/j.livsci.2008.07.008.
Schmidtmann, C., Thaller, G., Kargo, M., Hinrichs, D., Ettema, J., 2021. Derivation of economic values for German Dairy breeds by means of a bio-economic model- with special emphasis on functional traits. J. Dairy Sci. 104, 3144–3157. https://doi.org/10.3168/jds.2019-17635.
Schütte, J., 2023. Typology of German sheep farms-Differences in structure, characteristics, challenges and the provision of goods and services. Small Rumin. Res. 226, 107022. https://doi.org/10.1016/j.smallrumres.2023.107022.
Shephard, R., Webb Ware, J., Blomfield, B., Niethe, G., 2022. Priority list of endemic diseases for the red meat industry–2022 update. Final Report, Project B. AHE, 327. Meat & Livestock Australia (MLA).
Slavova, S., Stancheva, N., 2023. Profitability and economic values of productive and functional traits in sheep of Bulgarian dairy synthetic population. J. Hyg. Eng. Des. 43, 6–13.
Slavova, S., 2022. Bio-economic models for deriving economic values for sheep: a review. Agric. Sci. Technol. 14 (3), 3–9.
Sutherland, M.A., Tucker, C.B., 2011. The long and short of it: A review of tail docking in farm animals. Appl. Anim. Behav. Sci. 135 (3), 179–191. https://doi.org/10.1016/j.applanim.2011.10.015.
Venkatachalam, L., 2004. The contingent valuation method: a review. Environ. Impact Assess. Rev. 24, 89–124. https://doi.org/10.1016/S0195-9255(03)00138-0.
vit, 2024. ⟨https://www.vit.de/vit-fuers-tier/zuchtwertschaetzung/zws-sonstige-tierarten⟩ (accessed 15 October 2024).
Wolf, J., Wolfová, M., Krupová, Z., Krupa, E., 2024. User's Manual for the Program Package ECOWEIGHT (C Programs for Calculating Economic Weights in Livestock), Version 6.0.5. Part 2a: Expanded program EWSH1 for Sheep, Version 1.1.7. Institute of Animal Science, Prague Uhříněves, Czech Republic and Slovak Agricultural Research Centre, Nitra, Slovak Republic.
Wolfová, M., Wolf, J., Milerski, M., 2009a. Calculating economic values for growth and functional traits in non-dairy sheep. J. Anim. Breed. Genet. 126 (6), 480–491. https://doi.org/10.1111/j.1439-0388.2009.00815.x.
Wolfová, M., Wolf, J., Krupová, Z., Margetín, M., 2009b. Estimation of economic values for traits of dairy sheep: II. Model application to a production system with one lambing per year. J. Dairy Sci. 92 (5), 2195–2203. https://doi.org/10.3168/jds.2008-1411.
Wolfová, M., Wolf, J., Milerski, M., 2011. Economic weights of production and functional traits for Merinolandschaf, Romney, Romanov and Sumavska sheep in the Czech Republic. Small Rumin. Res. 99 (1), 25–33. https://doi.org/10.1016/j.smallrumres.2011.03.004.

CHAPTER 5

General Discussion

5 General Discussion

The following discussion serves on the one hand to provide an overarching interpretation of the results from chapters 2-4 and, on the other hand, to embed them in the current state of research. The analyses in this study shed light on the correlations and influencing factors with regard to breeding for short tails in Merino sheep.

Chapter 2 analysed the relationships between tail length and selected body characteristics, in particular body weight. Based on a structural equation model (SEM), phenotypic, environmental, and genetic factors were considered simultaneously in order to map a comprehensive structure of effects. The results indicate a high heritability of tail length (h^2=0.6), meaning that the trait responds well to selective breeding.

The economic evaluation of breeding traits in sheep breeding is addressed in chapters 3 and 4. In chapter 3, the preferences of sheep breeders were surveyed using the contingent valuation method, and based on this, an overall breeding value was developed that explicitly includes health traits for the first time.

The results show that health traits are weighted similarly highly by respondents as classic production traits, reflecting the growing importance of animal health and welfare in the practical definition of breeding goals.

Chapter 4 presents an economic evaluation of new breeding goals using a bio-economic model. Health-related traits, including tail length, were considered in this modelling approach for the first time. The results illustrate that tail length as a breeding goal trait has a measurable economic impact on the profitability of sheep farming and is therefore important for the sustainable optimization of breeding programs.

The following section of this chapter takes a closer look at the breeding objective of tail length, explains its relationship to other traits, and assesses its economic impact. It also discusses the extent to which the findings can contribute to the further development and establishment of suitable breeding strategies. Finally, conclusions are drawn and recommendations for practical breeding work are formulated.

5.1 Genetic parameters and heritabilities for tail length and other breeding goal traits

Breeding for short tails is increasingly being addressed as a relevant topic in current research and is being investigated in depth in various studies. In this study, a heritability of 0.6 was determined, which is classified as high and therefore has a favourable effect on breeding. This opens up the possibility of reducing tail docking procedures and pursuing breeding goals relevant to animal welfare. A recent study by Hodge et al. (2025) reports similarly high heritabilities (0.35-0.67). Greef et al. (2015) and Jonsohn et al. (2023) also report high heritabilities for tail length between 0.58 and 0.68. A higher heritability than that found in the present study is reported by Mainzer et al. (2025) at 0.85, which can be explained by the low number of animals.

The high heritabilities for tail length reported in chapter 2, in conjunction with the confirmed results of previous authors, indicate moderate to high heritability for this trait. These results support the approach of selecting for shortened tail length in sheep.

5.2 Genetic correlations between tail length and breeding goal traits

The correlation between traits plays a central role in breeding for short tails, meaning that targeted selection for shorter tails can lead to measurable changes within a few generations (Lagler et al., 2022; Eck, 2020). As shown in chapter two, there is a positive genetic correlation between tail length and weaning weight (0.23 +- 0.12). Hodge et al. (2025) come to similar conclusions. For breeding, this means that breeding for shorter tails also has a negative effect on weight. In addition to body weight, Eck (2020) also found positive correlations between tail length on the one hand and withers height, back length, or the quotient of tail length and withers height on the other hand in sheep. Lagler et al. (2022) recorded body length in addition to tail length and body weight and also found a positive correlation between the traits. Other authors confirm the positive correlations between tail length, body length, and body weight (Hümmelchen et al., 2022; Haverkamp, 2015). In addition, Hümmelchen et al. (2023) phenotyped the tail using sonographic data and also recorded the number of tail vertebrae using X-rays. The presence of wedged and block vertebrae was found to be significantly correlated with tail length. Hümmelchen et al. (2023) found a high prevalence of caudal spine fractures and block or wedged vertebrae in Merinoland lambs; although the study did not measure pain directly, the authors highlighted, that such skeletal breaks are a welfare concern and likely to be painful.

Mainzer et al. (2025) reported heritabilities of 0.23 for the trait number of vertebrae and 0.85 for tail length. For the trait tail abnormalities, a heritability close to zero was found, which in this case is favourable in terms of breeding for short tails. According to the authors, the abnormalities are highly likely to be caused by husbandry-related influences. In addition, there is a negative correlation between the traits tail length and number of vertebrae, which is due to the thickness of the tail. Thinner tails often have more and longer vertebrae than thicker tails (Mainzer et al., 2025). This thesis is supported by Amane et al. (2023), who report a significant influence on the number and length of vertebrae in relation to tail thickness. In addition, the authors conclude that length in cm is sufficient as a recording characteristic, as there is a positive correlation between the vertebral characteristics and these characteristics can be estimated using a model. Accordingly, it is possible to use tail length alone as a predictive parameter to estimate osteology.

As described in chapter 2, tail length was therefore recorded as the sole trait in this study. The aforementioned study by Amane et al. (2023) supports this study design, which eliminates the need to record additional tail traits. According to Eck (2020), tail length measurement is highly reliable, which further justifies the sole recording of tail length in this study. This method of measuring the tail using a centimeter ruler, as used in chapter 2, is therefore practical and reliable. In 2020, Grant et al. assessed the pain response of docked lambs using qualitative behavioural assessment (QBA), with the result, that painkillers had no effect after docking. The absence of an analgesic effect underscores the need to breed for shorter tails.

With regard to further trait correlations, it should be noted, that Hümmelchen et al. (2025) found no negative correlation between tail length and reproductive traits. Similarly, there is no significant correlation between wool quality traits and tail length (Medrado et al., 2021). The correlations between tail length and other breeding traits discussed in this paragraph have been exhaustively examined. To date, no negative consequences of selection for shorter tails have been found. However, further research is needed on the possible influence on tail length for future-oriented breeding traits such as parasite resistance and robustness.

5.3 Structural equation models for determining tail length and weight traits in sheep

In chapter 2, the factors influencing breeding traits are analysed in detail using a SEM. A negative correlation was found between tail length and weaning weight, as well as between tail length and slaughter weight. These relationships were discussed in detail in previous chapters. The negative correlation suggests that animals with shorter tails tend to have more favourable weight development. In addition, an intrauterine influence could play a role as a potential cause of the observed relationships.

SEM enable simultaneous consideration of recursive relationships between traits, thereby leading to more precise estimates (Gianola & Sorensen, 2004).

Apart from this work, there is no other publication to date, in which SEM have been used and tail length as a breeding trait was included. However, with regard to production-relevant parameters, in particular different body weights, there are several studies that follow similar methodological approaches. Mohammadi et al. (2020) use SEM to analyse causal relationships between body weights at defined stages of development in sheep. They report consistently positive effects between weight measurements at different times and also consider the 9-month and yearling weights, which were not included in the present study. The results presented in chapter 2 are consistent with the findings of Mokhtari et al. (2019) and Masari et al. (2021). Yazdanpanah et al. (2024) confirm these results and show that SEM enables more precise modeling of genetic and phenotypic relationships between growth parameters in sheep. In addition, the authors emphasize the importance of considering and optimizing environmental factors. In summary, it can be stated, that SEM is a powerful tool for mapping causal relationships between complex, interlinked breeding traits.

Further studies of this kind are needed to identify additional potential relationships between tail length and other traits, and to gain a deeper understanding of the underlying biological mechanisms. It would also be interesting to confirm in practice whether the recursive relationships between tail length and weight can be replicated.

5.4 Genes influencing tail length

Since TL is a highly heritable trait, it is interesting to look at the gene loci that can influence this trait in addition to the results discussed in chapter 2. The genetic architecture of this trait is complex. Several studies have shown that genes influencing tail morphology interact in a complex network that controls not only the number of vertebrae but also fat tail formation and general tail structure (Kalds et al., 2022; Wang et al., 2025; Qi et al., 2024; Xu et al., 2021; Zhu et al., 2024). QTL analyses identified significant associations with TL, particularly on chromosome OAR11 in the HOXB13 gene region (Lagler, 2022). Studies on short- and long-tailed Merino sheep also confirm several selection signals that correspond to the variability of tail morphology (Mainzer et al., 2025). A recent study by Wang et al. (2025) genotyped two sheep breeds for different tail lengths. Two genotypes were identified in short-tailed sheep, which had a detection accuracy of 70% for the method and thus offer new approaches to breeding for short tails.

The high heritability and identification of relevant gene regions make it clear that breeding for short tails is feasible in many populations without having to worry about negative effects on production parameters (Mainzer et al., 2025; Wang et al., 2025). In particular, breeds such as Merino sheep exhibit natural variations that can be specifically exploited to avoid tail docking in the long term (Eck, 2020; Lagler, 2022; Mainzer et al., 2025). Despite this genetic potential, there is still room for improvement in practical implementation, particularly with regard to clear phenotypic recording and reliable genotype-phenotype assignment.

In summary, breeding for short tails is feasible, when genetic influences are considered. However, further studies are needed on the causal relationships between phenotypes and gene loci that can influence tail length.

5.5 Derivation of economic breeding values for breeding goal traits

The economic evaluation of breeding goal traits in practical sheep breeding can be carried out using various methods. The methods used in this study to derive economic weights were discussed in detail in chapters 3 and 4. In chapter 3, the WTP for breeding goals was determined considering farm clusters. In chapter 4, a bio-economic model was used to calculate the economic values and profitability for functional, production, health, and welfare traits. This study was the first to include tail length and other health traits in a bio-economic model and evaluate them economically.

The evaluation of sheep farming systems is helpful for subsequent economic assessment; to this end, it is useful to classify the different farming systems. Chapter 3 showed that cluster analysis can be used to classify farming systems. In the study by Schütte et al. (2024), nine different sheep farming systems were classified using clustering. The study focuses primarily on extensive and semi-intensive farming systems, which are characterised by varying degrees of grazing and indoor housing. Extensive systems are mainly based on grazing, which reduces feeding costs and provides freedom of animal movement, while simple, functional shelters are used in winter and during transitional periods (Manoj et al., 2024; Schütte, 2023). The design of the barn has a significant impact on the well-being and productivity of the animals. For example, insufficient ventilation can cause respiratory infections and heat stress, while a floor, that is too hard, can lead to callus formation on the knees and hocks (Miguel et al., 2025). Thénard et al. (2024) underscores the findings of this study and also identifies three key farm profiles: small farms that pursue individual breeding goals, medium-sized farms with flexible selection criteria, and large farms that use established breeding indices to ensure the sustainability of their breeding systems.

Aouina et al. (2025) also clustered sheep farms. In addition to the farm characteristics and farm manager information described in chapter 3, the authors reported that hygiene practices, estrus management, and timing of mating emerged as key determinants in characterising the farming systems.

In other areas of animal husbandry, clustering methods are used to group other animal species according to specific characteristics. In buffalo, clusters were formed according to lactation profiles, which allowed conclusions to be drawn about individual feeding strategies and productivity (Krupová et al., 2025). Wolters et al. (2021) used a similar approach clustering cattle according to various criteria such as production systems, herd size, breed, or region. Clustering methods are also used in behavioral research on dogs aimed at identifying groups with similar behavioral patterns and correlate these with characteristics such as fear or aggression (Pereira et al., 2022).

Overall, it is clear that in animal science, both the design of housing systems and the use of cluster methods represent important starting points for improving animal welfare, productivity, and economic efficiency (Krupová et al., 2025; Manoj et al., 2024; Miguel et al., 2025; Pereira et al., 2022; Schütte, 2024; Wolters et al., 2021; Zhai et al., 2024).

5.6 Current breeding goals in sheep breeding

Modern sheep breeding today not only emphasizes classic performance traits such as production traits, but also increasingly integrates new breeding goals such as tail length and health traits, as described in chapter 3. Based on a contingent valuation survey of shepherds in Germany, a recommendation for a new total breeding value was developed in chapter 3. For the first time, this also considers health and welfare traits such as TL and disease resistance. The current overall breeding value in Germany does not include health and welfare traits in sheep breeding (VIT, 2025). This chapter will focus on the main areas of current breeding goals.

A recent African study by Phaladi et al. (2025) also deals with breeding objectives and reported, that health and welfare traits are not important to farmers. The focus there is on production and exterior traits of sheep. These results are similar to the findings of Bekuma et al. (2025) and once again confirm that health and welfare traits are not given any weighting. The study by Ragkos & Abas (2015) also did not include health and welfare traits in the breeding objectives for dairy sheep, but instead focused on production traits. Similar weightings of breeding traits to those used in this study were reported by Tabbaa et al. (2019): meat production, followed by disease resistance and adaptability to the rearing environment. In contrast, little importance was attached to the traits of conformation, milk production, and wool or fiber production. As mentioned in chapter 3, milk and wool production in particular play a minor role, as these traits are not of great economic importance in Germany. However, the above-mentioned breeding goals were influenced by the effects of breed, region, farm type, and herd structure and size.

Tail length was an important trait for the farmers surveyed, as pointed out in chapter 3. This result is supported by Adimasu et al. (2019), where tail length and the exterior of breeding rams were traits to be considered and, from the farmers' point of view, influenced the selection of breeding animals. A study by Rose et al. (2015) examines breeding goals for Merino sheep in different regions and concludes that breeding goals should be adapted to regional conditions in order to respond optimally to husbandry conditions and other economic influences. However, in chapter 3 this regional influence on breeding goals could not be substantiated.

5.7 Derivation of economic weights using bio-economic models

Chapter 4 dealt with the derivation of economic weights using a bio-economic model. This study was the first to consider health and animal welfare traits in a bio-economic model. Current studies on the topic also deal with the use of bio-economic models that take new breeding goal traits into account. Smith et al. (2025) use a bio-economic model to assess the resilience of Australian Merino sheep. Resilience was rated positively in the results but had a minor influence on the total value at 2.02%.

Another recent study by Amraei et al. (2025) confirms the findings presented in chapter 4, that production traits were most important and that the traits are strongly influenced by prices. The sale of lambs had the greatest economic significance, followed by milk production, which had no influence in this study because no dairy sheep were included. The economic significance of wool traits was very low (Amraei et al., 2025), which confirms the results reported in chapter 4.

Guo et al. (2025) define breeding objectives for Merino sheep with a focus on wool quality and weight traits. In agreement with the findings in chapter 4, they reported a high weighting for the WW, while yearlings' weight was associated with a merely low influence. Similar trait weightings in goats are also published by Tesema et al. (2023). Here production traits such as daily gain, weaning and various other weights were important. In addition, the goats´ coat colour was found to be relevant. However, Merinoland sheep are a single-colour breed, which is why colour could not be investigated in chapters 3 and 4.

Waters et al. (2024) calculated expected breeding values (EBVs) for robustness, a breeding goal trait in sheep. They used hair thickness as an indicator of robustness. While robustness was not investigated in this study, it could be an interesting issue to be addressed in future research. One drawback of using hair thickness as a surrogate marker in sheep is, that it has a high intraindividual variance and cannot easily be assessed in practice.

Recent studies show that the development and application of bio-economic models are of central importance not only for sheep farming but also for other livestock breeds (Bohan et al., 2019; Gizaw et al., 2018; Krupová et al., 2013; Slavova, 2021). These models are becoming increasingly important, particularly in the optimization of husbandry systems and the development of location-adapted breeding strategies. The integration of environmental and animal welfare aspects into the derivation of breeding goals is considered promising, as it contributes to more sustainable and economically viable production systems.

5.8 Future-relevant traits in sheep breeding

According to Smith et al. (2025), resilience factors in sheep represent a breeding trait, that will be influential in the future. The study demonstrates, that the integration of resilience into breeding programs is feasible, but requires careful evaluation to avoid compromising productivity.

Cunha et al. (2024) deal with parasite resistance in sheep, focusing in particular on resistance to gastrointestinal nematodes (GIN). Four traits are mentioned as indicators of resistance (egg count per gram of feces, hematocrit, FAMACHA score, and DAG score), which exhibit low to moderate heritability. The FAMACHA score, which is particularly easy to record in practice, would be a trait, that could be effortlessly implemented in the future, enabling selection. In the present study, various traits related to disease resistance were considered in chapters 3 and 4. On the one hand, the survey reported in chapter 3 revealed a weighting for disease resistance; on the other hand, as described in chapter 4, it has a measurable economic impact on profitability and should therefore be considered in the future.

Another trait, that was not addressed in this study but still has an economic impact, is heat tolerance. Oyieng et al. (under peer review) investigated the economic impact of heat stress on sheep in Africa. The authors describe a significant influence of heat on the weight of the animals and recommend that this trait should be considered when selecting breeding animals. In addition, the authors describe breed-related differences in heat tolerance.

Finally, a topic not covered in this study is the use of AI for data collection. Emsen et al. (2025) used AI to record the behavior of sheep. The authors consider the use of these new technologies to be beneficial, as conventional data collection is often time-consuming and AI can be very helpful. In addition to saving time, the authors state, that AI tools can improve the health and well-being of the animals.

5.9 Conclusion

The present results highlight the potential of integrating genetic and economic analyses to optimise breeding strategies in Merinoland sheep. Considering direct and maternal genetic effects alongside covariate structures enabled precise estimation of heritabilities and correlations, particularly for tail length and body weight traits. Tail length was found to be genetically highly modifiable, but it was also found to have an unfavourable correlation with growth traits. SEM analyses indicated complex, sometimes contradictory, phenotypic correlations influenced by environmental and health factors.

Concurrently, cluster analysis revealed distinct differences between production systems, influenced by farm size, husbandry type, and the socioeconomic circumstances of farm managers. This heterogeneity is reflected in significant variations in economic weights, particularly with regard to the growing importance of functional, health, and welfare traits compared to traditional performance traits. While it was found that tail length is genetically highly modifiable, the low relative economic values for tail length, health and parasite traits emphasise the need to expand the data base through system-wide surveys and to consider genotype-environment interactions more specifically in the future.

Overall, the results demonstrate that future breeding programmes for Merino land sheep must be based on a holistic integration of genetic, economic and management-related components to promote sustainable progress in animal welfare and production.

References

Adimasu, E., Almayehu, K., & Getachew, T. (2019). Breeding objective, breeding practices and selection criteria of indigenous sheep in Western Amhara, Ethiopia. Int J Sustain Agric Res, 6, 172-182.

Amane, A., Belay, G., Kebede, A., Dessie, T., Worku, S., Hanotte, O., & Vila, E. (2023). Analysis of tail morphology and osteology in Ethiopian indigenous sheep. Journal of Archaeological Science: Reports, 47, 103776.

Amraei, F., Vafaye Valleh, M., Dashab, G. R., Baneh, H., & Ahmadpanah, J. (2025). Estimation of Economic Values for Important traits of Lori-Bakhtiari Sheep in the Rural Rearing System. Research On Animal Production, 16(3), 13-23.

Aouina, K., Nabi, M., Hadj Omar, K., Kebbal, S., Khelifi Touhami, N. A., & Ouchene, N. (2025). Characterizing sheep farming systems to improve sustainability approaches and enhance policy implementation. Tropical Animal Health and Production, 57(4), 1-14.

Bekuma, A., & Tadesse, T. (2025). Breeding objectives, selection criteria and reproductive performance of indigenous sheep in west Wallaga zone, Oromia, Ethiopia. Journal of Applied Animal Research, 53(1), 2467108.

Bohan, A., Shalloo, L., Creighton, P., Berry, D. P., Boland, T. M., O'Brien, A. C., ... & McHugh, N. (2019). Deriving economic values for national sheep breeding objectives using a bio-economic model. Livestock Science, 227, 44-54.

Cunha, S. M. F., Willoughby, O., Schenkel, F., & Cánovas, Á. (2024). Genetic Parameter Estimation and Selection for Resistance to Gastrointestinal Nematode Parasites in Sheep—A Review. Animals, 14(4), 613.

Eck, K. S. (2020). Untersuchung der natürlichen Schwanzlängenvariation beim Merinolandschaf als mögliche Zuchtalternative zur tierschutzrelevanten Praktik des Schwanzkupierens (Dissertation). Ludwig-Maximilians-Universität München.

Emsen, E., Kutluca Korkmaz, M., & Odevci, B. B. (2025). Artificial intelligence-assisted selection strategies in sheep: Linking reproductive traits with behavioral indicators. Animals, 15(14), 2110.

Gianola, D., & Sorensen, D. (2004). Quantitative genetic models for describing simultaneous and recursive relationships between phenotypes. Genetics, 167(3), 1407-1424.

Gizaw, S., Abebe, A., Bisrat, A., Zewdie, T., & Tegegne, A. (2018). Defining smallholders' sheep breeding objectives using farmers trait preferences versus bio-economic modelling. Livestock Science, 214, 120-128.

Grant, E. P., Wickham, S. L., Anderson, F., Barnes, A. L., Fleming, P. A., & Miller, D. W. (2020). Preliminary findings on a novel behavioural approach for the assessment of pain and analgesia in lambs subject to routine husbandry procedures. Animals, 10(7), 1148.

Greeff, J. C., Karlsson, L. J. E., & Schlink, A. C. (2015). Inheritance of tail length in Merino sheep.

Guo, T., Li, W., Yuan, C., Wang, X., Liu, J., & Liang, B. (2025). Defining Multi-Trait Breeding Objectives and Selection Indexes to Develop More Efficient Breeding Programs for Superfine Wool Sheep. Animals, 15(13), 1873.

Hodge, M. J., Brown, D. J., & Walkom, S. F. (2025). Genetic evaluation of tail length in Australian sheep. In Proceedings of the AAABG 26th Conference (p. 407). Association for the Advancement of Animal Breeding and Genetics.

Hümmelchen, H., Wagner, H., Brügemann, K., König, S., & Wehrend, A. (2025). Effects of Breeding for Short-Tailedness in Sheep on Parameters of Reproduction and Lamb Development. Veterinary Medicine and Science, 11(1), e70138.

Hümmelchen, H., Wagner, H., König, S., & Wehrend, A. (2022). Bedeutung der Schwanzlänge beim Schaf und Zucht auf Kurzschwänzigkeit. Tierärztliche Praxis Ausgabe G: Großtiere/Nutztiere, 50(03), 187-194.

Hümmelchen, H., Wenisch, S., Brügemann, K., König, S., & Wagner, H. (2023). Phenotyping the sheep tail-Presentation of characterization methods in the context of breeding for short-tailedness. Tierärztliche Praxis. Ausgabe G, Großtiere/Nutztiere, 51(1), 6-14.

Kalds, P., Huang, S., Chen, Y., & Wang, X. (2022). Ovine HOXB13: expanding the gene repertoire of sheep tail patterning and implications in genetic improvement. Communications Biology, 5(1), 1196.

Krupová, Z., Krupa, E., & Kubínová, J. (2025). Comparison of K-Means and Hierarchical Clustering in Buffalo Lactation Profiles. *Animals*, 15(11), 1897. https://pmc.ncbi.nlm.nih.gov/articles/PMC12649460/

Krupová, Z., Krupa, E., & Wolfová, M. (2013). Impact of economic parameters on economic values in dairy sheep.

Lagler, D. K., Hannemann, E., Eck, K., Klawatsch, J., Seichter, D., Russ, I., ... & Medugorac, I. (2022). Fine-mapping and identification of candidate causal genes for tail length in the Merinolandschaf breed. Communications Biology, 5(1), 918.

Mainzer, J., Yin, T., Giambra, I., Hümmelchen, H., Engel, P., Wagner, H., ... & König, S. (2025). Genetic parameters, genome-wide associations and potential candidate genes for additive and dominance effects of tail traits in Merinoland sheep based on whole-genome sequence data in a selection experiment. Animal Genetics, 56(5), e70041.

Manoj, S., Singh, D., & Singh, R. (2024). Housing of Sheep and Goat Under Different Management Systems. *Biovet Innovator*, 10(2), 42–49. https://biovetinnovator.in/wp-content/uploads/2024/09/42-49-Manoj-.pdf

Masari, H. A. P. E., Hafezian, S. H., Mokhtari, M., Mianji, G. R., & Abdollahi-Arpanahi, R. (2021). Inferring causal relationships among growth curve traits of Lori-Bakhtiari sheep using structural equation models. Small Ruminant Research, 203, 106489.

Medrado, B. D., Pedrosa, V. B., & Pinto, L. F. B. (2021). Meta-analysis of genetic parameters for economic traits in sheep. Livestock Science, 247, 104477.

Miguel, D. C., de Brito, J. M., & de Almeida, R. M. (2025). Impact of housing and breeding conditions on the welfare of sheep. *Animal Science Papers and Reports*, 41(4), 313–319. https://asp.zut.edu.pl/pdf/asp-2023-22-4-01.pdf

Mohammadi, Y., Saghi, D. A., Shahdadi, A. R., Rosa, G. J. D. M., & Mokhtari, M. S. (2020). Inferring phenotypic causal structures among body weight traits via structural equation modeling in Kurdi sheep. Acta Scientiarum. Animal Sciences, 42, e48823.

Mokhtari, M., Barazandeh, A., Moghbeli Damaneh, M., Roudbari, Z., & Kargar Borzi, N. (2019). Inferring causal relationships among growth traits in Kermani sheep applying structural equation modeling. Journal of Livestock Science and Technologies, 7(2), 29-35.

Oyieng, E., Ojango, J. M. K., Gauly, M., Ekine-Dzivenu, C. C., Mrode, R., Clark, E. L., ... & König, S. (under peer review) The Impact of Heat Stress on Growth and Resilience Phenotypes of Sheep Raised in a Semi-Arid Environment of Sub-Saharan Africa. Available at SSRN 5218498.

Pereira, T., Santos, R., & Costa, P. (2022). Clustering for Automated Exploratory Pattern Discovery in Livestock. *Frontiers in Veterinary Science*, 9, 884437. https://pmc.ncbi.nlm.nih.gov/articles/PMC9260587/

Phaladi, A. M., Tyasi, T. L., Tada, O., & Mogashoa, S. (2025). Breeding practices and trait preferences of sheep farmers from two villages in Lepelle-Nkumpi municipality, Limpopo Province, South Africa. South African Journal of Animal Science, 55(2), 74-84.

Qi, Y., He, X., Wang, B., Yang, C., Da, L., Liu, B., ... & Liu, Y. (2024). Selection signature analysis reveals genes associated with tail phenotype in sheep. Frontiers in Genetics, 15, 1509177.

Ragkos, A., & Abas, Z. (2015). Using the choice experiment method in the design of breeding goals in dairy sheep. Animal, 9(2), 208-217.

Schütte, J. (2023). Typology of German sheep farms-Differences in structure, characteristics, challenges and the provision of goods and services. Small Ruminant Research, 226, 107022. https://doi.org/10.1016/j.smallrumres.2023.107022

Slavova, S. (2021). Estimation of the economic efficiency of Lacaune sheep farms, based on theoretical bio-economic models. Agricultural Science & Technology (1313-8820), 13(2).

Smith, E. G., Walkom, S. F., & Clark, S. A. (2025). Estimating the Value of Including Resilience in a Multi-Trait Selection Index Designed for Australian Merino Sheep. Journal of Animal Breeding and Genetics.

Tabbaa, M. J., Barakeh, F. S., & Baker, M. M. (2019). Factors influencing farmers decision on breeding objectives and selection criteria for sheep breeds in Abu Dhabi Emirate, UAE.

Tesema, Z., Derbie, B., Shenkute, A., Gobeze, M., Kefale, A., & Gizaw, S. (2024). Breeding objectives for Central Highland goats using participatory and bio-economic modelling approaches. Journal of Animal Breeding and Genetics, 141(1), 1-12.

Thénard, V., Quénon, J., Arsenos, G., Bailo, G., Baptista, T. R., Byrne, T., … & Vouraki, S. (2024). Identifying selection strategies based on the practices and preferences of small ruminant farmers to improve the sustainability of their breeding systems.

VIT, 2025. https://www.vit.de/vit-fuers-tier/zuchtwertschaetzung/zws-sonstige-tierarten (accessed 23 December 2025).

Havercamp, H., Brandt, H.R., Erhardt, G. (2015) Variation in tail length in Merinoland sheep as a basis for breeding activities at the Vortragstagung der Deutschen Gesellschaft für Züchtungskunde e. V. und der Gesellschaft für Tierzuchtwissenschaften e.V., Berlin, Germany

Wang, D., Zhao, Y., Fang, W., Liang, J., Li, K., Wang, C., & Cao, G. (2025). Association of Sheep Tail Type with the T Gene Single Nucleotide Polymorphisms Loci. Life, 15(3), 342.

Waters, D. L., Clark, S. A., Brown, D. J., Walkom, S. F., & Van Der Werf, J. H. (2024). Validation of reaction norm breeding values for robustness in Australian sheep. Genetics Selection Evolution, 56(1), 4.

Wolters, S., van der Werf, J., & Bijma, P. (2021). Herd clustering strategies and corresponding genetic gains in dairy cattle. *Journal of Dairy Science*, 104(6), 6522–6532. https://pmc.ncbi.nlm.nih.gov/articles/PMC8182665/

Xu, S. S., Gao, L., Shen, M., & Lyu, F. (2021). Whole-genome selective scans detect genes associated with important phenotypic traits in sheep (Ovis aries). Frontiers in genetics, 12, 738879.

Yazdanpanah, A., Fayazi, J., Roshanfekr, H., Rashedi, A., & Mokhtari, M. (2024). Genetic analysis of growth curve traits in Iran-Black sheep breed: Comparison of standard multivariate and structural equation models. Journal of Livestock Science and Technologies, 12(1), 69-80.

Zhai, X., Zhang, L., & Wang, Y. (2024). A key-feature-based clustering approach to assess the welfare of sheep. *Frontiers in Animal Science*, 5, 1421299. https://www.frontiersin.org/journals/animal-science/articles/10.3389/fanim.2024.1421299/full

Zhu, Q., Liu, P., Zhang, M., Kang, Y., Lv, L., Xu, H., ... & Lan, X. (2024). The detection of a functional 168 bp deletion of the HOXB13 gene determining short tail and its association with senior growth traits in sheep breeds worldwide. Animals, 14(11), 1617.

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Der Lebenslauf wurde aus der elektronischen Version der Arbeit entfernt.

The curriculum vitae was removed from the electronic version of the paper.

Formal Declaration

Erklärung gemäß § 17 (2) der Promotionsordnung des Fachbereichs 09 vom 07.07.2004 in der Fassung des 2. Änderungsbeschlusses vom 19.05.2019

Ich erkläre: Ich habe die vorgelegte Dissertation selbständig und ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt, die ich in der Dissertation angegeben habe.
Alle Textstellen, die wörtlich oder sinngemäß aus veröffentlichten Schriften entnommen sind, und alle Angaben, die auf mündlichen Auskünften beruhen, sind als solche kenntlich gemacht. Bei den von mir durchgeführten und in der Dissertation erwähnten Untersuchungen habe ich die Grundsätze guter wissenschaftlicher Praxis, wie sie in der „Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis" niedergelegt sind, eingehalten.

Datum: 27.12.2025

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Unterschrift

Jennifer Oberpenning