



# Principles of sheep behaviour: An overview from a welfare perspective

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## ABSTRACT

The behaviour of sheep, like that of other animals, is the result of a complex interaction between causal mechanisms, their specific function, their development throughout life and their phylogenetic prevalence in the species. Within the domain of animal welfare, behaviour is of paramount importance, as they provide key insights into how individuals cope with environmental challenges and the way these challenges impact their mental states, biological functioning, and species-typical behavioural repertoires. The aim of this review is to critically and narratively examine key aspects of sheep behaviour to enhance the understanding of their biological needs and support improvements in the welfare of sheep raised under different production systems. The review emphasises the fundamental role of sensory systems in animal behaviour and welfare, along with the motivational systems, underlying individual, social, and maternal behaviours. It's also examines abnormal behaviours in sheep and their implications for human-animal interactions within the production context. The integration of sheep behaviour knowledge with contemporary flock management is strategic to enhance both welfare and productive efficiency. Future research should focus on improving behavioural assessments, improved handling techniques and the possible implementation of precision farming to monitoring sheep behaviour.

## 1. Introduction

The domestication of sheep, estimated to have begun around 11,000 years ago in the agricultural Neolithic societies of the Fertile Crescent, marked a fundamental shift from a nomadic to a sedentary lifestyle, facilitating the transition from foraging and hunting to farming and breeding (Alberto et al., 2018). The domestication process followed the "prey pathway," whereby humans initially focused on hunting and later transitioned to breeding and flock management for certain species that were receptive to domestication (Zeder, 2012). Sheep were initially raised for meat, but by approximately 6000 years ago, archaeological evidence indicates a shift towards specialisation in secondary products such as wool and milk (Helmer et al., 2007). Since its domestication, sheep has accompanied humans in their expansion to almost all continents, different climatic zones and altitudes (Simões et al., 2021). However, the process of domestication has resulted in changes that extend beyond the physical characteristics and physiological mechanisms of sheep (González et al., 2013). These changes also encompass behavioural alterations, including modifications in fear responses to humans, anti-predator strategies, and the alignment of circadian

rhythms with human activities (Wang et al., 2023). In the contemporary era, sheep ranks as the second most extensively bred mammal globally, surpassed only by cattle, with a global population estimated at approximately 1.2 billion (FAOSTAT, 2021). This phenomenon can be attributed to various factors, including their remarkable adaptability to harsh environments, their docile nature, their medium size, their resilience, their capacity to utilise low-nutrient forage, and, more recently, an increase in their productivity (Robinson et al., 2014). The high productivity of sheep is linked to the specialisation, intensification and mechanisation of production developed particularly in Europe (Miranda-de la Lama and Estévez-Moreno, 2022), and more recently expanded in major producing countries such as China, influencing global intensification trends (DuBois and Gao, 2017).

Sheep farming is practised across a variety of production systems, which are shaped by climatic, economic, and cultural factors, as well as consumer preferences (Alanís et al., 2022). A broad categorization of sheep farming systems reveals three dominant types: intensive and extensive production for milk, meat, or wool, and transhumance (Kilgour et al., 2008). Intensive systems are designed to maximise efficiency and are based on rearing animals in controlled environments with

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high-energy feeding and confinement (Morris, 2017). Extensive systems, on the other hand, are characterised by grazing over large areas, ranging from small lowland farms to flocks in open, unfenced pastures, where feeding primarily depends on natural pastures and other forage species (Kilgour et al., 2008; Estévez-Moreno et al., 2019). Transhumance, on the other hand, is defined as a seasonal grazing system based on livestock movement between different geographic areas according to forage availability, contributing to ecosystem maintenance and pastureland productivity in mountainous and semi-arid regions (Fernández-Guisuraga et al., 2022). The evolution of both intensive and extensive systems has been characterised by specialisation, intensification, and mechanisation in response to global trends in the sheep farming sector (Miranda-de la Lama and Estévez-Moreno, 2022). Furthermore, hybrid systems have been developed (e.g. extensive grazing of ewes combined with intensive rearing of lambs), integrating strategies based on commercialisation, resource utilisation, and product standardisation. From a biological standpoint, each production system and agroecosystem pose a distinct challenge to the adaptive capacity of sheep.

Since approximately 1990, research on animal welfare has generated substantial evidence on the behaviour, sentience and biological limits of farm animals across diverse production systems. These findings, in conjunction with the intensification of animal production and the globalisation of information, have elevated animal welfare to the status of a primary global social concern (Estévez-Moreno et al., 2022). From a scientific perspective, animal welfare is a multidimensional concept that encompasses animals' responses and ability to cope with environmental challenges, assessed on a continuum from good to poor using physiological, morphological, and behavioural indicators (Broom, 2021). However, behaviour is particularly relevant for assessing animal welfare, as it provides insights into both proximate causes (mechanism and ontogeny) and ultimate causes (function and phylogeny) (Galindo, 2024). A wide range of behavioural indicators can be used to detect changes in individuals without invasive methods and to reveal the biological limits of animals in different management scenarios (e.g. handling, transport) or living conditions (e.g. production system). Furthermore, the mounting consumer interest in production systems that respect animal welfare, particularly those facilitating the expression of natural behaviours (Madau et al., 2022), underscores the necessity to comprehensively understand what is common and what is abnormal in sheep behaviour. Nevertheless, despite the increasing number of scientific publications on sheep behaviour and welfare, information remains scattered. The aim of this review was to critically and narratively present key aspects of sheep behaviour, thereby enhancing the understanding of their biological needs to support improvements in the welfare of sheep raised in different production systems.

## 2. Sensory systems

Because all behavioural responses arise from the processing of environmental stimuli by the sensory systems, an animal's welfare state is determined by the way in which those stimuli are perceived and evaluated (Broom, 2021). In this review, we describe the sensory modalities that have been most extensively studied in sheep, namely vision, hearing, olfaction, taste, tactile perception and pain, and summarise how these systems shape their behavioural responses to environmental stimuli.

### 2.1. Vision

Sheep share the typical vertebrate eye structure (lens, cornea, iris and retina), and their laterally placed eyes together with the horizontally rectangular retina and pupil confer the wide lateral visual field typical of prey species (Jacobs et al., 1998). Binocular panoramic vision allows for a field of view of approximately 270° to 320°, whereas monocular vision is limited to a range of 40° to 60° (Piggins and Phillips,

1996). Additionally, the eyes possess a tapetum lucidum, which is essential for optimal crepuscular and nocturnal vision. The sheep's visual system is capable of stereopsis and depth perception, although it lacks an accommodation reflex and requires a well-focused retinal image for the perception of nearby objects (Piggins and Phillips, 1996). Notwithstanding the characteristics and the relatively poor visual acuity, sheep can distinguish between dark and light herbage, as well as between tall and short swards. This ability is likely attributable to the brightness of their vision (Bazely and Ensor, 1989). Moreover, sheep can differentiate between food-related stimuli and other types of stimuli, such as those from animals or humans, at approximately 1 m (Kendrick, 1994). This species demonstrates superior kinetic visual acuity compared to static stimuli, exhibiting heightened reactivity to moving stimuli as opposed to static ones (Clarke and Whitteridge, 1976).

The colour vision is dichromatic, as is the case for several other ungulates, with two types of cones mediating this function (Jacobs et al., 1998). Consequently, sheep are unable to perceive the colour red, which ranges in shade from grey to yellow according to intensity and perceive green as shades of yellow. These characteristics indicate that there is no optical distinction between grass in the pasture and hay with respect to colour (Kendrick, 2008). Vision is also important for social recognition, as adult ewes can identify images of conspecifics (including familiar lambs) and discriminate emotional expressions (e.g. Bellegarde et al., 2017). However, three-month-old lambs do not prefer pictures of their mothers over those of familiar ewes, suggesting that facial-image recognition develops later (e.g. Ungerfeld et al., 2021). The position of a sheep's ears and tail are useful visual indicators of its emotional state. In situations perceived as negative, the sheep's attention is focused on its surroundings, and the position of its ears changes more frequently, while lambs in pain exhibit tail wagging (Molony et al., 2002). Conversely, during positive experiences, the ears adopt more passive positions and are more relaxed. The position of the tail is also indicative of heightened emotional arousal, manifesting as a raised tail in both positive and negative conditions (Reefmann et al., 2009).

### 2.2. Hearing

The auditory capabilities of sheep encompass a frequency range from 42 kHz to 125 Hz, with a sensitivity of approximately 10 dB (Heffner and Heffner, 1992). This enables them to perceive ultrasound. This, in conjunction with the external ear functioning as a directional filter, is significant for the capture of specific sounds (Kendrick, 2008). It is thus imperative to consider the potential stress-inducing effects of ultrasound, which is not perceptible to humans, in agricultural settings (e.g., machinery). Auditory cues play an important role in social dynamics, and lambs and ewes use vocalisations for mutual recognition (Searby and Jouventin, 2003).

### 2.3. Olfaction

Sheep can distinguish and identify individual flock members and humans based on their voices (Kendrick et al., 1995). Sheep possess two anatomically and physiologically distinct olfactory systems: the olfactory epithelium, which transmits information to the main olfactory bulb, and the vomeronasal organ, which transmits information to the accessory olfactory bulb. The epithelium is responsible for detecting volatile odorous molecules, whereas the vomeronasal organ is involved in the detection of pheromones, which are semiochemical molecules that convey information between individuals of the same species (Brennan and Keverne, 2004). Furthermore, olfactory cues are also employed extensively in sheep communication (Salazar et al., 2007). Indeed, the olfactory system enables sheep to discriminate between unfamiliar conspecifics, as shown by their ability to distinguish the odour of different individuals (Baldwin and Meese, 1977), and to recognise familiar flock members, demonstrating fine-scale social recognition within the group (Adamczyk et al., 2015). Olfactory signals are of great

importance in maternal recognition, as ewes identify their lambs within hours of birth through scent cues, enabling selective nursing and preventing mismothering (Lévy, 2022). Recent findings also demonstrate that newborn lambs are inherently attracted to the odour of inguinal wax, thereby supporting the role of olfaction in neonatal orientation and teat-seeking behaviour (Alary et al., 2025). Moreover, olfactory stimuli play a major role in sexual communication. Rams can identify which ewes in the flock are in oestrus by the odour of their urine (Blissitt et al., 1994). In ewes that are seasonally in anoestrous, exposure to sexually active males results in synchronised ovulation. This phenomenon is known as the "male effect" and is primarily conveyed by olfactory cues (Gelez and Fabre-Nys, 2004).

#### 2.4. Taste

The perception of flavour is facilitated by the tongue, which in sheep contains two distinct types of taste buds: fungiform, distributed in a bilateral manner across both halves of the tongue and on the tip, and circumvallate (Ünsal et al., 2003). Early studies identified the receptors responsible for the four basic taste modalities in sheep as bitter, sweet, sour and salty (Bell and Kitchell, 1966). Subsequent studies have also identified the ability to perceive the umami taste (Favreau et al., 2010). Among the preferred tastes of sheep are umami and specific types of sour, including malonic and butyric acids (Gherardi and Black, 1991). Regarding bitter and salty tastes, experimental evidence indicates that sheep initially display indifference, later avoiding these stimuli with increasing doses (Favreau et al., 2010). Sheep are not attracted to or exhibit preferences for sweet-tasting stimuli (Burritt et al., 2005). These preferences may result in sheep selecting specific plants and avoiding toxic substances in vegetation (Ginane et al., 2011). Moreover, sheep can generalize flavour experiences, transferring preferences or aversions from one tasted plant to others with similar sensory properties (Ginane and Dumont, 2006). Understanding sheep's taste preferences can help optimize foraging strategies and prevent the consumption of harmful plants.

#### 2.5. Somatosensation and pain perception

Among the somatosensory modalities, pain is the most critical for sheep welfare, as nociception encompasses mechanical, thermal and chemical stimuli whose perception has a direct and profound impact on the animal's physical and affective state (Miranda-de la Lama, 2025). The experience of pain is complex and individualistic, depending not only on the severity of the damage and external stimulus, but also on previous pain experiences (Guesgen et al., 2013) and on social position within a flock (Fitzpatrick et al., 2006). Consequently, the evaluation of pain in sheep frequently represents a significant challenge (McLennan, 2024). This is since sheep are prey animals and, by evolutionary development, can mask pain signals to potential predators (Stubsjøen et al., 2009). There are several methods that can be employed to assess pain in animals. These include behavioural scales (Silva et al., 2020) and studies of facial expressions (Häger et al., 2017). The manifestations of pain sensations include a reduction in sociability, a decrease in food consumption, tremors, abnormal vocalisation, lameness or altered gait and locomotion (Steagall et al., 2021). Two models have recently been developed for the assessment of pain in sheep: Sheep Pain Facial Expression Scale (SPFES) and Sheep Grimace Scale (SGS). Both tools evaluate specific facial action units associated with pain (e.g., orbital tension, ear and lip position), classified as absent, partially present or present (Zufferey et al., 2021). The SPFES has shown high accuracy and inter-rater reliability in detecting chronic pathological pain (McLennan et al., 2016), while the SGS has proven valid and reliable for identifying postoperative pain (Häger et al., 2017).

#### 2.6. Sensory experiences and welfare implications

The implications of sensory systems on sheep welfare can be seen in Table 1. Although precognition represents a valuable tool for enhancing the management and husbandry of sheep, the necessity for developing techniques and indicators of positive welfare has recently been underscored. A key component of positive welfare is the enhancement of positive experiences, such as physical contact with humans, while avoiding negative interactions (Mattiello et al., 2019). Brushing appears particularly beneficial in sheep, as rams brushed before and during electroejaculation show calmer behavioural responses and reduced stress, together with improvements in sperm motility and kinetics (Orihuela et al., 2024). Chaumont et al. (2021), observed that rams displayed increased relaxation and a willingness to interact with the individual providing the positive stimulus. Moreover, during grooming sessions, the animals displayed a greater degree of calmness and reduced restlessness when groomed by the familiar individual. This emphasises the significance of positive handling in fostering trust and alleviating fear in sheep. Additionally, research indicates that repeated and gentle physical contact can modify the behavioural response of lambs, increase their level of curiosity while simultaneously reduce their anxiety levels (Sokołowski et al., 2023). Finally, the sensory perception of sheep is fundamental to their welfare, influencing their ability to recognise conspecifics, detect food and respond to pain. Stressors associated with sensory experiences, such as loud noises or painful procedures, can affect both welfare and productivity. The application of validated pain scales and positive handling, such as brushing and social context, promote confidence and reduce fear. The integration of this knowledge into

**Table 1**

Summary of the main sensory systems in sheep and their implications for animal welfare, including key behavioural functions and practical applications in handling.

Sensory System	Impact on Animal Welfare	Application Examples
Vision	<ul style="list-style-type: none"> <li>– Panoramic vision (270°–320°) and depth perception.</li> <li>– Limited visual acuity, better at detecting moving objects.</li> <li>– Distinguish between vegetation by light intensity.</li> </ul>	<ul style="list-style-type: none"> <li>– Improve lighting in pens/pastures.</li> <li>– Minimize visual distractions.</li> <li>– Design spaces to aid navigation.</li> </ul>
Hear	<ul style="list-style-type: none"> <li>– Sensitive to frequencies from 42 kHz to 125 Hz (including ultrasound).</li> <li>– Crucial for social communication and threat detection.</li> <li>– Excessive noise causes stress.</li> </ul>	<ul style="list-style-type: none"> <li>– Minimize exposure to high-frequency noises.</li> <li>– Progressive noisy flocking.</li> <li>– Control sound environment to reduce stress.</li> </ul>
Smell	<ul style="list-style-type: none"> <li>– Detect pheromones and recognize conspecifics.</li> <li>– Important for social cohesion, ewe-lamb bond and reproduction (e.g., "male effect").</li> </ul>	<ul style="list-style-type: none"> <li>– Control odours in breeding/slaughter areas.</li> <li>– Use olfactory signals to enhance social cohesion.</li> <li>– Key to the sheep-lamb recognition and adoption of orphans.</li> </ul>
Taste	<ul style="list-style-type: none"> <li>– Prefer umami and sour flavours; avoid bitter or salty in high doses.</li> <li>– Influences plant selection and prevention of poisoning.</li> </ul>	<ul style="list-style-type: none"> <li>– Design diets based on taste preferences.</li> <li>– Feed enrichment in intensive systems.</li> </ul>
Touch	<ul style="list-style-type: none"> <li>– Ear and tail positions reflect emotional state.</li> <li>– Tactile interaction of animals with environmental enrichment elements.</li> </ul>	<ul style="list-style-type: none"> <li>– Optimize foraging strategies.</li> <li>– Use gentle physical contact to reduce fear and handling stress.</li> <li>– Petting or brushing helps to reduce anxiety.</li> </ul>
Pain	<ul style="list-style-type: none"> <li>– Pain is individual and often hidden (due to prey instincts).</li> <li>– Pain affects sociability and cognitive skills.</li> <li>– Accurate pain assessment improves welfare.</li> </ul>	<ul style="list-style-type: none"> <li>– Use pain scales (SPFES, SGS).</li> <li>– Refinement or replacement of handling techniques that can potentially cause pain and/or suffering.</li> </ul>

the training of farmers and technicians would facilitate the development of management practices that value these characteristics, thereby promoting more sustainable production systems.

### 3. Behavioural motivational systems

The identification of the causal factors underpinning any given behaviour necessitates an understanding of how the internal state of the organism is integrated with external stimuli perceived through sensory processes (Broom, 2021). In a manner analogous to physiological homeostasis (e.g. regulation of temperature, osmotic state or nutrient balance), behaviour is also regulated through mechanisms of negative and positive feedback, whereby the performance of an action reduces or increases the motivation to continue it (Galindo, 2024). These systems are subject to the influence of motivation, a process within the brain that determines which behaviours, and physiological changes occur and when they occur, or the tendency to perform a behaviour (Mason and Bateson, 2017). Therefore, the motivational state and the behaviours it engenders are determined by how environmental stimuli are perceived through biological, physical and chemical receptors located in the sensory organs (e.g., mechanoreceptors, photoreceptors, chemoreceptors), which in turn generate changes in neuroendocrine activity (Galindo, 2024). Consequently, the term “motivational system” refers to the processes that regulate and shape behavioural responses (Broom, 2021). In this review, the focus will be on behaviour in relation to the three major motivational systems: individual, social (including sexual) and maternal behaviours.

#### 3.1. Individual behaviours

Individual behavioural motivational system refers to the patterns of behaviour that an animal performs for itself, including feeding, body care, exploration, rest, elimination behaviour, activity time budgeting and temperament (Broom, 2021). Sheep are diurnal animals, with most of their activity concentrated during daylight hours across different farming systems (Piccione et al., 2008). Furthermore, peak activity is associated with feeding and grazing (Umstätter et al., 2008). In intensive systems, animals alternate sleep cycles with nocturnal activities of lower intensity and shorter duration than those performed during the day. Furthermore, the period of peak activity is midday (Piccione et al., 2008). In extensive systems, the circadian rhythm is more susceptible to environmental fluctuations. For example, during the autumn and winter months, when daylight hours are reduced, nocturnal activity increases (Sarout et al., 2018). During the winter months, when adverse weather conditions prevail, such as rain, cold, humidity and fog, sheep reduce their daily activity levels, opting instead to remain under shelter (Dwyer and Bornett, 2004). Furthermore, elevated summer temperatures can disrupt sheep behaviour, particularly about feeding patterns. During the summer months, sheep exhibit reduced movement during the midday period (Plaza et al., 2022). The urination and defecation behaviours of sheep remain poorly understood. However, in contrast to other ungulates (Miranda-de la Lama and Villarroel, 2023), they do not exhibit latrine behaviour, which is the repeated use of specific defecation/urination sites. It appears that sheep tend to defecate near their resting area during the night (White and Hall, 1998). Although the faeces are more concentrated in the nocturnal resting area, the sheep also defecate on the pasture, even if they avoid grazing in the vicinity of fresh faeces (Boag et al., 1989). Furthermore, urination occurs with less frequency in the grazing area and in specific locations (Betteridge et al., 2010).

In intensive systems, it is essential to provide an area of the appropriate size for the individual animal and the flock, with the dimensions of this area varying according to the age and weight of the animals in question (Petherick and Phillips, 2009). These systems are unvarying, barren and unstimulating for the animals, which affects maintenance and social behaviours, and stimulates the occurrence of abnormal or stereotypic behaviours (Miranda-de La Lama et al., 2012). In extensive

sheep farming systems, sheep tend to establish defined grazing areas (Gonyou, 1984). This can be considered a form of cognitive mapping of the pasture (Plaza et al., 2022). Feeding behaviour is influenced by social facilitation, a collective motivational state arising from the strong daily synchrony observed among individuals within a flock (Ramseyer et al., 2009). Consequently, when a sheep commences grazing, the others will imitate this behaviour (Agreil and Meuret, 2004). This phenomenon is referred to as social facilitation, although in the case of sheep, it is also recognised as a synchronised behavioural repertoire at the outset. The mean time spent grazing is 8 h, with an upper limit of 12–13 h in the event of changes in other activities, such as rumination (Dias-Silva and Abdalla Filho, 2020), or in the event of poor feed quality and quantity (Silva et al., 2016). The grazing time is divided into two principal periods, with shorter intervals in between. During these intermissions, the sheep graze at a maximum distance of one metre apart (Sales-Baptista et al., 2022). In this manner, all ewes consume the same type of plant during the feeding period. Sheep navigate pasture environments mainly through visual cues and show marked selectivity in plant choice, readily consuming easily digestible forage (Jamieson and Hodgson, 1979) and favouring plant species they have previously encountered (Gluesing and Balph, 1980). According to Hofmann (1989), sheep are classified as roughage eaters, preferring the tender and palatable parts of grasses, broadleaf plants, herbaceous plants and shrubs.

It is well documented that woolly breeds (e.g. Merino, Rambouillet) tend to move considerable distances in search of specific food sources, alone or in small groups. These breeds spend approximately one third of their day ruminating (eight hours), mostly during the night; however, the duration can fluctuate between four and nine hours, with 15- to 20-minute intervals (Fraser, 1983). Also, these breeds demonstrate a marked preference for small plants, while hair breeds (e.g. Katahdin, Pelibuey) exhibit a higher consumption of shrubs and legumes (Dias-Silva and Abdalla Filho, 2020). Approximately one-third of the day is dedicated to rumination (8 h), particularly during nocturnal hours; however, the duration can fluctuate between 4 and 9 h, with intervals of 15–20 min (Fraser, 1983). Sheep possess a high tolerance for drought and extreme heat, which enables them to thrive in arid environments (Henry et al., 2018). In pastures lacking access to water, sheep exhibit a tendency to engage in longer periods of daytime rest and nocturnal grazing (Clark and Jay, 1975). In the intensive system, access to feed sources is more strictly regulated, and the diet is more precisely calibrated. In this condition, sheep spend a longer time eating and forage consumption is more uniform and distributed more evenly throughout the day than with concentrates (Minervino et al., 2014). Furthermore, the supplementation of concentrates in this breeding system tends to alter forage intake, reducing it (Silva et al., 2015) and increasing the resting time (Minervino et al., 2014). Providing animals with three daily feedings, rather than one or two, increases the population of rumen ciliate cells and may be an effective way to raise feeding frequency, particularly at night (Gonyou, 1984). Thus, developing feeding strategies that optimise rumination is especially important in intensive and arid production environments.

The palatability of the feed is a significant factor, as some feed has been rejected due to its smell or taste (Arnold et al., 1980). Although sheep deprived of smell or taste were still able to maintain normal feed intake and meal size (Baldwin and Meese, 1977), sensory stimulation remains important because varying odour and flavour cues influences the hedonic value of foods, thereby shaping intake, preferences and learning independently of post-ingestive effects (Favreau et al., 2013). In the context of confinement feeding, the introduction of alternative forms of feeding may result in alterations to the duration of rumination. Research indicates that the supply of fresh grass results in increased feeding and rumination times when compared to hay (Fanchone et al., 2010). Furthermore, other studies have demonstrated that silage with a shorter chop length increases both rumination and intake when compared to long silage (Krone et al., 2024). These findings emphasise

the importance of varied feed types and presentation to optimise feed intake, rumination, and overall welfare in ruminants, especially under confinement conditions.

The temperament of a sheep is indicative of stable individual differences in the activation of underlying motivational systems, such as fear, exploration, and sociability. These systems shape behavioural responses to handling and other potentially challenging situations (Estévez-Moreno et al., 2021; Atkinson et al., 2022). The following traits are typically assessed: activity and vocalisation. These traits emerge from distinct motivational processes. For instance, activity levels may reflect variation in fearfulness versus boldness or exploration versus avoidance when animals face novel environments or human presence (Réale et al., 2007). The arena test is a valuable tool that can provide insights into an animal's motivational systems, allowing for the assessment of sociability, fear, and curiosity simultaneously. Studies have shown that bolder animals tend to explore more and exhibit lower fear responses (Beausoleil et al., 2008), which also relates to a greater willingness to take grazing risks (Michelena et al., 2009). Although vocalisations were initially proposed as a personality marker, evidence indicates they are mainly expressions of social motivation, functioning as calls to conspecifics during isolation rather than reflecting general activity levels (Atkinson et al., 2022). It is important to note that even shy animals may modify their behavioural output through habituation, showing reduced fear and increased approach behaviour when repeatedly exposed to the same stimulus (Erhard et al., 2006). Finally, it should be noted that both intensive and extensive systems have a significant impact on individual sheep behaviour, which can in turn affect their welfare. While intensive systems may reduce stimulation and alter time budgets for individual behaviours, extensive systems allow for greater expression and adaptation to the environment. However, it is crucial to consider individual differences in both systems to effectively address welfare issues.

### 3.2. Social behaviour

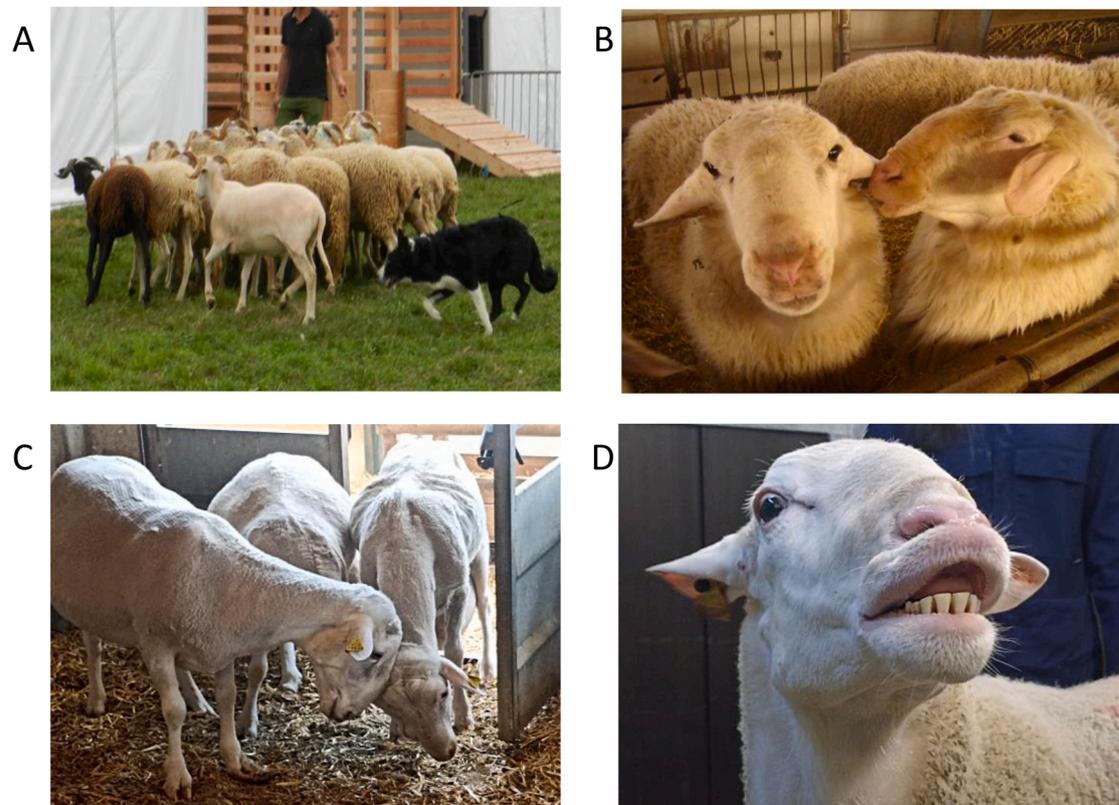
The regulatory system of social behaviour includes three main categories: agonistic behaviours (dominance–subordination and flight responses), affiliative behaviours (social bonding and cohesion), and sexual behaviours (Galindo, 2024). In sheep, the social group is a central component of the animal's environment, offering evolved survival advantages such as improved predator detection and dilution, access to social information for coordinated foraging and movement, and enhanced social and thermal comfort that support both individual fitness and group stability (Miranda-de la Lama, 2025). They include more effective protection against predators, greater efficiency in foraging, access to sexual mates and more effective defence of offspring (Miranda-de la Lama and Mattiello, 2010). Sheep are highly gregarious, forming cohesive groups, although the intensity of this behaviour varies with age and sex, as differences in responses to social isolation have been documented between males and females at different developmental stages (Viérin and Bouissou, 2003). This behaviour is driven by social facilitation, a collective motivational state resulting from the high behavioural synchrony of flock members (Ramos et al., 2021). Weaned lambs readily form groups even without prior familiarity, reflecting the strong gregariousness and social cohesion characteristic of sheep (Miranda-de la Lama et al., 2012). Furthermore, when an adult ewe is introduced into a group of lambs and/or kids, they immediately follow and imitate her behaviour (Pascual-Alonso et al., 2015). This strong tendency to follow adult conspecifics also has practical implications: in many lamb feedlots, adult ewes are kept on-site because lambs quickly follow them, facilitating unloading procedures and movement into pre-slaughter pens (EFSA et al., 2022).

Group living offers protection from predators, as predicted by the selfish flock theory. This theory states that large groups can reduce the risk of predation by diluting the likelihood of an individual being attacked (King et al., 2012). Domestic sheep have an attenuated

perception of danger compared to their wild relatives. This is a result of artificial selection and familiarity with humans (Dwyer, 2004). Furthermore, flock size has been found to influence anti-predator behaviour, with an increase in the number of sheep leading to a reduction in response to predation stimuli, a phenomenon referred to as the 'buffer effect' (González et al., 2013). Several social behaviours have been identified as anti-predator mechanisms (Fig. 1A), including modifications in recovery time, flight distance, scanning, alarm, observation and freeze responses (Wang et al., 2023). The intensity and frequency of these behaviours vary according to the type of stimulus and predator, as well as the breed of sheep (Zambra et al., 2021).

The ewe is a seasonally polyoestrous species whose reproductive activity is stimulated by decreasing day length, meaning that oestrus begins as daylight hours shorten (Ramírez et al., 2021). The seasonality of sheep displays considerable variation across different latitudes. In tropical and subtropical environments, certain breeds appear to be almost fully or completely aseasonal (Rosa and Bryant, 2003). In wild sheep, outside the breeding season, groups of males and females typically occupy separate habitats and often utilise non-overlapping grazing areas (Ruckstuhl, 1998). However, during the breeding season, the two groups intermingle, and males engage in agonistic behaviours to gain access to females (Bon et al., 1993; Rowell and Rowell, 1993). As a promiscuous species, in which multiple males mate with multiple females, social dominance within a group plays a key role in regulating access to resources (Mauleón et al., 2023). Dominant individuals have been shown to obtain greater amounts of food, utilise preferred areas such as shade or resting sites, and gain priority access to mates (Price et al., 2001). The number of members in male groups is subject to variation from year to year, due to the splitting and reforming of groups (Fisher and Matthews, 2001). Female groups comprise ewes of varying ages and reproductive status, and lambs of both sexes (Nowak et al., 2008). In agricultural settings, adult sheep are typically maintained in unisexual groups comprising individuals of similar age and sexual maturity. However, there are exceptions to this, such as ewe-lamb groups during the lambing period and ewe-ram groups during the mating period (Ozella et al., 2022).

Because the composition of these groups shapes social organisation, the concept of dominance becomes essential to understand how individuals interact within them. Social dominance establishes a hierarchical structure (either linear or non-linear) whose formation depends on several factors, including breed, sex, social alliances and environmental conditions (Miranda-de La Lama et al., 2012). A linear hierarchy is a structure in which animal A is dominant over animal B, which in turn dominates all other animals except A, and animal Z is not dominant over any other animal (Miranda-de la Lama, 2025). This structure has been observed with regularity in small, heterogeneous groups of sheep (Mauleón et al., 2023). In contrast, non-linear hierarchies are characterised by the presence of multiple individuals occupying equal positions within the group, or triangular and/or polygonal relationships formed with multiple individuals exerting dominance over others in a non-sequential manner. This form of dominance has been documented in medium to large homogeneous flocks (Miranda-de La Lama et al., 2019). The maintenance of social relationships between individuals in a flock depends on the occurrence of affiliative (Fig. 1B) and aggressive patterns (Fig. 1C) (Miranda-de la Lama, 2025). The agonistic patterns observed among the various breeds are similar, as are those observed between males of the same size and social position (Fisher and Matthews, 2001). Dominant individuals typically begin by displaying threat behaviours, such as tongue flicks and kicks, followed by mounts and head butts, which may elicit reciprocal butting or chasing from subordinates (McClelland, 1991). Affiliative behaviours such as rubbing and grooming may also occur during low-tension social interactions (Miranda-de la Lama, 2025), whereas in all-ewe groups agonistic exchanges are infrequent and brief, typically involving only short butting episodes (Eccles and Shackleton, 1986). In intensive systems, the predominant social unit is a group of ewes of similar size and age. The social



**Fig. 1.** Different key aspects of social behaviour: A) Defensive behaviour as a social strategy during exposure to potential predators (unknown dog and human). B) Affiliative behaviours such as licking and sniffing. C) Aggressive behaviours with head-butting. D) The flehmen reflex especially important in social recognition and sexual behaviour (Photos by Genaro C. Miranda-de la Lama).

organisation and level of cohesion of these groups are depending upon the breed. For example, in Mediterranean breeds, animals are in closer proximity and the flock's organisation is more dependent on species characteristics than in English breeds, where social dominance is of greater importance (Lynch et al., 1989, 1985). It can be reasonably deduced that the most cohesive breeds will experience greater difficulties if they are isolated in small groups of four to five animals. In general, an increase in flock size does not affect behaviour unless the available space is insufficient.

In intensive farming, the hierarchy is more rigid due to competition for resources, particularly feed (Miranda-de La Lama et al., 2012). The integration of multiple flocks may necessitate a period of adjustment for the animals involved. In the case of different breeds, integration between flocks may never occur (Arnold and Pahl, 1974). This is because breeds exhibit varying degrees of gregariousness, a behavioural trait related to feeding behaviour, which prevents them from achieving the same level of social synchrony. For example, Ortiz-Plata et al. (2012) observed that sheep of the Columbia and Suffolk breeds engaged in disparate activities within a mixed flock, despite having resided together for several years. Additionally, the Suffolk grazed in a more dispersed manner, while the Columbia grazed in compact groups. During the mating period, competition increases, and rams may engage in more frequent and intense fights as access to ewes becomes more contested (Mauleón et al., 2023), while ewes themselves may form temporary subgroups (Fisher and Matthews, 2001). In contrast, the social hierarchy of castrated males is more flexible and resembles that of females (Dove et al., 1974; Squires and Daws, 1975).

In sheep, social personality profiles have been documented in unisexual groups of both ewes and rams. Miranda-de La Lama et al., (2019) identified four consistent profiles in multiparous ewes—avoidant, affiliative, aggressive and pragmatic—each reflecting distinct strategies in social interaction and resource use. These profiles were also

associated with different reproductive patterns and behavioural responses, and showed consistent differences when animals were re-exposed to a simple cognitive task, suggesting that social personality influences broader aspects of behaviour. In rams, Papadaki et al. (2023) identified two distinct personality profiles, designated as "dynamic" and "responsive". The authors observed that individuals exhibiting a "dynamic" personality were more likely to engage in aggressive behaviours and vocalise more frequently, whereas those exhibiting a "responsive" personality were more submissive and spent a greater proportion of time lying down. These findings suggest that an understanding of social personality profiles in sheep could have important implications for flock management, as different personality types may respond differently to management, social dynamics and environmental challenges.

Socio-sexual behaviours are defined as those exhibited for the purpose of reproduction and are associated with attraction, courtship and copulation. These behaviours include intraspecific communication signals, such as postures, vocalisations, pheromones and visual displays, which facilitate interaction between males and females (Broom and Fraser, 2007a). They also encompass sexual selection strategies, such as male competition and mate choice. Rams typically display dominant sexual behaviour towards ewes, approaching them in a low-stretch posture (often accompanied by a slight head twist) followed by nosing and sniffing of the perineal region (Fisher and Matthews, 2001). In addition to seasonal fluctuations, the oestrus cycle of ewes can be triggered by their exposure to a sexually active ram, whose specific odours can reactivate the gonadotropic axis of anoestrous ewes. This phenomenon is referred to as the "ram effect" (Cann et al., 2023). When ewes are in oestrus, rams show increased courtship activity, including following, close approaches and mounting attempts. Subsequently, the male displays the flehmen reflex (Fig. 1D), which involves raising the upper lip to direct pheromones to the vomeronasal organ. This allows the male to ascertain the reproductive state of the ewe. The intensity and duration of

the flehmen reflex vary irrespective of the reproductive status of the ewe (Bland and Jubilan, 1987). García-Mahecha et al. (2023), observed that rams exhibited a higher prevalence of the flehmen's reflex following the ingestion of a feed that was highly preferred in comparison to a feed that was less preferred.

In the event of an unwelcome approach, the female may exhibit head-shaking behaviour or flee (Fisher and Matthews, 2001). Typically, the female does not select the male. However, recent evidence suggests that when an oestrus ewe can choose the ram without the influence of other individuals, she tends to prefer a subordinate male over a dominant one (Díaz et al., 2021). The female displays oestrus and seeks out the male, later following him. On occasion, the ewe may engage in self-rubbing against the ram (Broom and Fraser, 2007b). Three mating strategies have been described based on the hierarchical position of the individual within the group (Hogg, 1984). The tending strategy is performed by the highest-ranking males and consists of following one oestrus ewe while distancing all the other rams. The second strategy, courting, is observed in males of lower rank, who congregate around the dominant ram and the oestrus ewe, attempting to mount the female. The blocking strategy is employed by rams of all ages and involves the blocking and isolation of the female, preventing her from returning to the flock (Hogg, 1984). During the act of mating, the presence, sight, and interaction between dominant and subordinate rams influence the behaviour of the subordinate ram, increasing the likelihood of ejaculatory behaviour (Ungerfeld et al., 2019). In summary, social behaviour in sheep reflects a balance between evolved strategies that enhance group cohesion and resource access in extensive systems and the stress-inducing effects of social mixing, isolation and competition that arise in more restrictive housing environments (Miranda-de la Lama, 2025).

### 3.3. Maternal behaviour

The behaviour of maternal animals is fundamental to the survival of their offspring in mammals and thus represents an essential aspect from an animal production perspective (Cansian et al., 2024). Sheep are considered a precocial species, as lambs are born with open eyes, functional sensory capacities and the ability to stand and follow the dam shortly after birth, enabling them to perform the basic behaviours required for early survival (Broom, 2021). After birth, sheep display a "follower" anti-predator strategy in which lambs rapidly attach to and follow their mother and the maternal group, showing escape responses like adults when threatened (Nowak et al., 2023). Prior to parturition, the ewe, despite the effects of domestication, moves away from the rest of the flock in search of a sheltered and isolated location, thereby avoiding interference from other ewes and increasing the likelihood of bonding with the lamb (Poindron and LeNeindre, 1980). The period during which maternal bonding and subsequent recognition and acceptance of the lamb occurs is limited to a few hours and is crucial for reproductive success (Fisher and Matthews, 2001). Immediately following parturition, the female displays olfactory recognition behaviours, including licking, sniffing and grooming, which are all critical for the recognition of the birth fluid's attractiveness (Poindron et al., 2007). The lambs, following standing, commences the initial attempts at sucking, which facilitate attachment (Goursaud and Nowak, 1999). During suckling, the lamb wags its tail vigorously to disperse pheromones to the mother, who smells the anogenital area (Ewbank, 1967). Furthermore, auditory stimuli also contribute to the formation of the maternal bond between ewe and lamb, because of the emission of specific vocalisations, termed maternal vocalisations (Dwyer, 2014). In extensive breeding, normal socialisation that would occur in the wild, including lambs weaning and separation of sexes, is disrupted due to human interference (Kilgour et al., 2008). Even in the intensive breeding, where milk is the main product, the timing and methods for weaning lamb must be well managed. Indeed, abrupt weaning is associated with an increase in activity, especially vocalisation, and

disruption of circadian rhythms of activity (Kilgour et al., 2008).

After the recognition of the lamb, the attachment by the ewe is defined as "selective," whereby the female does not accept other lambs as her own (Poindron et al., 2007). The bond that is established results in an increase in maternal vigilance, maintenance of short spatial proximity, and frequent suckling interactions by the lamb (Dwyer and Lawrence, 2005). Nevertheless, several factors can influence an ewe's maternal capacity; under extensive conditions, primiparous ewes show shorter periods of maternal responsiveness than multiparous ewes, a pattern associated with an increased risk of lamb abandonment and mortality (Freitas-de Melo et al., 2021). Several studies have demonstrated that ewes subjected to malnutrition or isolation stress, particularly during the latter third of gestation, exhibit elevated levels of aggression towards lambs and diminished levels of grooming, resulting in a compromised feeding time (Hild et al., 2011). Ultimately, prolonged and arduous deliveries may culminate in the rejection of the lamb by the mother (Darwish and Ashmawy, 2011). Upon rejoining the group, the lamb may be subject to aggressive interactions by other ewes or vulnerable to predation, thus emphasising the importance of the mother's role in maintaining the selectivity of the mother-lamb relationship (Dwyer et al., 2003). Following a period of approximately two weeks, the ewe and lamb are no longer in close contact with one another. This is followed by the mother using her vision and hearing to identify her offspring (Fisher and Matthews, 2001). Several weeks later, lambs begin to form social groups within the flock's home range, where they display a range of juvenile social behaviours including play, sexual interactions, agonistic encounters and allelomimetic activities (Papadaki et al., 2024). Berger (1980) posited that movements such as neck twists, heel kicks and playful jumping indicate an invitation to play. The period of peak play behaviour is observed between the ages of 9 and 11 weeks (Hass and Jenni, 1993). Males display a greater propensity for mounting and playing behaviour than females, who, in contrast, exhibit a higher frequency of gambolling (Sachs and Harris, 1978).

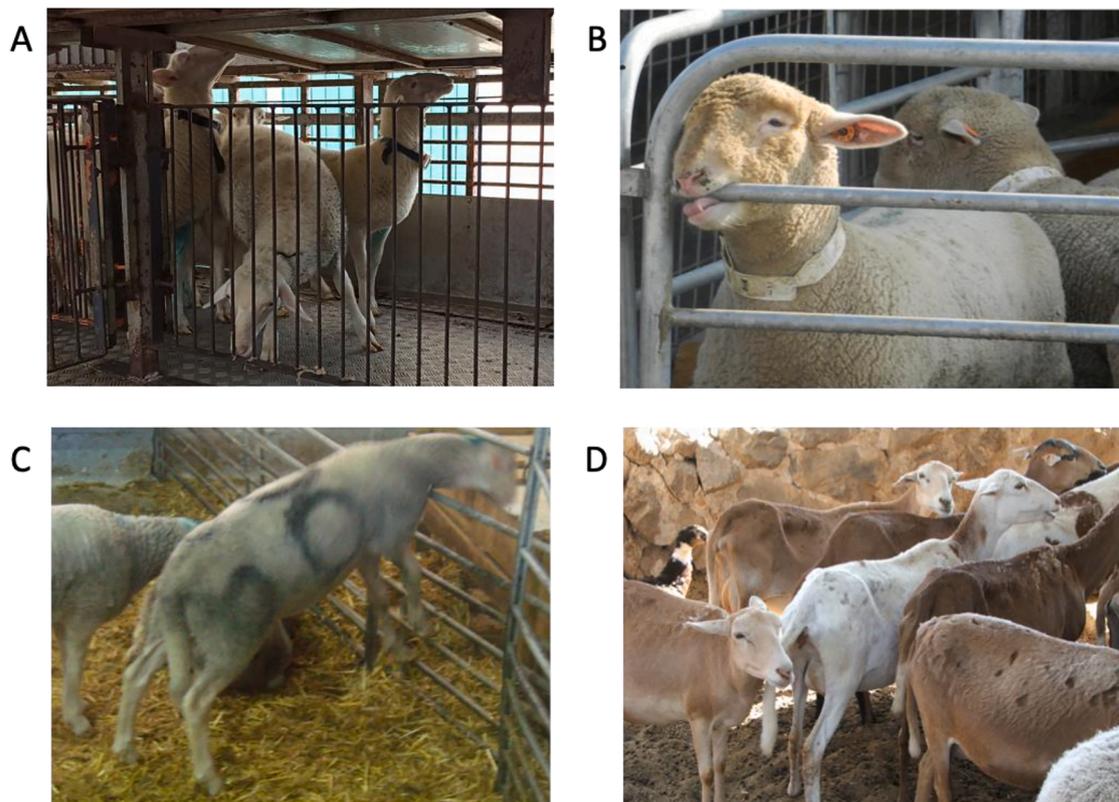
The ewe is particularly susceptible to the effects of breeding and management conditions, particularly towards the end of pregnancy. It is therefore essential to avoid any nutritional or psychological stressors that could interfere with the physiological changes associated with pregnancy, as well as any managerial activities in the immediate post-partum period that could affect the recognition of the lamb and the formation of the ewe-lamb bond (Dwyer, 2014). The likelihood of lambs being exchanged or stolen increases when large numbers of pregnant ewes' lambs are present within a narrow time window under high-density conditions that limit their ability to isolate for parturition, as demonstrated in commercial flocks (Lockwood et al., 2020). In addition to management practices, the individuality of animals may also influence the survival of the lamb. Indeed, a correlation between maternal care and temperament has already been demonstrated, although the precise nature of this relationship remains unclear. Nevertheless, it appears that sheep with superior maternal capabilities exhibit reduced fear responses when confronted with an arena test (Cloete et al., 2020). The incidence of difficulty during delivery may also be a trait that can be selected to decrease lamb mortality. Some breeds (e.g., blackface) experience less difficulty during the birthing process (Dwyer and Bünger, 2012). Furthermore, the degree of difficulty experienced during parturition varies between individuals and is of clinical significance, with a moderate heritability (Matheson et al., 2012). Several perinatal behavioural latencies in both ewes and lambs have been shown to be heritable and to respond to genetic selection. For instance, latency to parturition in ewes and latency to stand and suckle in lambs show favourable genetic correlations with the number of lambs weaned per ewe mated and with lamb survival, respectively (Pickup and Dwyer, 2011). Importantly, some of these behavioural traits have already been incorporated into formal breeding programmes, such as maternal behaviour scores (Bunter et al., 2019) and lambing ease scores (Li and Brown, 2015).

#### 4. Abnormal behaviours

Normal behaviour refers to those behaviours that are typical of a species in its environment (e.g., exploration; Fig. 2A), whereas abnormal behaviour refers to those behaviours that deviate from these established patterns and are usually out of context (Miranda-de la Lama, 2025). These include stereotypic and redirected behaviours (Keeling and Jensen, 2009), often associated with negative mental states such as stress, frustration or motivational conflict. Stereotypic behaviours are characterised by repetitive, invariant patterns with no apparent function, typically arising under conditions of environmental restriction. Displacement behaviours arise when an animal experiences a motivational conflict and responds by performing an activity unrelated to the immediate context. In contrast, redirected behaviours occur when the appropriate behavioural response cannot be directed toward its original target and is instead expressed toward another accessible object or individual (Mason, 2006). Identifying these behaviours in cryptic species such as sheep remains a considerable challenge. Consequently, in this species, behaviours that could be considered "abnormal" are instead classified as normal behaviours occurring with an abnormal frequency and incidence. These behaviours have the potential to cause damage and problems to the animal that implements them, despite their role in coping with an unsuitable situation. The prevalence of these behaviours was higher in animals kept in an intensive system with no opportunity for external grazing compared to those kept on pasture (Lauber et al., 2012). For example, sheep kept in individual pens exhibit high rates of pacing behaviour, and those relocated from grazing areas to enclosed spaces may begin to chew on pen fixtures (Done-Currie et al., 1984). Artificially reared lambs may also develop abnormal oral behaviours, such as sucking the navel or the scrotum of pen mates, particularly under early weaning or limited oral stimulation (Napolitano et al., 2008). Moreover, the absence of cereal straw as bedding material in fattening

lambs resulted in an increased frequency of stereotypical behaviours (Teixeira et al., 2014). It has also been reported that lambs subjected to social mixing in industrial feedlots can affect locomotor activity and alter their circadian rhythms (Abecia et al., 2024). In addition, this practice also increases the frequency of oral stereotypies (Fig. 2B), such as repeatedly licking or gnawing feed troughs, walls and fences (Fig. 2C), as well as rubbing their bodies (up and down) against fences or walls (Miranda-de La Lama et al., 2012).

Insufficient or inadequate opportunities for sheep to wield feeding is one of the primary hypotheses explaining abnormal behaviour. Moreover, the fibre and protein content of the diet may influence the emergence of abnormal behaviours (Yurtman et al., 2002). The consumption of diets comprising a high proportion of concentrates has been linked to an increased prevalence of wool-biting (or hair-biting) and pen furniture chewing behaviours (Cooper and Jackson, 1996; Vasseur et al., 2006). Insufficient levels of activity or oral stimulation result in the reorientation of behaviours towards alternative objects, including pen fixtures and other animals' wool (Vasseur et al., 2006). Wool or hair biting and eating are regarded as stereotypical behaviours (Fig. 2D), characterised by their repetitive and continuous nature as well as the absence of any discernible purpose or function (Mason and Latham, 2004). These behavioural patterns are associated with excessive density and typically manifest initially in one or a few animals, subsequently spreading to the remainder of the group (Parés et al., 2023). The behaviour in question is the biting and consumption of the fleece of other sheep, typically those situated at the lower echelons of the flock hierarchy. This can lead to gastrointestinal issues and an increased risk of parasitic infection (Broom and Fraser, 2007c). Another abnormal behaviour observed in ewes kept in chronic and close confinement is polydipsia, which is characterised by an intense sensation of thirst accompanied by the ingestion of fluid that is disproportionate to the body's water requirements. This may potentially result in a dilution of the nutritional



**Fig. 2.** Some key aspects to understand the abnormal behaviour. A) Normal oral and tactile exploratory behaviours when animals are first exposed to a new space (i. e. transport operations). B) Oral stereotypies in a familiar and unstimulating environment. C) Body rubbing. D) Wool or hair chewing as a redirected behaviour (Photos by Genaro C. Miranda-de la Lama).

value of the ration (Broom and Fraser, 2007d). The high prevalence of these behaviours in intensive systems underscores the necessity for enhanced management strategies.

One such strategy is environmental enrichment, which has been shown to help mitigate abnormal behaviours while increasing the diversity and complexity of the environment. Structures such as platforms and ramps (Aguayo-Ulloa et al., 2014), foraging substrates (Pascual-Alonso et al., 2015a), different bedding materials (Teixeira et al., 2015), and management practices such as weaning with foster ewes or human nursing (Pascual-Alonso et al., 2015b) have been shown to be associated with more diverse maintenance behaviours, reduced stereotypical behaviour and increased affiliative interactions (Aguayo-Ulloa et al., 2015). These strategies have also been linked to enhancements in growth, feed efficiency, immune function and even meat quality in lambs, in comparison with finishing systems that provide minimal stimulation. Furthermore, greater environmental complexity has been shown to influence the emotional states of sheep. For instance, housing enrichment has been demonstrated to modify their responses in cognitive bias tasks, suggesting more positive judgments under enriched conditions (Stephenson and Haskell, 2022).

## 5. Human-animal relationships and handling

The human-animal relationship is frequently overlooked in the assessment of animal welfare. Evidence is emerging that the relationship between humans and animals has a significant impact on their welfare, facilitates manipulation and improves productivity. Indeed, animals that receive gentle contact from humans display reduced levels of fear and agitation, particularly during loading and transport, veterinary procedures and when in proximity to humans (Nowak and Boivin, 2015). This reduction in stress can have direct productive benefits, as animals that are less fearful are easier to handle, leading to fewer injuries and more efficient handling during these events. In intensive farming, the relationship with humans assumes a key role in ensuring the welfare of animals and the smooth functioning of the system (Nowak et al., 2008). In these systems, human contact occurs much more frequently than under extensive conditions, making the quality of this contact even more crucial for animal welfare. The positive predisposition of the stockperson, but also the temperament of the sheep, contribute to the welfare of the animals during milking and other contact situations (Kilgour et al., 2008). A calm and patient approach from handlers can significantly reduce the animals' stress levels, improving both their welfare and the efficiency of milking. Even in a stressful environment, such as slaughter, the relationship with humans is of importance. Training staff to develop positive attitudes towards animals has been shown to reduce stress and fear, leading to improved productivity, such as higher-quality meat and fewer health complications (Hemsworth et al., 2011).

The social nature of sheep is advantageous in several contexts, including handling, management and flocking (Schiller and Horback, 2024). By demonstrating a unified response to potential threats, it becomes more feasible to manage them effectively (Fisher and Matthews, 2001). This gregarious behaviour allows efficient guidance with minimal human intervention; yet even though larger flocks keep greater distances from humans (Nowak et al., 2008), sheep can still recognise individual people visually, enabling positive interactions when habituated (Knolle et al., 2017). Furthermore, the sheep can recognise its breeder and conspecifics not only in person but also in photographic images, which may be in black and white and from different angles (Kendrick et al., 2001; Knolle et al., 2017). Furthermore, when sheep perceive the human as attentive, they increase their level of activity and display more glancing behaviour, which can lead to more manageable, less anxious sheep (Beausoleil et al., 2006). Sheep can be readily habituated to human presence (González-Pech et al., 2018). Furthermore, research indicates that in dairy sheep, habituation to handling and the development of a positive relationship can result in the animals becoming calmer and less reactive, thereby enhancing welfare and

improving production (Dimitrov-Ivanov and Djorbineva, 2003). This highlights the importance of consistent, positive interactions in improving production outcomes through reduced stress and better animal cooperation during handling and milking (Jardat and Lansade, 2022). The potential for positive attitudes in working with sheep to reduce flight distance from humans has also been investigated (Napolitano et al., 2011). Reducing the flight distance can lead to faster handling times, lower stress for the animals, and reduced risks of injury. Initiating habituation to human handling at an early age markedly improves animals' manageability, resulting in calmer and more compliant behavioural responses during routine procedures (Caroprese et al., 2012; Coulon et al., 2013).

Sokolowski et al. (2023) demonstrated that positive physical contact with lambs resulted in increased curiosity and decreased fear levels, which is significant because socially acclimated sheep exhibit a greater capacity to assess environmental stimuli, leading to better decision-making and enhanced flock management (Kozak et al., 2019). Nevertheless, it is essential to consider the specific breed in question (Pulido et al., 2019). Indeed, different breeds have different needs and behaviours and respond variably to the same stimuli (Kozak et al., 2019). Research indicates that, according to livestock transporters, facilities have a significant impact on handling ease, with the experience of the individual sheep and the breed also playing a role (Pulido et al., 2019). Well-designed facilities can reduce stressful interactions, facilitate smoother handling and increasing the productivity of the operation. Furthermore, the study under discussion indicates that transporters consider patience and experience to be key factors influencing their ability to manage challenging sheep, thereby emphasising the role of handler training in enhancing animal welfare and productivity (Burnard et al., 2015). Over time, handling procedures have evolved to improve human-animal relationships and animal welfare. New procedures, such as hoof care while standing, machine milking, loading via ramps, and shearing with clippers, have been introduced to reduce physical stress and increase handling efficiency. These innovations not only enhance animal welfare but also improve operational productivity, as they allow stockpersons to manage the animals more efficiently and with less stress (Yardimci et al., 2013). In conclusion, it is crucial to acknowledge the central role of the human-animal relationship in enhancing both welfare and productivity. While the merits of this approach are evident, further research is necessary to adapt practices to the characteristics of each breed and productive system.

## 6. Future priorities

The behavioural, motivational and sensory concepts reviewed above provide a basis for identifying practical handling applications and future research needs. Building on this foundation, the following section outlines key avenues for advancing sheep welfare and improving production systems. Future research directions will focus on the development of valid and reliable tools related to artificial intelligence and real-time monitoring systems. These tools will facilitate the early identification of changes in different motivational behavioural systems and will even allow for the automated detection of social and personality strategies. Such strategies may help to detect profiles of animals at risk of welfare problems or animals resilient to specific production scenarios (e.g., Çakmakçı et al., 2023). As demonstrated in the present review, recent research has indicated that positive or neutral human-sheep interactions will be of crucial importance in minimising fear responses and enhancing the animals' quality of life and resilience. Another research opportunity is the development of genetic improvement programmes that will not only focus on productivity (as is already the case in other livestock species), but also on pro-social behavioural traits, calm temperaments and behavioural resilience in this context, which are associated with a greater capacity to adapt to diverse productive environments. Furthermore, it is imperative to acknowledge the repercussions of climate change, which will necessitate the development

of novel management strategies that are aligned with the natural behaviours of sheep. These strategies should prioritize the utilization of behavioural indicators to identify potential risks, particularly those associated with the individual motivational systems of sheep. The future of sheep production will require an interdisciplinary approach, where the study of behaviour improves animal welfare, optimises production efficiency and strengthens the sustainability of the sector. This is in accordance with the European Union's Farm to Fork strategy, which includes MOP+ (production method with animal welfare indicators). In the near future, the implementation of new technologies for the measurement of sheep behaviour could provide useful phenotypes to include in balanced breeding objectives applied to the field of welfare genetics (Visser, 2025).

## 7. Conclusions

In conclusion, our review confirms that behaviour is a key indicator of animal welfare, and that its integration into the training of veterinarians, farmers, and other stakeholders can improve flock management and handling practices, reduce stress, and prevent the development of abnormal behaviours. Furthermore, the human-animal relationship is crucial in sheep farming, highlighting the need for rational and sustainable management strategies to meet the biological needs of the sheep across different production systems. Furthermore, the increasing demand for ethically sourced and sustainable animal products is likely to encourage the adoption of welfare-focused practices, in which behaviour plays a key role.

## CRedit authorship contribution statement

**Genaro C. Miranda-de la Lama:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Conceptualization. **Silvia Miretti:** Writing – original draft, Supervision, Resources, Project administration, Funding acquisition. **Paola Toschi:** Visualization, Validation, Formal analysis. **Isabella Manenti:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Conceptualization.

## Declaration of Competing Interest

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

We understand that the Corresponding Author is the sole contact for the Editorial process (including Editorial Manager and direct communications with the office). He is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs.

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