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Sensory factors involved in mother-young bonding in sheep: a review

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ABSTRACT: The aim of this review is to discuss sensory recognition (olfaction, vision, vocalisation, hearing and direct contact) in relation to the ewe-lamb bond, and the relevance of this information for animal management, considering that sensory recognition between ewes and their offspring is a key element of lamb welfare. In some parental care strategies, parents promote recognition of their own young in order to ensure their survival by providing them – and only them – with food, while the young simultaneously learn features of the environment. In the specific case of sheep, mother-young bonding is established during the sensitive period of the first 4 h after birth. The ewe prints a distinctive signal on her lambs that marks her as the legitimate mother, while stimulating the offspring's learning processes through olfactory, visual and acoustic cues. However, the sensory basis for proximal recognition of lambs changes over time as they learn to recognise the signals emitted by the mother. After 4 h – or less – the ewe becomes maternally selective; this means that she accepts only her own lambs at the udder, while actively rejecting alien newborns. Likewise, newborn lambs develop a preference for their mothers in less than one day. This preference is regulated by the difference between the acceptance behaviour manifested by the lamb's own mother and the aggressive rejecting behaviour shown by alien ewes. This early discriminative ability allows the lamb to avoid the aggressive actions of alien dams and maintain close contact with its own lactating mother. At around one week of age, lambs learn to develop the sensory cues that allow them to recognize their mother. These include olfactory, visual, acoustic and tactile information. Mutual ewe-lamb recognition at an early age also ensures that newborns will be fed and cared for by their own mother, which satisfies some of the requirements for their survival and welfare. For all these reasons, any disruption of ewe-lamb bonding during parturition is detrimental to lamb welfare and survival.

Keywords: ewe-lamb bond; welfare; recognition; olfactory; vocalisation; vision

Contents

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1. Introduction

The offspring of mammals of different species are born with distinct degrees of maturity in terms of motor or sensory development or thermoregulation. Consequently, the behaviour of the mother, which must be perfectly adapted to the needs of the newborn, differs according to the degree of development of her young at birth (Poindron 2005; Mora-Medina 2016). Maternal behaviour is a process that results from a combination of neuronal, humoral and sensory factors, and is designed to lead the individual mother to nourish and take care of her progeny by manifesting diverse behavioural patterns oriented towards ensuring the viability of the young (Ramirez et al. 2011). The developmental status of neonates also varies with litter size, as do the patterns of mother-young interaction (Nowak et al. 2000). Thus, in altricial species (i.e., canids, felids, most rodents and lagomorphs, among others), the mother builds a nest, or seeks a sheltered area where she gives birth to a large litter of young that are not fully-developed and have only limited sensory and locomotor abilities. Given that mother-young interaction begins inside the nest, it does not usually depend strongly on mutual recognition but, rather, on contiguity (Gonzalez-Mariscal and Poindron 2002; Numan et al. 2006). In an intermediate type of mammals, called carried-by-the-mother, the sensory systems of neonates are functional, but thermoregulation is inefficient – as in swine – and their locomotor capabilities are limited. This is characteristic of marsupials (internal matricolia), and primates (external matricolia). The mothers and neonates of these types of mammals must, therefore, resolve both shared and individual challenges during the perinatal period (Nowak et al. 2000; Gonzalez-Mariscal and Poindron 2002; Numan et al. 2006).

Precocial species (most ungulates) are characterised by a small litter of fully-developed young that are able to follow the mother shortly after birth (just 30 min), and that begin to suckle within 1 h (Nowak et al. 2000). These young are also capable of perceiving olfactory, acoustic, visual and tactile cues from the environment (Gonzalez-Mariscal and Poindron 2002; Numan et al. 2006). In lambs, the mother's interest in her young is strongest immediately after parturition and declines as her offspring ages, whereas the interest of the lambs shows an inverse relationship (Maldonado et al. 2015). After birth, the mother accepts only her own young at the udder and actively rejects any alien newborn that attempts to suckle. In sheep, goats and cattle, this aspect of maternal behaviour is called maternal selectivity (Nowak et al. 2000; Hernandez et al. 2002; Lambert 2012).

In the specific case of sheep, members of a precocial species, the ewe-lamb bond is key to the survival of the young (Numan et al. 2006). Because sheep are seasonal breeders that live in large social groups, many young are born around the same time, so it is critical for their reproductive success that the mother is able to immediately recognise and bond with her own offspring (Bielsky and Young 2004). Maternal selectivity exists to ensure that lambs will be cared for by their own mother, thus increasing their chances for survival. Maternal selectivity in ewes is understood as the capacity of the mother to accept only her lamb, or lambs, at the udder, while rejecting any alien lamb or lambs that try to nurse. This capacity is controlled, in part, by the offspring's recognition of olfactory cues (Ramirez et al. 2011).

The care that the mother provides to her young is also important for the latter's physiological and psychological development (Poindron 2005). Elements of newborn welfare include the condition of the animal's body and mind, and the extent to which its natural needs (i.e., genetic traits manifested according to breed and temperament) are satisfied (Hewson 2003). Therefore, beyond the simple survival of the young, the quality of maternal care will also influence their physiological and psychological development in the short, medium, and long term. In addition, mother-progeny interaction represents the offspring's first social experience and so can influence later preferences during adulthood (Charrier et al. 2003; Poindron 2005; Numan et al. 2006).

These neonates are entirely dependent on the care and resources provided by their mothers, for whom care of offspring entails substantial costs, including the expenditure of metabolic energy for milk production, thermal regulation, and the increased risk of predation due to the presence of conspicuous neonates and limited mobility (Nowak et al. 2000). For the young, meanwhile, recognising their own parents is essential for their survival because among gregarious animals, parents are the only individuals responsible for feeding them. This ability to bond thus implies some degree of recog-

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nition (mutual or unilateral), though this seems to vary among species and according to environmental conditions (Alexander and Borgia 1978).

In social species, close interactions – such as sensitivity to the signs or cues emitted by other members of the group (especially parents) – are highly-complex and constitute a fundamental element of the normal development of mother-young relationships. Socialisation takes place during the sensitive period of the early stages of the life-cycle of the young. In some mammals, the mother is the most important source of stimulation for the offspring, and is responsible for the first phases of their social sensitisation (Numan et al. 2006). However, while it is true that young mammals cannot survive without maternal resources, they are not simply passive recipients of parental care, for soon after birth neonates participate actively in nipple localisation and sucking, and influence the caregiving behaviour of their mother by communicating their needs to her (Nowak et al. 2000).

In all mammalian species, mothers also constitute the most important social contact for their young during the first month of life, as they facilitate the acquisition of information regarding the physical and social environments (Coulon et al. 2013; Mora-Medina et al. 2015; Mora-Medina 2016). At lambing, ewes (*Ovis aries*) tend to isolate themselves from the flock, an act that benefits the early relationship with their young. Later, they return to the flock and their lambs progressively interact with other conspecifics (Poindron et al. 1994; Val-Laillet and Nowak 2006). Isolation with no interference from other ewes is indeed of the utmost importance for the onset of the mother-young relationship and for lamb survival because it facilitates mutual recognition and rapid access to the udder. Newborn lambs develop a preference for their mothers in less than one day (Nowak et al. 1987), and this discriminative ability allows them to avoid potentially aggressive alien dams and maintain close contact with their own nursing mothers (Val-Laillet and Nowak 2006; Mora-Medina et al. 2015). Thus, soon after parturition, a mutual, long-lasting ewe-lamb bond is established (Poindron et al. 2007; Hernandez et al. 2012). Mothers can identify their young through the use of different sensory modalities, but the sensory basis for proximal recognition of lambs differs from those used in distal recognition (Ferreira et al. 2000; Keller et al. 2003; Mora-Medina et al. 2015). In light of these antecedents, the aims of this review are to discuss sensory recognition (olfaction, vision, vocalisation, hearing and direct contact) and the relevance of this information for animal management in relation to the ewe-lamb bond and lamb welfare.

2. Olfaction

2.1 Importance of chemical communication

Much of what is known about the neural basis of olfactory learning in mammals has come from studies of a small range of species, especially rodents and sheep (Rosenblatt 1983; Kendrick et al. 1992), in which learning occurs in specific contexts that are often vital for reproductive success. While this involves cues for individuality it also takes place in the context of other arousing sensory signals. Somatosensory stimulation plays an important role in many contexts of olfactory learning; however, attractant chemical signals may also be significant in olfactory recognition by promoting attention towards the chemical signals of individuality that need to be learned (Porter et al. 1991; Ferreira et al. 1999; Brennan and Kendrick 2006).

For most mammals, olfaction is important in many aspects of life, including mate attraction and recognition, mother-infant bonding, navigation, and detection of predators (Booth and Katz 2000; Gelez et al. 2004; Mateo 2006). Mammals achieve recognition of conspecifics by detecting species-specific chemical cues using their olfactory systems. It is widely-held that certain olfactory memories for cues related to mating, birth, or maternal care involve structural and functional changes in the olfactory bulb, triggered by noradrenaline (Kendrick et al. 1992; Keverne and Kendrick 1992; Gelez et al. 2004; Keller et al. 2004a; Keller et al. 2004b), which may result in the subsequent suppression of aversive behaviours towards the remembered individual and related stimuli (Pedersen 1997; Tibbetts and Dale 2007).

In most mammalian species, information regarding sex, age and other species-specific social and reproductive characteristics is conveyed by pheromones, which are detected by the vomeronasal and olfactory systems. Traditionally, pheromone signals were thought to possess intrinsic rewarding meanings and to trigger "innate", hardwired social-behavioural responses. In contrast, odorants are

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considered to possess mostly neutral reward value, but may induce approach or avoidance behaviours as a result of experience, or through conditioning when paired with stimuli that possess intrinsic rewarding properties (Beny and Kimchi 2014; Liberles 2014).

Chemical communication is particularly important in the management of mother-young relationships (Numan et al. 2006; Arteaga-Castaneda et al. 2007), and in various domestic mammals, parturient mothers clearly respond to the odours of their young (Mora-Medina et al. 2015; Mora-Medina 2016). While olfactory cues certainly inhibit maternal behaviour in non-pregnant females, at parturition the mother develops a state of high responsiveness to olfactory cues from the young that become important determinants in modifying her behaviour toward the neonate, which can range from avoidance to indifference or maternal care-giving (Levy et al. 2004).

2.2 Mutual mother-young olfactory recognition

In sheep, the amniotic fluid that covers the newborn lamb is very attractive for parturient ewes (Levy et al. 1983; Levy and Poindron 1987), such that within approximately four hours after giving birth the mother learns to recognise her own lamb by its smell, and will reject all other lambs (Poindron 1976; Poindron et al. 2007; Hernandez et al. 2012). Indeed, lambs may be rejected by their mothers if the amniotic fluid is washed off. Likewise, a mother may accept an alien lamb within four hours of giving birth if the young animal is impregnated with amniotic fluid. Interestingly, this suggests that the source of the amniotic fluid (i.e., whether it comes from the biological mother or another ewe) is not important, and that what truly matters is that the amniotic fluid contains attractive chemical cues that serve to facilitate individual recognition of the lamb (Poindron et al. 1980; Levy et al. 1983; Poindron et al. 1984; Arteaga-Castaneda et al. 2007; Poindron et al. 2010). Keller et al. (2003) have demonstrated that the presence of individual olfactory cues in amniotic fluids may also explain why about 30% of mothers display maternal selectivity from the very moment at which the foetus is expelled. This means that the amniotic fluid conveys individual as well as supra-individual cues.

The strong bond between ewe and lamb that forms shortly after parturition is a key factor in lamb survival. Offspring recognition via olfaction in most female animals is based on the young's individual olfactory signature, which is thought to emanate from its body coat; more specifically, from the anal region, which seems to be an especially attractive area since the dam licks it more than any other part of the lamb's body (Ramirez et al. 2011). However, Vazquez et al. (2015) found that if licking on some area of the body is impeded, the mother will compensate by increasing this activity on other areas. Studies in sheep have also demonstrated that the perception of olfactory cues is processed by the main olfactory systems (Levy et al. 1995), though other authors suggest that this could be mediated by accessory olfactory systems. This hypothesis relies on the finding that several chemical compounds that emanate from the anal region have been associated with pheromones that are detected by the vomeronasal organ and are responsible for influencing various types of behaviour, from sexual maturation to maternal behaviour (Levy et al. 1995; Ferreira et al. 1999; Ferreira et al. 2000). The vomeronasal organ is used as the confirming determinant for the recognition of neonates during nursing in sheep (Booth and Katz 2000). Other studies with sheep have induced anosmia (i.e. temporal destruction of the olfactory mucosa) during pregnancy to impede the olfactory learning process after birth. Results show that this affects only the main olfactory system, leaving the accessory systems intact. In those experiments, the dams were unable to learn and process the olfactory cues from their lambs, and so ceased to be selective in terms of differentiating between their own and alien young (Levy et al. 1995; Ferreira et al. 1999; Ferreira et al. 2000).

Ruminant mothers acquire the ability to recognise their own young rapidly, and reject any alien neonates that attempt to suckle. In sheep and goats, this discrimination is established within 2–4 h after birth (Nowak and Poindron 2006). However, in these species olfaction ceases to be efficient at distances greater than 0.25 m (Alexander 1978; Poindron et al. 2003). Studies performed with both sheep and goats have demonstrated that when the dam is farther than 0.25 m from its own young it is no longer able to recognise them by odour cues. However, under this condition the mothers utilised acoustic/visual cues to recognise their own lambs.

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In those experiments, the anosmic dams studied using a selective test were unable to discriminate between their own lambs and alien ones, but when they were tested in a distal recognition pen, they used visual and acoustic cues to recognise their neonates (Ferreira et al. 2000; Poindron et al. 2003).

With regards to the lamb, few studies have been conducted to evaluate the role of olfactory cues in maternal recognition. Nowak (1991) demonstrated that for lambs the role of smell is not important for recognising the mother during the first 24 h after birth. In that study, the olfactory function of a group of lambs was temporally impaired by applying topical anaesthesia in each nostril. The results demonstrated that the lambs so affected were still able to discriminate their mother from an alien one in a double-recognition test.

2.3 Complex olfactory mosaic and maternal selectivity

The neural substrates that control the expression of maternal responsiveness have been found mainly in the hypothalamic regions. Lambing, or the experimental induction of maternal behaviour in non-gestating ewes, increased c-*fos* mRNA expression in the hypothalamus, including the medial pre-optic area, and the paraventricular and supra-optic nuclei of the hypothalamus. In a recent study, Fos immunochemical expression has been measured in anosmic parturient ewes who are maternal but do not form a memory of their lambs. Heightened Fos immunochemical expression persists in the medial pre-optic area, and in the paraventricular and supra-optic nuclei of the hypothalamus of anosmic ewes, suggesting that these structures represent the core of maternal circuitry in sheep (Keller et al. 2004b).

These activations occur when mothers are exposed to a lamb after parturition, but not when the lamb is removed immediately after birth, or if the ewes are rendered anosmic (Keller et al. 2004b). Ewes develop a selective bond with their newborn offspring even when direct physical contact is prevented, as long as they have access to the lamb's salient odour. This suggests that the lamb's olfactory signature is partly volatile. The recognisable odour profile of a lamb reflects a complex mosaic of chemical by-products of bodily processes. Indeed, a recent study identified a list of 133 volatile organic compounds associated with the wool of Dohne Merino lambs that are presumably involved in offspring recognition (Burger et al. 2011). Quantitative analyses and comparisons of odour profiles reveal that the wool volatiles of twins are remarkably similar, but differ from those of other twins or non-twin lambs. Nonetheless, when alien lambs were dressed in jackets sprayed with synthetic mixtures formulated to match the chemical composition of the scents of the ewes' own lambs, the alien lambs were rejected (Burger et al. 2011; Keller and Levy 2012).

As pointed out above, there is no doubt that all mammals must initiate suckling soon after birth to survive. In rodents, this innate behaviour is critically dependent on uncharacterised, maternally-derived chemosensory glands, but recently a classic suckling pheromone was identified in a non-model system using the European rabbit (Schaal et al. 2003; Charra et al. 2012). This finding supports the role of specialised olfactory cues, or pheromones, in triggering the first episode of naive suckling behaviour (Logan et al. 2012). Regarding the establishment of maternal selectivity, it is hypothesised that down-regulation of cell proliferation occurs in specific areas of the sheep's brain, as well as in the main olfactory bulb, during the early postpartum period. This could facilitate the development of a perpetual olfactory memory that is retained to favour survival of the newborn through neurons that somehow assist the learning process (Archunan et al. 2014). Therefore, the olfactory system's capacity to generate new interneurons is thought to fulfil an important function in social situations in which olfaction plays a pivotal role (Keller and Levy 2012).

3. Vision

3.1 Visual perception in ungulates

Vision allows organisms to perceive the qualities of luminous bodies in accordance with certain laws of light. Also, this sense enables second-order perception of some mathematical elements, such as situation, size, form and volume (Rovira-Castro 1973). The retina is a multi-layered extension of the brain that plays a key role in vision (Komaromy 2010). In ungulates, vision, in combination with the auditory, olfactory and gustatory system, is vital for environmental perception, individual recognition, and the selection of the ecological resources necessary for survival and reproduction (Sugnaseelan et al. 2013).

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A wide visual field is a common characteristic of ungulates such as goats, cattle, horses and sheep, and may be an adaptation by prey animals that enables early detection of predators (Kendrick et al. 1995). Sheep have excellent eyesight due to the angle of approximately 48° between the optic axis and the midline, which indicates that they have a wide, though not panoramic, monocular field, and a binocular field of about 60° (Hutson 2007). This allows sheep to scan the horizon constantly using their monocular vision with no need for head and eye movement. This is advantageous for scanning the flock and for opportune detection of predators (Piggins and Phillips 1996; Shinozaki et al. 2010). The retinal topographies and distribution of the tapetum are specialised in the horizontal and dorso-temporal fundus, which suggests that sheep have better visual acuity in the horizontal and antero-inferior fields, and that this specialisation is related to the species' visual ecology. Thus, the retina provides basically good photopic vision as an adaptation to diurnal activity, while the presence of the tapetum and dense rods also provides good mesopic vision (Shinozaki et al. 2010).

3.2 Mutual mother-young visual recognition

Experiments by Kendrick et al. (1995) have shown that sheep can distinguish between sheep and human faces, different breeds of sheep, and sexes of the same breed. Eyesight appears to play the most important role in recognition, as in humans. In a 1996 study, Kendrick et al. found that ewes are able to discriminate between pictures of their own lamb and an alien one when they are only 3-week old. However, in research by Keller et al. (2003), primiparous ewes that were selective at suckling at 4 h postpartum did not recognise their lambs at a distance because maternal experience has a differential effect on the dynamics of these learning processes.

Sheep discriminate objects in the frontal visual field by binocular fixation with the centralis area for optimal visual acuity, and are well-equipped to detect movement in the postero-inferior and postero-superior visual fields (Shinozaki et al. 2010). Like primates, sheep have specialized neural circuits in the temporal cortex that facilitate the recognition of individuals by their faces. Electrophysiological recordings from single cells in this region have demonstrated small populations of cells that respond preferentially to faces as opposed to other classes of objects (Broad et al. 2000). In lambs, meanwhile, sight is well-developed by one week of age, and neonates are able to recognise their mother using only visual cues (Arnold et al. 1975; Shillito 1975; Alexander and Shillito-Walser 1978).

Terrazas et al. (2002) demonstrated that at around 24 h of age lambs use a combination of visual and acoustic cues to discriminate their mothers from other ewes. These findings, added to the fact that lambs are able to select their mother from a distance at just three days of age (Nowak 1991), indicate that recognition based on distal individual features develops rapidly. Therefore, lambs seem to gradually develop their ability to recognise their dams, initially through orientation based on rather general cues that do not necessarily depend on individuality, but later come to rely on a more complete and individual representation of the mother (Terrazas et al. 2002). During the first two or three days of the lamb's life, the newborn also learns the individual physical features of its mother and so develops the ability to recognise her from a distance at an age ranging from three to seven days (Nowak 1991).

In another study, Terrazas et al. (1999) attempted to test whether ewes would discriminate between their own and an alien lamb in a situation in which olfactory cues could not be used. To this end, mothers were given the choice between their own and an alien lamb when separated by a minimum distance of 1 m. The ewe to be tested was placed in a Y maze enclosure fitted inside a triangle delimited by plain metal hurdles, while her own lamb and an alien lamb of approximately the same age were placed in each of the individual pens at the other corners of the enclosure. In that study, mother ewes spent significantly more time close to their own lamb than to an alien young of the same age, indicating that they were able to discriminate between them. This behaviour was present in the groups of ewes tested as early as 8 h after parturition, suggesting that they are already able to recognise their lambs on the basis of visual and acoustic cues at this early stage.

4. Hearing

4.1 Information contained in vocalisations

Vocal communication plays a particularly important role in regulating social interaction and

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coordinating activities in many mammals and birds that are organised in social groups (Fichtel and Manzer 2010). Animals produce sounds for various purposes and most of their vocalisations have distinctive characteristics that are used in systematics (i.e., the study of the units of biodiversity), and are therefore useful in documenting biodiversity (Ferreira-Pereira 2011).

A broad range of animals produce sounds (McComb and Reby 2005), and in many animal species hearing is essential for receiving acoustic signals from other individuals and the environment. In this process, socialization and the learning of specific vocalisations by conspecifics play predominant roles in species survival (Arch-Tirado and Collado-Corona 2002; Moura et al. 2008; Arch-Tirado et al. 2009).

Animal vocalisations can convey information about context and events in the environment, as well as multiple pieces of information about the sender; including identity, physical characteristics, and emotional or motivational states (Fay and Popper 2000). Vocalisations are specifically attributed to particular inner states, as shown by the study conducted by Schrader and Todt (1998), who demonstrated that the rate of particular vocal types in domesticated pigs indicates different endocrine stress responses, and that non-human primates may show a more creative use of vocalisations under certain circumstances (Schrader and Todt 1998).

Vocalisations may also enable recognition of conspecifics. One example of such recognition is that newborn animals of certain species develop an auditory memory as a result of interaction with other members through vocalisations (Sebe et al. 2008).

According to Marx et al. (2003), emission parameters related to energy, frequency and duration are particularly effective for characterising call types. For example, low-tone vocalisations, such as grunts by sheep, are used to maintain social contact with members of the group, while many high-pitched screams are similar to those used in an excited state (Ferreira et al. 2000; Charrier et al. 2001; Long 2007; Martinez et al. 2011).

4.2 Mutual mother-young vocal recognition

It has been shown that mother-young vocal communication and acoustic recognition promote preferential nursing and are important components in regulating early mother-young interactions, based on findings that both mother and neonate show an intense peak of vocal activity in the first 3 h following birth (Nowak 1990; Dwyer et al. 1998; Val-Laillet and Nowak 2006; Nowak et al. 2007; Sebe et al. 2007; Sebe et al. 2010). Therefore, vocal communication appears to be a key factor for mother-offspring recognition (Carter et al. 1992; Dwyer et al. 1998; Sebe et al. 2010). In sheep, maternal bleats and proximity to young to allow access to the udder are characteristic maternal responses (Bridges 2015). Ewes begin to vocalise in the final 3 h preceding parturition, emitting mainly high-pitched bleats. However, this bleating becomes most intense during the first 3 h following birth, though at that point it consists mainly of low-pitched bleats. Thereafter, it decreases sharply until 24 h postpartum, with most of the activity coming from the mother (Sebe et al. 2007).

Furthermore, during vocal interactions with 48-h-old lambs, ewes produce two categories of bleats: high-pitched and low-pitched (Mukasa-Mugerwa et al. 2000, Terrazas et al. 2003; Sebe et al. 2007; Dwyer 2008; Sebe et al. 2008). These are related to the degree of mouth opening and are easily distinguishable by humans; i.e., low-pitched bleats are quiet vocalisations produced with the mouth closed, while high-pitched bleats are loud calls produced with the mouth wide open. It is generally accepted that low-pitched bleats are an expression of maternal care and have a calming effect on lambs (Carter et al. 1992; Terrazas et al. 2002; Sebe et al. 2007).

The numerous low-intensity vocalisations emitted during parturition are thought to orient the young towards the maternal body and to provide cues for later recognition of the mother. It has been further suggested that, in prey species like sheep, natural selection has favoured low-intensity vocal communication between mother and young as a strategy to avoid attracting predators, as these sounds can be perceived only under conditions of close proximity (Nowak et al. 2000; Nowak 2006).

Furthermore, soon after parturition, ewes and lambs display a preference for each other based solely upon vocal cues (at 24 h in ewes and 48 h in lambs; Sebe et al. 2007) and recognise the individual acoustic signature of their kin soon afterwards (Searby and Jouventin 2003). Taken together, these results suggest that mutual vocal recognition plays a significant role in the development of pref-

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erential nursing by ewes of their own lambs, and that this may occur quite rapidly after parturition (Nowak et al. 2000; Manteuffel et al. 2004; Nowak and Poindron 2006).

Hence, animal calls have evolved, in part, as communication signals used to indicate some type of "need", and are relatively easy to remember. It seems reasonable to regard vocalisations as clear indicators of an animal's state of welfare. However, evaluating welfare requires that, in a given environment, the physical and physiological conditions of the vocalising animal can be clearly attributed to its condition. Whereas high-pitched, tonal sounds are thought to signal appeasement in fear-associated contexts, low-pitched, harsh sounds are attributed to more aggressive emotions (Manteuffel et al. 2004).

5. Somatosensory stimulation

5.1 At parturition

In mammals, the manifestation of maternal behaviour at parturition is facilitated by the physiological changes that occur in the mother at that time. Thus, the prepartum increase of oestradiol concentrations in maternal blood is a key factor in the activation of maternal behaviour in several species (Gonzalez-Mariscal and Poindron 2002; Numan and Insel 2003). This has been especially well-documented in rats and sheep (Meurisse et al. 2005). A major neurotransmitter that increases markedly in the cerebrospinal fluid at parturition is oxytocin (Nowak et al. 2000). Oxytocin and vasopressin are members of a large group of ancient neuropeptides with proven effects on a variety of mnemonic and social processes. Among their established roles in mammals, these two peptides control an organism's ability to remember individuals they have encountered previously. This form of social recognition is essential for all complex relationships, including the development of lifelong pair bonds in monogamous mammals (Winslow and Insel 2004). In addition, the intracerebral release of oxytocin that results from the vagino-cervical stimulation caused by the expulsion of the foetus is another critical determinant of the activation of maternal behaviour (in sheep and rats; Meurisse et al. 2005). Research indicates that oxytocin is released into the bloodstream and the brain in response to very specific types of somatosensory stimulation, such as vagino-cervical stimulation during birth and sexual behaviour, nursing, feeding, and tactile contact (touch, warmth or vibration; Kendrick and Keverne 1991; Winslow and Instel 2004; Coulon et al. 2013). Although oxytocin-induced maternal nurturing is mediated by some of the same brain regions in rodents and sheep, it also modulates maternal bond selectivity by altering neurotransmitter activity in the olfactory bulb, essentially priming the olfactory systems for the selective learning of the offspring's scent (Broad et al. 2006). Furthermore, the influence of maternal experience on ewes' ability to display maternal care could be crucial. It is not uncommon for ewes giving birth for the first time to show inadequate maternal behaviour towards their neonate, or even abandon it, though this is very rare in multiparous dams (Meurisse et al. 2005).

5.2 Maternal licking/grooming

Peripartum behaviour in ruminants is characterised by a number of typical components. For example, within just a few minutes of parturition, the mother begins to lick the neonate and the foetal fluids spilled on the ground. The birth membranes are also consumed during this cleaning process. Studies have shown that in ewes – less clearly in cows – birth fluids are normally repulsive but become temporarily attractive at parturition (Nowak et al. 2000). In primiparous ewes, the absence of foetal fluids on the newborn discourages licking, and may provoke a refusal to nurse or even aggressive behaviour. While several functions of grooming have been postulated, most have as yet little or no experimental evidence. Grooming usually begins at the head, perhaps because the failure to remove foetal membranes from the face could lead to suffocation. Removal of the birth fluids may also help dry the coat of the neonate and reduce heat loss, and licking may stimulate teat-seeking activity in the young (Nowak et al. 2000).

In sheep, the mother's behaviour must be synchronised with the movements of the newborn lamb, which has to stand in order to locate and reach the mammary gland. Most lambs stand up within the first 30 min of delivery and begin to suckle 1–2 h later. They find the udder by exploring the underside of the ewe's body from chest to

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udder, guided by various cues that emanate from the mother's body. Many ewes help the neonate by lowering their back and bending a hind leg to facilitate access to the teat (Vince 1993). Lambs learn the position and shape of the udder very quickly, and this learning is sustained by the dynamics of mother-young interaction and the reinforcing properties of suckling (Nowak et al. 2007). Thereafter, udder-seeking behaviour is guided by thermo-tactile and olfactory cues (Vince 1993). Touching the face strongly activates oral exploration and orientation movements of the head, but the intensity of responses depends on the characteristics of the stimulus: i.e., lambs respond preferentially to warm, smooth, non-woolly, intermediate yielding surfaces.

The key role played by tactile contact in social bonding is potentially facilitated by oxytocin (Goncalves et al. 2008) since oxytocin-induced maternal behaviour, such as licking, grooming and nursing pups, are activities that the mother performs in order to ensure the normal development and survival of her offspring. Moreover, recent studies suggest that this hormone is essential for social recognition, and that pregnancy, birth and lactation all improve spatial memory in the female rat. A study by Tomizawa et al. (2003) showed that even aspects of the role of oxytocin in synaptic plasticity and long-term memory could be intimately linked to its role in maintaining maternal social behaviour. That study also revealed a new function of oxytocin; namely, that it causes plastic changes in hippocampal synapses during motherhood.

In another vein, discriminative social bonds between twin lambs are mediated to a great extent by the mutual familiarisation that results from direct contact (Dwyer and Bornett 2004). Lambs appear to have individually distinct (olfactory) signatures, but those of twin siblings may be sufficiently similar to enable the mother to detect a resemblance (Boivin et al. 2001).

With respect to direct contact, early mother-young interaction in combination with birth- and suckling-related stimulations compose an ideal substrate for the development of mutual bonding (Nowak et al. 2007; Nowak and Boivin 2015). Bonding is important for survival and behavioural development, and the mother plays a key role in fostering such social cohesion. Therefore, the development of social familiarity is perhaps the earliest stage in the process of developing social relations and, consequently, is crucial to normal social development (Winslow and Instel 2004). After the periparturient phase, ewes never – or only exceptionally – groom their lambs, but tactile stimulation can be provided in different ways. For example, young lambs are often seen sleeping against their mother's body, or sometimes even on top of her, or against the body of other lambs. They obviously have a need for body-to-body contact when resting, though the biological importance of such touching is still unknown (Nowak and Boivin 2015).

6. Lamb welfare

There is no species of mammal in which the young can survive in the absence of maternal care (Nowak et al. 2000). As a result, the early development and survival of newborn lambs depend entirely on the care provided by their mothers. In sheep, which are gregarious, this begins with the ewes' tendency to separate from the flock as parturition approaches. Even under intensive management, pre-lambing ewes choose to isolate themselves if they are given the opportunity to do so through the provision of cubicles in the shed. Under non-intensive conditions, however, it is not always clear whether parturient ewes actively seek isolation or are left behind by the flock (Nowak and Poindron 2006). Considering that the primary, immediate functions of the mother-young relationship are to provide the offspring with a secure source of nutrition, protection against predators, and guidance (Nowak et al. 2000), it is important that this bond develops as quickly as possible after birth. It is imperative that the mother recognise its own lamb and that the lamb recognise its mother. However, it should be underlined that the development of early recognition of the dam varies according to breed, sex, and litter size. For example, twin lambs commonly take more than two days to begin to show a preference for their dam. Even then, behavioural differences persist between singles and twins (Nowak and Poindron 2006).

After parturition, a series of events occurs that involve sensory signals that can ensure or compromise the lamb's welfare. One of the most important of these signals is the grooming of the newborn lamb. This appears to be an extension of the attraction to the spilt foetal fluids, and usually begins with

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consumption of the remnants of the foetal membranes, before developing into a thorough licking of the newborn, usually beginning with the head, the first part of the lamb that moves, and continuing along the body once the newborn is standing, with particular attention paid to the ano-genital region. This behaviour includes stimulation of respiration, muscle tone, circulation and excretion, drying to reduce heat loss, removal of birth odour to avoid attracting predators, hair-care to increase thermal insulation and, finally, the bonding and learning of offspring's odour by the mother (Alexander 1988).

The lamb's survival and development can be affected by the ewe's maternal behaviour, as von Borstel et al. (2011) demonstrated in their research on differences in maternal behaviour in ewes (n = 602) from five different breeds during periods of separation from their lambs (n = 1003), in which the behaviour measurements of ewes were related to the productivity traits of the lambs. The sheep tested in that study belonged to one of the following German breeds that have evolved under different husbandry intensities (in order from most- to least-intensive): Merino Landschaf, Deutsches Schwarzkopfiges Fleischschaf, Weisses Deutsches Bergschaf, Rhonschaf, and Graue Gehornte Heidschnucke. Prior to lambing, the ewes were kept together in groups of 30–60 in a barn with straw bedding (1.5 m^2/ewe). All lambs were born indoors. One day after birthing, the lambs were taken from the lambing pens for 10 min and held by a human handler at a distance of 5 m from the ewes. Then they were returned to their mothers, and the ewes' behaviour was observed for 1 min. These researchers demonstrated that most of the ewes, regardless of breed, manifested agitation when the lambs were separated (71.8%), and that 87.2% vocalised during separation. Almost all the ewes (96.2%) sniffed and licked their offspring after they were returned to the lambing pen. Graue Gehornte Heidschnucke showed the highest rates ($P < 0.001$) of vocalisation during separation, whereas Deutsches Schwarzkopfiges Fleischschaf showed the lowest. Also, Deutsches Schwarzkopfiges Fleischschaf and Rhonschaf showed lower rates of activity during separation than Merino Landschaf and Graue Gehornte Heidschnucke. This study concluded that maternal behaviour differed among the breeds studied, potentially implying animal-welfare benefits for some breeds under given husbandry conditions.

Another condition that has repercussions on lamb welfare is the number of offspring born and the ewe's breed-dependent ability to care for them. Alexander et al. (1983), observed the behaviour of four breeds of sheep – Merino, Dorset Horn, crossbreed (Border Leicester × Merino) and New Zealand Romney – to provide information on whether these separations are common in sheep in general, or are characteristic of only fine-woolled Merinos. Their study demonstrated that 46% (32/70) of the Merino ewes that produced live twins became permanently separated from at least one lamb. Also, temporary separation (ewes being more than 30 m away from lambs and showing no response to their presence) of up to 6 h was observed in 34% of ewes, while only 20% were never seen to be separated from either twin. In contrast, few ewes with single lambs were observed to separate at any time, and 90% were never seen to separate. All but one of the 16 temporary and permanent separations from singles observed occurred on the first day after birth. Nonetheless, it is important to point out that weakness of lambs at birth, difficulties during parturition, or interference with, or by, other sheep, appeared to contribute to permanent separation in 12 of the 26 twin-bearing ewes for which the separation circumstances were verified. Turning to the Dorset Horn and crossbreed types, researchers observed that those ewes presented greater ability, since the incidence of permanent separations was significantly lower than in the Merinos. They concluded that the failure of ewes and lambs to remain together is clearly prejudicial to lamb survival, although some abandoned or stray lambs may be mothered by other ewes. Birth difficulties were an important cause of separation in the Romney and Merino breeds with single lambs, and observations indicate that moderately prolonged births extend the period of maternal receptiveness that precedes delivery; thus increasing a ewe's possibility of mothering a stray lamb or stealing a lamb from its own mother; while markedly prolonged births suppress maternal behaviour and can lead to recumbency, when the newborn lambs are not cared for.

With respect to the conditions in which the births of these lambs evolved, we know that they can impede the adequate development of the ewe-lamb bond and, as a result, affect the survival of offspring, as Darwish and Ashmawy (2011) demonstrated in ewes with prolonged labour and complicated de-

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liveries that failed to show good maternal care or abandoned their newborns more frequently than those with short labour and unassisted births. In normal conditions, the ewe is expected to show intense licking and grooming of the still-wet lamb and to emit frequent low-pitched bleats (the so-called "caregiver" bleat emitted by the ewe to strengthen bonding with the lamb). However, the findings from that study showed that these behaviours are likely to be less frequent in ewes with prolonged, difficult births compared to those with short, uncomplicated deliveries. Those researchers also observed that lambs from prolonged, difficult births were similarly, and significantly, less vigorous after birth, as they required more time to stand, reach the udder and suck successfully. In addition, they showed a reduced ability to maintain body temperature after birth; an effect that persisted during the first three days of life and is associated with higher neonatal mortality in the first week after birth (11.54%), compared to lambs from short, non-stressful birth processes.

Malnutrition suffered by the mother during the gestation period also results in poor lamb welfare. This was demonstrated by Dwyer et al. (2003) in their research on the effects of a moderate (35%) reduction in ewe nutritional intake during pregnancy on the expression of ewe-lamb bonding behaviours in primiparous Scottish Blackface ewes. Those authors concluded that even a moderate level of undernutrition impairs attachment between ewes and lambs by affecting maternal behaviours expressed at birth. In addition, their results suggest that levels of undernutrition that cause a decrease in birth weight will affect the evolution of the behaviour of neonatal lambs.

The ewe's milk is the only source of nutrition for the lamb, but because newborn mammals have very limited energy reserves, they must begin to feed just minutes after birth. A major factor that affects survival is the difficulty in maintaining homeothermy. In this regard – especially in ungulates like sheep – colostrum provides not only a key source of energy but also immunoglobulins that help ensure passive systemic immunity. For this reason, an essential priority for neonate survival is early access to the udder. Behavioural patterns acquired early in life through imitation of the mother – e.g., development of food preferences and predator avoidance – have advantages over inborn behaviour or learning by trial-and-error (Nowak et al. 2000).

One example of how the mother serves as a guide in learning for her lambs was described by Thorhallsdottir et al. (1990), who observed that individual learning by trial-and-error has been the most efficient and permanent way for lambs to learn about harmful foods. In their study, after control lambs had a single experience with the harmful food, they avoided that food for at least two months. However, the lambs that were allowed to observe their mothers during exposure to the harmful food ate significantly less than when they were exposed in isolation. This indicates that they learned to avoid the food from observing that their mothers did not ingest it. In other experiments conducted by these researchers, lambs that were exposed with their mothers to a food that the dams rejected ate less of that food after weaning than the lambs of mothers that readily ate the food. This provides additional evidence that observational learning of food avoidance is important in lambs.

In a study by Pfister et al. (2006), ewes were fed 10% locoweed pellets (*Oxytropis* and *Astragalus* spp.), which contain plants that are toxic from day 100–130 of gestation. Animals that ingest this food for more than two weeks show a loss of motor skills, diminished proprioception, emaciation, and reproductive disorders; thus, those researchers decided to observe its effects on the behaviour of lambs. Their work demonstrated that intoxicated lambs appeared to be unable to develop appropriate neonatal bonds with their dams because they spent less time with them once contact was made, compared to control lambs, even at 36 h after birth. The treated lambs were also slower to cross a maze to reach their dams, slower to reach their mothers when impeded by a barrier, and unable to discriminate their mothers from alien ewes at 12 h postpartum. These findings demonstrate the poor level of welfare of those lambs due to the fact that development of the sheep's central nervous system peaks in mid- to late gestation and is affected by maternal swainsonine ingestion (an indolizidine alkaloid). Also, the lambs from intoxicated mothers had lower birth weights and some required assistance to nurse. Clearly, it is important to emphasise that any disruption of ewe-lamb bonding during parturition is detrimental to lamb welfare and survival.

Reinforcement of vocal activity by nursing is also consistent with the shaping of neonatal behaviour through the stimuli associated with suckling, which can have a calming effect and facilitate learning, as has been reported for a wide range of species, including humans, rats, rabbits, dogs and sheep

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(Nowak et al. 2007). In contrast, vocalisations that present a higher frequency are used in a wide variety of contexts, ranging from the excitement caused by anticipating or receiving food, to warning the flock of the presence of intruders, or signalling that they are experiencing stress, fear or pain. For example, a study by Terrazas et al. (2002) showed that a higher frequency of high-pitched bleats elicited aversive behaviour in the lambs, since such bleating is normally associated with maternal agitation and rejection of alien lambs. It is possible, therefore, that in these experiments the difference in maternal vocal activity between a lamb's own mother and alien mothers served as an important cue for lambs to discriminate and prefer their own dam.

On the other hand, emotionally relevant external events, hormone concentrations affecting mood, and appetitive behaviours such as thirst and hunger, can all stimulate a complex central nervous network that proximately regulates endocrine feedback and behaviour in order to maintain, or re-establish, homeostasis (Manteuffel et al. 2004). Thus, physiological stress responses may provoke the emission of modulated vocalisations that could be considered vocal expressions of stress (Marx et al. 2003). One example of this is the fact that animals tend to emit more vocalisations when isolated, and as cortisol and norepinephrine concentrations increase in their blood plasma (Arch-Tirado and Collado-Corona 2002; Moura et al. 2008; Arch-Tirado et al. 2009). In this regard, Bergamasco et al. (2005) have shown that even brief maternal separation in goats (10 min) produced significant increases in both behavioural and physiological measures, suggesting that such separation may be an effective psychogenic stressor for growing kids that provokes situations with negative effects on neonate welfare.

In another vein, social bonds or attachments are commonly defined as differential behaviours or emotional interactions that occur in the presence, or absence, of a partner. Social attachments function to facilitate reproduction and social cohesion, provide a sense of security, and reduce feelings of stress and anxiety. Attachment has been described primarily in terms of mother-infant bonding (e.g. mother-offspring relationships in sheep; Coulon et al. 2013), where the dam plays a prominent role in the development of her offspring's social relationships with siblings and other age-mates. For example, twin births are a common occurrence in domestic breeds of sheep, and suckling lambs interact preferentially with their twins rather than other age-mates.

One final area involved in improving offspring welfare is the condition of suffering that lambs may experience; a factor that may favour attracting the attention of the mother, as Hild et al. (2011) demonstrated when they sought to detect whether maternal care by ewes could be effective in mitigating psychological or physiological stress or pain in their offspring. To this end, they studied ewes that had given birth to twins so that they could have a control and a treatment animal. The treatments consisted of either an intravenous injection of LPS (lipopolysaccharide) or social isolation. Their study showed that the amount of attention given to a lamb by the ewe correlated positively to the amount of pain-related behaviour expressed by the tail-docked and castrated lambs. Results showed that on the baseline day the ewes were able to discriminate between a lamb experiencing pain and its control twin, or the same lamb. The positive correlation between maternal behaviours and pain-related behaviours in the lambs suggested that more attention from the ewe is drawn by more pain-related behaviours.

In relation to the effects of separation from the mother on lamb welfare, the results of a series of studies conducted by Keller et al. (2005) showed that recognition of the lamb at suckling consolidates over time into a memory that resists mother-young separation. At the neurobiological level, those studies suggest that such consolidation processes induce time-dependent reorganisations in the network involved in lamb recognition. Retrieval of consolidated memory shows an enhanced engagement of the frontal regions compared to retrieval of labile memory.

As has been described, the ewe-lamb bond is very important for neonate survival, so any situation that inhibits recognition and the ensuing development of this bond immediately after birth will have negative effects on the lamb's welfare.

7. Conclusion

Ewe-lamb recognition includes the exchange of sensory stimuli (olfactory, tactile, visual and auditory stimuli) between the mother and her neonate. The welfare and survival of lambs depend on the

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rapid recognition and establishment of the ewe-lamb bond, which takes place during the sensitive period that begins immediately after birth and lasts for no more than 16 h. It is essential that the dam provides maternal care and food to her offspring, so it is vitally important that the pair remain together and are not disturbed or separated. If this sensitive period ends before the dam and her neonate have the opportunity to achieve mutual recognition, the probability of successful development of the ewe-lamb bond will be altered, putting the lamb's welfare at risk.

Likewise, deficient maternal behaviour has been identified as a possible cause of mortality in neonates, since the absence of maternal care and food would force lambs to make greater physiological expenditures, while their survival would depend on their own capacity to successfully confront adverse stimuli in the environment.

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9. References

Alexander G (1978): Odour, and the recognition of lambs by Merino ewes. Applied Animal Ethology 4, 153–158.

Alexander G (1988): What makes a good mother? Components and comparative aspects of maternal behaviour in ungulates. Proceedings of Australian Society of Animal Production 17, 25–41.

Alexander RD, Borgia G (1978): Group selection, altruism, and the levels of organization of life. Annual Review of Ecology and Systematics 9, 449–474.

Alexander G, Shillito-Walser EE (1978): Visual discrimination between ewes by lambs. Applied Animal Ethology 4, 81–85.

Alexander G, Stevens D, Kilgour R, De Langen H, Mottershead BE, Lynch JJ (1983): Separation of ewes from twin lambs: incidence in several sheep breeds. Applied Animal Ethology 10, 301–317.

Arch-Tirado E, Collado-Corona MA (2002): Analysis of vocalizations in newborn guinea pigs with normal hearing and deafness caused by periods of solitude. Cirugia y Cirujanos 70, 442–448.

Arch-Tirado E, Verduzco-Mendoza A, Taboada-Picazo V, Mota-Rojas D, Alonso-Spilsbury M, Alfaro-Rodriguez A (2009): Analysis of normal and denerved laryngeal vocalization in guinea pigs (Cavia porcellus). Journal of Voice 23, 34–39.

Archunan G, Rajanarayanan S, Karthikeyan K (2014): 16 Cattle pheromones. In: Caretta C (ed.): Neurobiology of Chemical Communication. 1st edn. CRC Press, New York. 461–479.

Arnold GW, Boundy CAP, Morgan PD, Bartle G (1975): The roles of sight and hearing in the lamb in the location and discrimination between ewes. Applied Animal Ethology 1, 167–176.

Arteaga-Castaneda ML, Martinez-Gomez M, Guevara-Guzman R, Hudson R (2007): Chemical communication in domestic mammals. Veterinaria Mexico 38, 105–123.

Beny Y, Kimchi T (2014): Innate and learned aspects of pheromone-mediated social behaviours. Animal Behaviour 97, 301–311.

Bergamasco L, Macchi E, Facello C, Badino P, Odore R, Pagliasso S, Bellino C, Osella MC, Re G (2005): Effects of brief maternal separation in kids on neurohormonal and electroencephalographic parameters. Applied Animal Behaviour Science 93, 39–52.

Bielsky IF, Young, LJ (2004): Oxytocin, vasopressin, and social recognition in mammals. Peptides 25, 1565–1574.

Boivin X, Nowak R, Garcia AT (2001): The presence of the dam affects the efficiency of gentling and feeding on the early establishment of the stockperson-lamb relationship. Applied Animal Behaviour Science 72, 89–103.

Booth KK, Katz LS (2000): Role of the vomeronasal organ in neonatal offspring recognition in sheep. Biology of Reproduction 63, 953–958.

Brennan PA, Kendrick KM (2006): Mammalian social odours: attraction and individual recognition. Philosophical Transactions of the Royal Society, B-Biological Sciences 361, 2061–2078.

Bridges RS (2015): Neuroendocrine regulation of maternal behavior. Frontiers in Neuroendocrinology 36, 178–196

Broad KD, Mimmack ML, Kendrick KM (2000): Is right hemisphere specialization for face discrimination specific to humans? European Journal of Neuroscience 12, 731–741.

Broad KD, Curley JP, Keverne EB (2006): Mother-infant bonding and the evolution of mammalian social relationships. Philosophical Transactions of the Royal Society, B-Biological Sciences 361, 2199–2214.

doi: 10.17221/255/2014-VETMED

Burger BV, Viviers MZ, Le Roux NJ, Morris J, Bekker JPI, Le Roux M (2011): Olfactory cue mediated neonatal recognition in sheep, Ovis aries. Journal of Chemical Ecology 37, 1150–1163.

Carter CS, Williams JR, Witt DM, Insel TR (1992): Oxytocin and social bonding. Annals of the New York Academy of Sciences 652, 204–211.

Charra R, Datiche F, Casthano A, Gigot V, Schaal B, Coureaud G (2012): Brain processing of the mammary pheromone in newborn rabbits. Behavioral and Brain Research 226, 179–188.

Charrier I, Mathevon N, Jouventin P (2001): Mother's voice recognition by seal pups – Newborns need to learn their mother's call before she can take off on a fishing trip. Nature 412, 873.

Charrier I, Mathevon N, Jouventin P (2003): Vocal signature recognition of mothers by fur seal pups. Animal Behaviour 65, 543–550.

Coulon M, Nowak R, Andanson S, Ravel C, Marnet PG, Boissy A, Boivin X (2013): Human-lamb bonding: Oxytocin, cortisol and behavioural responses of lambs to human contacts and social separation. Psychoneuroendocrinology 38, 499–508.

Darwish RA, Ashmawy TAM (2011): The impact of lambing stress on post-parturient behaviour of sheep with consequences on neonatal homeothermy and survival. Theriogenology 76, 999–1005.

Dwyer CM (2008): Individual variation in the expression of maternal behaviour: a review of the neuroendocrine mechanisms in the sheep (Ovis aries). Journal of Neuroendocrinology 20, 526–535.

Dwyer CM, Bornett HL (2004): Chronic stress in sheep: assessment tools and their use in different management conditions. Animal Welfare 13, 293–304.

Dwyer CM, McLean KA, Deans LA, Chirnside J, Calvert SK, Lawrence AB (1998): Vocalisations between mother and young in sheep: effects of breed and maternal experience. Applied Animal Behaviour Science 58, 105–119.

Dwyer CM, Lawrence AB, Bishop SC, Lewis M (2003): Ewe-lamb bonding behaviours at birth are affected by maternal undernutrition in pregnancy. British Journal of Nutrition 89, 123–136.

Fay RR, Popper AN (2000): Evolution of hearing in vertebrates: the inner ears and processing. Hearing Research 149, 1–10.

Ferreira G, Gervais R, Durkin TP, Levy F (1999): Postacquisition scopolamine treatments reveal the time course for the formation of lamb odor recognition memory in parturient ewes. Behavioral Neuroscience 113, 136–142.

Ferreira G, Terrazas A, Poindron P, Nowak R, Orgeur P, Levy F (2000): Learning of olfactory cues is not necessary for early lamb recognition by the mother. Physiology and Behavior 69, 405–412.

Ferreira-Pereira SM (2011): Influence of bioacoustics in the development of science in Portugal. Interface of bioacoustics and monitoring of biodiversity. [MSc Thesis.] Technical University of Lisbon, Portugal.

Fichtel C, Manzer M (2010): 2. Vocal communication in social groups. In: Peter K (ed.): Animal Behaviour: Evolution and Mechanisms. 1st edn. Springer-Verlag, Berlin. 29–54.

Gelez H, Archer E, Chesneau D, Campan R, Fabre-Nys C (2004): Importance of learning in the response of ewes to male odor. Chemical Senses 29, 555–563.

Goncalves L, Dafre AL, Carobrez SG, Gasparotto OC (2008): A temporal analysis of the relationships between social stress, humoral immune response and glutathione-related antioxidant defenses. Behavioural Brain Research 192, 226–231.

Gonzalez-Mariscal G, Poindron P (2002): Parental care in mammals: immediate internal and sensory factors of control. In: Pfaff DW, Arnold AP, Etgen AM, Fahrfbach SE, Rubin RT (eds): Hormones, Brain and Behavior. 1st edn. Academic Press, San Diego. 215–298.

Hernandez H, Serafin N, Terrazas AM, Marnet PG, Kann G, Delgadillo JA, Poindron P (2002): Maternal olfaction differentially modulates oxytocin and prolactin release during suckling in goats. Hormones and Behavior 42, 232–244.

Hernandez H, Terrazas A, Poindron P, Ramirez-Vera S, Flores JA, Delgadillo JA, Vielma J, Duarte G, Fernandez IG, Fitz-Rodriguez G, Retana-Marquez S, Munoz-Gutierrez M, Serafin N (2012): Sensorial and physiological control of maternal behavior in small ruminants: sheep and goats. Tropical and Subtropical Agroecosystems 15, S91–S102.

Hewson C (2003): What is animal welfare? Common definitions and their practical consequences. Canadian Veterinary Journal 44, 496–499.

Hild S, Clark CCA, Dwyer CM, Murrell JC, Mendl M, Zanella AJ (2011): Ewes are more attentive to their offspring experiencing pain but not stress. Applied Animal Behaviour Science 132, 114–120.

Hutson GD (2007): 10. Behavioural principles of sheep handling. In: Grandin T (ed.): Livestock Handling and Transport. 3rd edn. CAB International, Boston. 155–174.

Keller M, Levy F (2012): The main but not the accessory olfactory system is involved in the processing of socially relevant chemosignals in ungulates. Frontiers in Neuroanatomy 39, 1–8.

Keller M, Meurisse M, Poindron P, Nowak R, Ferreira G, Shayit M, Levy F (2003): Maternal experience influences the establishment of visual/auditory, but not olfactory

doi: 10.17221/255/2014-VETMED

recognition of the newborn lamb by ewes at parturition. Developmental Psychobiology 43, 167–176.

Keller M, Meurisse M, Levy F (2004a): Mapping the neural substrates involved in maternal responsiveness and lamb olfactory memory in parturient ewes using Fos imaging. Behavioral Neuroscience 118, 1274–1284.

Keller M, Perrin G, Meurisse M, Ferreira G, Levy F (2004b): Cortical and medial amygdala are both involved in the formation of olfactory offspring memory in sheep. European Journal of Neuroscience 20, 3433–3441.

Keller M, Meurisse M, Levy F (2005): Mapping of brain networks involved in consolidation of lamb recognition memory. Neuroscience 133, 359–369.

Kendrick KM, Keverne EB (1991): Importance of progesterone and estrogen priming for the induction of maternal-behavior by vaginocervical stimulation in sheep – effects of maternal experience. Physiology and Behavior 49, 745–750.

Kendrick KM, Levy F, Keverne EB (1992): Changes in the sensory processing of olfactory signals induced by birth in sheep. Science 256, 833–836.

Kendrick KM, Atkins K, Hinton MR, Broad KD, Fabre-Nys C, Keverne B (1995): Facial and vocal discrimination in sheep. Animal Behaviour 49, 1665–1676.

Kendrick KM, Atkins K, Hinton MR, Heavens P, Keverne B (1996): Are faces special for sheep? Evidence from facial and object discrimination learning tests showing effects of inversion and social familiarity. Behavioural Processes 38, 19–35.

Keverne EB, Kendrick KM (1992): Oxytocin facilitation of maternal-behavior in sheep. Annals of the New York Academy of Sciences 652, 83–101.

Komaromy AM (2010): Day blind sheep and the importance of large animal disease models. The Veterinary Journal 185, 241–242.

Lambert KG (2012): The parental brain: Transformations and adaptations. Physiology and Behavior 107, 792–800.

Levy F, Poindron P (1987): The importance of amniotic fluids for the establishment of maternal behaviour in experienced and inexperienced ewes. Animal Behaviour 35, 1188–1192.

Levy F, Poindron P, Le Neindre P (1983): Attraction and repulsion by amniotic fluids and their olfactory control in the ewe around parturition. Physiology and Behavior 31, 687–692.

Levy F, Locatelli A, Piketty V, Tillet Y, Poindron P (1995): Involvement of the main but not the accessory olfactory system in maternal behavior of primiparous and multiparous ewes. Physiology and Behavior 57, 97–104.

Levy F, Keller M, Poindron P (2004): Olfactory regulation of maternal behavior in mammals. Hormones and Behavior 46, 284–302.

Liberles SD (2014): Mammalian pheromones. Annual Review of Physiology 76, 151–175.

Logan DW, Brunet LJ, Webb WR, Cutforth T, Ngai J, Stowers L (2012): Learned recognition of maternal signature odors mediates the first suckling episode in mice. Current Biology 22, 1998–2007.

Long CV (2007): Vocalisations of the degu Octodon degus, a social caviomorph rodent. Bioacoustics – The International Journal of Animal Sound and its Recording 16, 223–244.

Maldonado A, Orihuela A, Aguirre V, Vazquez R, Flores-Perez I (2015): Changes in mother-offspring relationships with the increasing age of the lamb in hair sheep (Ovis aries). Journal of Veterinary Behavior 10, 166–170.

Manteuffel G, Puppe B, Schon PC (2004): Vocalization of farm animals as a measure of welfare. Applied Animal Behaviour Science 88, 163–182.

Martinez MG, Gonzalez RS, Massot PP, Ramirez LA, Mendez JD, Diaz FR, Garcia AM (2011): Maternal behaviour around birth and mother-young recognition in Pelibuey sheep. Veterinaria Mexico 42, 27–46.

Marx G, Horn T, Thielebein J, Knubel B, von Borell E (2003): Analysis of pain-related vocalization in young pigs. Journal of Sound and Vibration 266, 687–698.

Mateo JM (2006): The nature and representation of individual recognition odours in Belding's ground squirrels. Animal Behaviour 71, 141–154.

McComb K, Reby D (2005): Vocal communication networks in large terrestrial mammals. In: McGregor P (ed.): Animal Communication Networks. Cambridge University Press, Cambridge. 372–389.

Meurisse M, Gonzalez A, Delsol G, Caba M, Levy F, Poindron P (2005): Estradiol receptor-α expression in hypothalamic and limbic regions of ewes is influenced by physiological state and maternal experience. Hormones and Behavior 48, 34–43.

Mora-Medina P (2016): Animal welfare in lambs: mother-young separation. [PhD Thesis.] Metropolitan Autonomous University, Mexico City, Mexico.

Mora-Medina P, Mota-Rojas D, Arch-Tirado E, Orozco H (2015): Animal welfare in lambs: ewe-lamb separation. Large Animal Review 21, 39–44.

Moura DJ, Silva WT, Naas IA, Tolon YA, Lima KAO, Vale MM (2008): Real time computer stress monitoring of piglets using vocalization analysis. Computers and Electronics in Agriculture 64, 11–18.

Mukasa-Mugerwa E, Lahlou-Kassi A, Anindo D, Rege JEO, Tembely S, Tibbo M, Baker RL (2000): Between and within breed variation in lamb survival and the risk factors associated with major causes of mortality in indigenous Horro and Menz sheep in Ethiopia. Small Ruminant Research 37, 1–12.

doi: 10.17221/255/2014-VETMED

Nowak R (1990): Lamb's bleats: important for the establishment of the mother-young bond? Behaviour 115, 14–29.

Nowak R (1991): Senses involved in the discrimination of Merino ewes at close contact and from a distance by their newborn lambs. Animal Behaviour 42, 357–366.

Nowak R (2006). Suckling, milk, and the development of preferences toward maternal cues by neonates: from early learning to filial attachment? Advanced Study Behavior 36, 1–58.

Nowak R, Boivin X (2015): Filial attachment in sheep: Similarities and differences between ewe-lamb and human-lamb relationships. Applied Animal Behaviour Science 164, 12–28.

Nowak R, Poindron P (2006): From birth to colostrum: early steps leading to lamb survival. Reproduction Nutrition Development 46, 431–446.

Nowak R, Poindron P, Le Neindre P, Putu IG (1987): Ability of 12-hour-old merino and crossbred lambs to recognise their mothers. Applied Animal Behaviour Science 17, 263–271.

Nowak R, Porter RH, Levy F, Orgeur P, Schaal B (2000): Role of mother-young interactions in the survival of offspring in domestic mammals. Reviews of Reproduction 5, 153–163.

Nowak R, Keller M, Val-Laillet D, Levy F (2007): Perinatal visceral events and brain mechanisms involved in the development of mother-young bonding in sheep. Hormones and Behavior 52, 92–98.

Numan M, Insel TR (eds) (2003): The Neurobiology of Parental Behavior: Hormones, Brain, and Behavior. 1st edn. Springer-Verlag, New York. 428 pp.

Numan M, Fleming A, Levy F (2006): Maternal behavior. In: Neill JD (ed.): Knobil and Neill's Physiology of Reproduction. Academic Press, San Diego. 1921–1994.

Pedersen CA (1997): Oxytocin control of maternal behavior – Regulation by sex steroids and offspring stimuli. Integrative Neurobiology of Affiliation 807, 126–145.

Pfister JA, Davidson TW, Panter KE, Cheney CD, Molyneux RJ (2006): Maternal ingestion of locoweed III. Effects on lamb behaviour at birth. Small Ruminant Research 65, 70–78.

Piggins D, Phillips CJC (1996): The eye of the domesticated sheep with implications for vision. Animal Science 62, 301–308.

Poindron P (1976): Effects of odor removal, without damaging the olfactory bulbs and the selectivity of maternal behavior of the ewe (in French). Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences, Serie D 282, 489–491.

Poindron P (2005): Mechanisms of activation of maternal behaviour in mammals. Reproduction Nutrition Development 45, 341–351.

Poindron P, Le Neindre P, Raksanyi I, Trillat G, Orgeur P (1980): Importance of the characteristics of the young in the manifestation and establishment of maternal behaviour in sheep. Reproduction Nutrition Development 20, 817–826.

Poindron P, Le Neindre P, Levy F, Keverne EB (1984): The physiological-mechanisms of the acceptance of the newborn among sheep. Biology of Behaviour 9, 65–88.

Poindron P, Caba M, Gomora Arrati P, Krehbiel D, Beyer C (1994): Responses of maternal and non-maternal ewes to social and mother-young separation. Behavioural Processes 31, 97–110.

Poindron P, Gilling G, Hernandez H, Serafin N, Terrazas A (2003): Early recognition of newborn goat kids by their mother: I. Nonolfactory discrimination. Developmental Psychobiology 43, 82–89.

Poindron P, Levy F, Keller M (2007): Maternal responsiveness and maternal selectivity in domestic sheep and goats: the two facets of maternal attachment. Developmental Psychobiology 49, 54–70.

Poindron P, Otal J, Ferreira G, Keller M, Guesdon V, Nowak R, Levy F (2010): Amniotic fluid is important for the maintenance of maternal responsiveness and the establishment of maternal selectivity in sheep. Animal 4, 2057–2064.

Porter RH, Levy F, Poindron P, Litterio M, Schaal B, Beyer C (1991): Individual olfactory signatures as major determinants of early maternal discrimination in sheep. Developmental Psychobiology 24, 151–158.

Ramirez M, Soto R, Poindron P, Alvarez L, Valencia JJ, Gonzalez F, Terrazas A (2011): Maternal behaviour around birth and mother-young recognition in Pelibuey sheep. Veterinaria Mexico 42, 27–46.

Rosenblatt JS (1983): Olfaction mediated developmental transition in the altricial newborn of selected species of mammals. Developmental Psychobiology 16, 347–375.

Rovira-Castro CE (1973): Phylogenetic evolution of vision life. Revista Medica de Costa Rica 445, 477–499.

Schaal B, Coureaud G, Langlois D, Ginies C, Semon E, Perrier G (2003): Chemical and behavioural characterization of the rabbit mammary pheromone. Nature 424, 68–72.

Schrader L, Todt D (1998): Vocal quality is correlated with levels of stress hormones in domestic pigs. Ethology 104, 859–876.

Searby A, Jouventin P (2003): Mother-lamb acoustic recognition in sheep: a frequency coding. Proceedings of the Royal Society B-Biological Sciences 270, 1765–1771.

Sebe F, Nowak R, Poindron P, Aubin T (2007): Establishment of vocal communication and discrimination between ewes and their lamb in the first two days after parturition. Developmental Psychobiology 49, 375–386.

Sebe F, Aubin T, Boue A, Poindron P (2008): Mother-young vocal communication and acoustic recognition promote

doi: 10.17221/255/2014-VETMED

preferential nursing in sheep. Journal of Experimental Biology 211, 3554–3562.

Sebe F, Duboscq J, Aubin T, Ligout S, Poindron P (2010): Early vocal recognition of mother by lambs: contribution of low- and high-frequency vocalizations. Animal Behaviour 5, 1055–1066.

Shillito EE (1975): A comparison of the role of vision and hearing in lambs finding their own dams. Applied Animal Ethology 1, 369–377.

Shinozaki A, Hosaka Y, Imagawa T, Uehara M (2010): Topography of ganglion cells and photoreceptors in the sheep retina. Journal of Comparative Neurology 518, 2305–2315.

Sugnaseelan S, Prescott NB, Broom D, Wathes CM, Phillips CJC (2013): Visual discrimination learning and spatial acuity in sheep. Applied Animal Behaviour Science 147, 104–111.

Terrazas A, Ferreira G, Levy F, Nowak R, Serafin N, Orgeur P, Soto R, Poindron P (1999): Do ewes recognize their lambs within the first day postpartum without the help of olfactory cues? Behavioural Processes 47, 19–29.

Terrazas A, Nowak R, Serafin N, Ferreira G, Levy F, Poindron P (2002): Twenty-four-hour-old lambs rely more on maternal behavior than on the learning of individual characteristics to discriminate between their own and an alien mother. Developmental Psychobiology 40, 408–418.

Terrazas A, Serafin N, Hernandez H, Nowak R, Poindron P (2003): Early recognition of newborn goat kids by their mother: II. Auditory recognition and evidence of an individual acoustic signature in the neonate. Developmental Psychobiology 43, 311–320.

Thorhallsdottir AG, Provenza FD, Balph DF (1990): Ability of lambs to learn about novel foods while observing or participating with social models. Applied Animal Behaviour Science 25, 25–33.

Tibbetts EA, Dale J (2007): Individual recognition: it is good to be different. Trends in Ecology and Evolution 22, 529–537.

Tomizawa K, Iga N, Lu YF, Moriwaki A, Matsushita M, Li ST, Miyamoto O, Itano T, Matsui H (2003): Oxytocin improves long-lasting spatial memory during motherhood through MAP kinase cascade. Nature Neuroscience 6, 384–390.

Val-Laillet D, Nowak R (2006): Socio-spatial criteria are important for the establishment of maternal preference in lambs. Applied Animal Behaviour Science 96, 269–280.

Vazquez R, Orihuela A, Flores-Perez FI, Aguirre V (2015): Reducing early maternal licking of male lambs (Ovis aries) does not impair their sexual behavior in adulthood. Journal of Veterinary Behavior 10, 78–82.

Vince MA (1993): Newborn lambs and their dams: the interaction that leads to sucking. Advances in the Study of Behavior 22, 239–268.

von Borstel UK, Moors E, Schichowski C, Gauly M (2011): Breed differences in maternal behaviour in relation to lamb (Ovis orientalis aries) productivity. Livestock Science 137, 42–48.

Winslow JT, Insel TR (2004): Neuroendocrine basis of social recognition. Current Opinion in Neurobiology 14, 248–253.

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