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REVIEW [REVISIÓN]

SENSORIAL AND PHYSIOLOGICAL CONTROL OF MATERNAL BEHAVIOR IN SMALL RUMINANTS: SHEEP AND GOATS

[CONTROL FISIOLÓGICO Y SENSORIAL DE LA CONDUCTA MATERNA EN PEQUEÑOS RUMIANTES: OVEJAS Y CABRAS]

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SUMMARY

Contrary to rodents in which maternal behaviors is characterized by the nest formation and give birth to altricial offsprings, maternal behavior in sheep and goats is characterized by the establishment of a selective bond between the mother and their progeny during the first postpartum hours. In both species, maternal behavior ethogram at parturition consists of a series of behaviors that initiates with the prepartum isolation of the female from their coespecifics and that culminates with the successful exclusive nursing behavior toward their newborn during postpartum. The sensory and physiological factors that control the expression of maternal behavior are very similar in both sheep and goats, although in the goats there is little information generated about this aspect. The increased peripherical concentrations of oestradiol at the end of gestation and the vaginocervical stimulation are two primary physiological events that are very important to the expression of the maternal behavior. However, olfactory cues from the offspring also are involved in the maintenance of maternal responsiveness once the birth takes place. Although mother-young spatial relationships during postpartum are different between sheep (followers) and goats (hiders) the maternal behavior had many similarities and their sensorial and physiological control are basically identical for many aspects.

Keywords: Maternal care; sheep; goats; oestradiol; olfactory cues; suckling.

RESUMEN

Al contrario de lo que ocurre en roedores, en los cuales la conducta materna se caracteriza por la construcción de un nido y paren crías altriciales, en ovejas y cabras esta conducta es caracterizada por el establecimiento de un vínculo selectivo entre la madre y su progenie dentro de las primeras horas postparto. En ovejas y cabras el etograma de la conducta materna al parto está compuesto de una serie de conductas que comienza con el aislamiento preparto de la hembra y que culmina con el amamantamiento exclusivo del recién nacido. Los factores fisiológicos y sensoriales que controlan la expresión de la conducta materna son muy similares en ovejas y cabras, aunque en la cabra existe poca información generada acerca de este aspecto. El incremento en las concentraciones periféricas de estradiol al final de la gestación y la estimulación vagino-cervical son dos eventos fisiológicos de gran importancia para el despliegue de la conducta materna. Sin embargo, también las señales olfatorias provenientes del recién nacido son implicadas en el mantenimiento de la respuesta maternal una vez que el parto ha ocurrido. No obstante que la relación espacial madre-cría durante el postparto son diferentes entre ovejas (seguidores) y cabras (escondedizos), la conducta materna presenta muchas similitudes y su control fisiológico y sensorial son básicamente idénticos en muchos aspectos.

Palabras clave: cuidados maternales; ovejas; cabras; estradiol; señales olfatorias; amamantamiento.

INTRODUCTION

Maternal behavior presents a wide variety of behavioral patterns among the mammals. Its ethological characteristics depend mainly on the degree of precocity of the young at birth, but also on the social nature of the specie. Thus, while mothers of altricial young build a nest (e.g. rodents), this is rarely the case in ungulates, whose maternal behavior is rather characterized by a rapid development of the inter-individual recognition and exclusive care (maternal selective behavior).

In this respect, they represent an interesting alternative to rodents for the study of mother-young interactions. Additionally, interest to study this aspect in small ruminants is furthermore enhanced by the fact that the onset of maternal behavior is strictly associated with the process of parturition by contrast to what observed in rodents. In fact, in this last specie, maternal behavior can be elicited by the only presence of the young (Numan, 1994).

In the fist part of this review will be focus on the characteristics of maternal behavior before, during and after parturition in sheep and to a lesser extent in goats. In the second part of this review concerns to the respective roles of physiological and sensorial roles on the maternal behavior studied in these species.

Prepartum Maternal Behavior

Sheep and goats are social animals and show strong gregarious tendencies. In both species when remain apart from conspecifics (social isolation) is highly stressful with very strong behavioral responses indicative of agitation (running, rearing against the sides of the open, escape attempts) and frequent, high-pitched vocalization (Price and Thos, 1980; Carbonaro *et al*., 1992; Le Neindre *et al*., 1993; Dwyer, 2009). However, pregnant ewes and goats show social isolation from the rest of the flock and a reduction of their behavioral response to social isolation (i.e social agitation index) between 24 h and about 1 h prepartum (Sheep: Arnold and Morgan, 1975; Echeverri *et al*., 1992; Lécrivain and Janeau, 1987; Shackleton and Haywood, 1985; goat: Das and Tomer, 1997; Lickliter, 1985; O´Brien, 1983, 1984; Ramirez *et al*., 1995; Rudge, 1970). Therefore, during this state of gestation the females show a clear a reduction in the gregariousness behavior (Poindron *et al*., 1997, 1998a,b).

The imminent labour of parturition in sheep and goats is characterized by an initial increase in restlessness, pawing, lip licking, frequency of vocalizations, and then straining in both standing, lying positions and the intolerance from conspecifics also increase (Collias, 1956; Herscher *et al*., 1963a; Smith, 1965; Das and Tomer, 1997; Dwyer, 2009). In ewes and goats, isolation from the rest of her conspecific could be beneficial to the early relationship with their young (Val-Laillet and Nowak, 2006; Dwyer, 2009). Furthermore, mother select a birth site and offspring survival is increased with increased duration spent on the birth site (Dwyer, 2009). This isolation improves the establishment of the mother-young bond by preventing separations of newborn young from their mothers and reducing interference or newborns stealing by other mothers or predators (Gonyou and Stookey, 1983, 1985; Poindron *et al*., 1993). Therefore, this isolation without interference from others ewes is indeed of the utmost importance for the onset of the mother-young relationship and this behavior may facilitate mutual recognition and rapid access to the udder at birth, improving the chances of newborn survival (Val-Laillet *et al*., 2006). Ewes can display full maternal behavior at three hours before parturition in the presence of the others newborn lambs (Arnold and Morgan, 1975).

Maternal and Neonatal Behavior at Birth

Maternal behavior towards the neonate is characterized by a number of very typical components; these behaviors are similar in sheep and goats (Hersher *et al*., 1963a,b). Immediately after birth the mothers show intense and focused interest in the newborn and in the amniotic fluids in its coat and on the ground. In this regard, amniotic fluids are important in experienced ewes not only for the establishment of maternal responsiveness as in primiparous, but also these fluids carries some chemosensory information to facilitate exclusive bonding (Poindron *et al.*, 2010). A few minutes after expulsion of the fetus the mother rises and starts to lick her kid very vigorously, generally beginning with its head and neck (Collias, 1956; Shillito and Hoyland, 1971; Lickliter, 1985). Licking is accompanied by numerous low and high pitched bleats and occasionally by flehmen behavior, especially when consuming urine from the neonate (Sambraus and Wittmann, 1989; Dwyer *et al*., 1998). These behaviors serve for two purposes: first, the mothers help to dry (facilities the remove of the fetal membranes from the face that could lead to suffocation), and stimulate the lamb (the teat-seeking activity of the young), and secondly they form an exclusive and selective attachment to her own offspring (Nowak *et al*., 2000; Dwyer, 2009). Furthermore, the mother must be coordinated with the movements of the neonate lamb which has to be able to stand before it can orient and reach the mammary gland (Nowak *et al*., 2007). The newborn stands on its feet, usually at 10 to 30 min after birth, it start to nuzzle its mother´s body and rapidly reaches the udder, to successfully suck in 30 to 60 min after birth

(Allan *et al*., 1991; Poindron *et al*., 1993). In sheep and does a selective attachment is formed within an hour or less of birth, this mother-young bonding is important for the rapidly learns to mutual recognition at distance (Nowak *et al*., 2000; Terrazas *et al*., 2003; Poindron *et al*., 2003). A disturbance in the maternal care, maternal selectivity or in the mutual recognition may have deleterious effects on the survival of the young during the first week of life (Nowak *et al*., 1997; Nowak *et al*., 2000; Poindron *et al*., 2007a,b; Nowak *et al*., 2007).

Formation of an exclusive mother-young bond and maternal behavior during the postpartum

The survival of the newborn is dependent on the coordinated expression of appropriate behaviors between both the ewe and the lamb that lead to the formation of a strong relationship between both partners (González-Mariscal and Poindron, 2002). In sheep and goats, expulsion of the fetus facilitates the formation of the maternal bond. Also, the vaginocervical stimulation (VCS) performed after the establishment of maternal selectivity allows mothers to form a new bond with an alien newborn (sheep: Kendrick *et al*., 1991; goat: Romeyer *et al*., 1994b).

Whether estrogen may participate in the establishment of maternal selectivity remains an open question. Some results in sheep suggest that they may modulate the establishment of bonding (Alexander *et al*., 1986, 1989) or allow bonding in the absence of VCS (Le Neindre *et al*., 1979). However, in studies of the sensitive period in which ewes were induced to lamb using high doses of estradiol, was found no evidence for an effect of estradiol on selectivity (Poindron and Le Neindre, 1980). Immediately after parturition mothers groom and nurse any kid, but then rapidly learn to discriminate and nurse only their own young (Collias, 1956; Herscher *et al*., 1963b). In sheep and goats, the maternal bond is established within the first 2 h leading to the later rejection of any infant that tries to suckle from a dam other than its own (Poindron *et al*., 1993). In some conditions, 5 to 10 min of contact with the neonate are sufficient for does to become selective (Gubernick, 1981) and mothers reject alien kids at 2 to 4 h postpartum, regardless of their age or the similarity of their coat to that of their own young (Romeyer and Poindron, 1992; Romeyer *et al*., 1994a; Poindron *et al*., 2007b). Previous studies have demonstrated that 30–60 min of immediate postpartum contact with a neonate may be sufficient for the ewe to become familiar with that lamb's unique signature and discriminate her lamb from alien ones (Keller *et al*., 2003). Maternal olfaction plays an important role; this full access to olfactory cues through licking facilitates the establishment of maternal selectivity. Of the mothers that remain maternal despite 4 h of licking deprivation, half fail to be selective and still accept alien kids, in contrast to mothers that have fully interacted with their neonate during the same period (Poindron *et al*., 2007a,b). It could be argued that the inability of mothers to display maternal care after deprivation of the neonate at birth is due to the fact that they have not had the opportunity to bond to their young. These in turn have higher incidence of separations and higher mortality of the offspring (Murphy *et al*., 1994; Alexander *et al*., 1983; Putu *et al*., 1988). Therefore, the first hours postpartum represent a critical time for the establishment of the maternal bond towards her young (Poindron *et al*., 2007b).

One way to assess whether the establishment of maternal selectivity depends on the sensitive period is to study the rapidity with which selectivity develops at various times during this period (Poindron *et al*., 2007b). The sensitive period is generally considered a transition from a control of maternal responsiveness by physiological factors internal in the mother, to a neurosensory control by sensory cues from the young (Poindron and Le Neindre, 1980; Rosenblatt *et al*., 1979). Hence, presenting or suppressing cues of the neonate during the sensitive period will provide valuable information about their importance for the maintenance of maternal responsiveness and selectivity beyond the sensitive period (Poindron *et al*., 2007a,b). The results of such studies will be discussed in the section "The sensitive period and sensorial control of maternal behavior" of the present review. Nonetheless, some results suggest that the sensitive period may be shorter in goats than in sheep (Ramírez *et al*., 1996).

Maintenance of maternal behavior relies on behavioral cues from the neonate, particularly sucking interactions, and mothers whose offspring die lose interest in the body of their young within a few hours (Dwyer, 2009). Thus, the ability of the neonate to attach rapidly to its mothers (as much as the reverse) is a primary condition for the maintain access to food and maintain maternal behavior in the postpartum, consequently increase the opportunity of survival of kid (Poindron *et al*., 1993; Nowak *et al*., 2000). Thus, 50% of mothers do not show maternal interest in their young after 4 h of separation beginning at birth and 75% of them reject their own young after 12 h of privation in sheep and goats (Poindron *et al*., 1979; Lickliter, 1982). Mother-young interactions at birth are important for the establishment of its mutual recognition after parturition. Thus, the establishment of early recognition of the dam may be vital for the lamb (Poindron *et al*., 1993; Nowak *et al*., 2007; Poindron *et al*., 2007a,b). However, the maintenance of maternal behavior during postpartum depends very much on the events immediately after parturition (Poindron *et al*., 2007b).

During the first week of life the mother allows the offspring to access the udder and suck whenever it approaches. Therefore, during first month of life the mothers will actively seek out her lamb when they are separated, and mother-young distances are generally no more than a few meters in lamb, and distances higher in kids (Nowak *et al*., 2000; Dwyer, 2009).
In ungulates, two main types of mother-young spatial relationships have been described, which depends on the behavior of the neonate. In some species as in sheep at birth the neonate start to follow their mothers as soon as she moves from the birth site classified as "followers" (Lent, 1974). This "follower" species spend less time in close physical proximity to their dams as they mature (Herscher *et al*., 1963b). Others species, for example goat neonates, do not follow their mothers when she goes foraging. Rather, for the first few days they lie down and hide, waiting for the mother to return for nursing, thus it mother-young spatial relationship is classified as "hiders" (Lickliter, 1987). This hider species gradually come to spend more time in close physical proximity to their mothers as they mature (Lickliter, 1984). However, contrary to a greater quantity of published studies on the onset of maternal behavior, mechanisms that contribute to their spontaneous disappearance in the mothers and the spontaneous weaning of the young in small ruminants are also little studied.

Physiological control of maternal behavior

Contrary to rodents, in sheep the activation of maternal motivation is completely controlled by the physiological events that accompany parturition. Thus, full maternal responsiveness is strictly related to the event of parturition, but fades after few hours in the absence of the new-born lamb (Poindron and Le Neindre, 1980). Thus, 4 h of separation beginning at birth induced disturbances of maternal responsiveness in half of the mothers and after 12 h of deprivation 75% of them rejected the lamb (Poindron *et al*., 1979). On the other hand, when 4 or 24 h of immediate postpartum contact is allowed, it was sufficient to maintain maternal responsiveness for the following 24-h period of separation (Poindron *et at*., 1979; Lévy *et al*., 1991). If immediately separated from their neonate, parturient goats display maternal behavior spontaneously only for a short time after giving birth, although the duration of this period of initial responsiveness towards the neonate is longer in multiparous mothers (Lickliter, 1982). This indicates the existence of a sensitive period for the establishment of the relationship between the newborn kid and its mother (Herscher *et al*., 1963b; Poindron *et al*., 2007b) and suggests that it is controlled by the physiological factors associated with parturition.

The physiological events around parturition

In sheep and goats, as in many others mammals, one of the physiological events that characterizes the parturient female is the rapid and important changes in steroid hormones (progesterone and oestrogens) that take place in the days or hours just before birth. Both preparturient ewes and does experience a fall in the peripheral plasma concentrations of progesterone few days prior to parturition, while oestradiol rises one day before parturition to reach a peak at parturition and return to basal levels within the first 4 h postpartum (Thorburn *et al*., 1972; Chamley *et al*., 1973; Shipka and Ford, 1991). As a result of the shift in balance in steroid exposure, being oestradiol dominant, serum prolactin (PRL) levels increase dramatically around one day before parturition in sheep (Chamley *et al*., 1973) and during the last 3 days in does (Currie *et al*., 1988), and are maintained at high levels during postpartum because of suckling stimulation (Davis *et al*., 1971).

The changes of concentration in estrogen and progesterone in the goat during late pregnancy and parturition are very similar to those found in sheep, in which these hormones play an important role in the display of maternal behavior (Poindron *et al*., 2007a). However, an exogenous treatment of estradiol and progesterone that induces lactation and facilitates maternal behavior in non-pregnant ewes is ineffective in the goat (Rosenblatt and Siegel, 1981). The alternative of inducing maternal behavior with treatments mimicking more closely the hormonal changes occurring at parturition has not been investigated.

Fetus expulsion and vaginocervical stimulation (vcs)

The importance of VCS for the activation of maternal behavior has been most extensively studied in sheep. The induction of maternal behavior in nonpregnant animals is achieved with some success only by using pharmacological doses of oestradiol (Poindron and Le Neindre, 1980; Kendrick *et al*., 1992). In addition, the type of behaviors induced, their latency and sequence of appearance, are quite variable, thus suggesting that additional factors are required for the activation of an adequate maternal behavior. Although a large number of physiological changes occur during parturition, some strong evidences indicate that VCS is the initial step that triggers the immediate onset of maternal behavior. The actual process of expulsion of the fetus appears of utmost importance. For example, the acceptance of a second neonate presented to a ewe 30 min after the birth of her own single lamb, it is not accepted as readily as an alien presented to a twin-bearing ewe at the time of expulsion of her second born (Poindron *et al*., 1980). The application of

artificial VCS for 5 min, to nonpregnant multiparous females, induced the maternal behavior in 80% of them within 30 min (Keverne *et al*., 1983). This facilitatory effect of VCS is evident only in multiparous ewes, primed with ovarian esteroids (Poindron *et al*., 1988; Kendrick and Keverne, 1991). In parturient ewes, expulsion of the second lamb enhances licking behavior toward any neonate (Poindron *et al*., 1980) as does additional vaginal stimulation applied one hour postpartum (Keverne *et al*., 1983). Conversely, the suppression of the sensory information associated with labor (by means of applying peridural anesthesia or performing a Cesarean section) results in the failure of parturient mothers to display maternal behavior, especially if they are primiparous (Alexander *et al*., 1988; Krehbiel *et al*., 1987). Similar results are obtained in goats (Poindron *et al*., 2007b), although the effects of peridural anesthesia are more variable, possibly due to interindividual variations of genital innervation in this species (Labussiere, 1999). Although the nervous pathways that convey the transmission of sensory information from the vagina and uterus to the brain are not known in detail, it is well established that one way by which VCS facilitates maternal behavior in sheep is through the intracerebral release of oxytocin (OT).

Main neurobiological events

The neurobiological role of oestradiol has been studied mainly in the rat, in which this hormone had a more facilitatory effect than in the ewe (Bridges, 1996; Rosenblatt *et al*., 1979; Rosenblatt *et al*., 1988). Thus, Numan (1994) had established that medial preoptic area (MPOA) is the target structure to facilitate the maternal behavior by the oestradiol. In fact, this structure showed an increase in the number of receptor for oestradiol (ER) at the end of pregnancy (Giordano *et al*., 1989). Furthermore, oestradiol implants in the MPOA facilitates the maternal behavior in virgin females (Numan, 1994), whereas applications of antiestrogens inhibit it (Ahdieh *et al*., 1987). In the ewe, the presence of ER during oestrus in the MPOA (between some others structures) is well established (Lehmann *et al*., 1993; Blache *et al*., 1994). In the sheep, contrary to mice, at parturition the number of cells with ER is low and this number does not depend on the previous maternal experience (Meurisse *et al*., 2005; Ehret and Buckenmaier, 1994). However, more recently Meurisse *et al*. (2005) indicated that in sheep ER expression is influenced by previous physiological and/or maternal experience at specific times of the reproductive cycle. They are also congruent with the higher ability of multiparous than nulliparous ewes to show maternal behavior several days prepartum.

The mechanical stimulation caused by the expulsion of fetus is associated with a short, but important, liberation of OT during the expulsion phase in the peripheral circulation, due to the Ferguson reflex (Kendrick *et al*., 1991). As with PRL, the later release of OT is also provoked by suckling. However, the physiological events associated with VCS, caused by the passage of the fetus through the birth canal, also have neurobiological correlates. A rise of OT is also found in the cerebrospinal fluid (CSF) and the olfactory bulbs (Kendrick *et al*., 1986, 1988). Furthermore, during parturition significant increases of the noradrenaline metabolite MHPG have been found at the CSF levels, and of noradrenaline (NA) in the median preoptic area, the bed nucleus of the stria terminalis, and the olfactory bulbs (Kendrick *et al*., 1992), which are structures involved in the manifestation of maternal behavior in rodents (Numan, 1990).

Besides the role of the steroids hormones and VCS, some other peripheral and central physiological parameters also participate in the activation of the maternal behavior at partum, even though their role may not be as determinant. For example, the decrease in the peripheral concentrations of progesterone facilitates the effects of VCS (Kendrick and Keverne, 1991; Poindron, 2005). This is the case for the central release of opiates, and also maybe for CRH, although for this factor, its intracerebral releasing at the moment of parturition has not yet been shown in the ewe. These physiological factors and probably others that have not yet been studied, result in a rapid increase of maternal motivation in the 3 or 4 h preceding parturition, culminating at delivery. Then, maintaining this motivation will depend on the possibility of the mother to interact with the newborn. In the following section, the participation of some sensory cues on the maintenance of maternal responsiveness is examined.

The sensitive period and sensorial control of maternal behavior

If a mother is not allowed to interact with her young at the time of internally driven maternal responsiveness, she losses her ability to care for her progeny until the next parturition. This phenomenon evidences the existence of a so called "sensitive period" presented in most mammals studied. The removal of the neonates at parturition results in the rapid fading of maternal responsiveness, in contrast to what occurs if the parturient dam is allowed to have some initial contact with her young. It is, internal factors render the mother sensitive to specific stimuli from the neonate and the perception of such stimuli allows her to gain experience necessary to maintain her maternal responsiveness once those internal factors have disappeared (González-Mariscal and Poindron, 2002). These effects of early mother-young separation have been confirmed in many studies and extended to other species (rats: Bridges, 1975; Fleming and Sarker, 1990; sheep: Poindron *et al*., 1979; goats: Klopfer *et*

al., 1964; Lickliter, 1982; Ramírez *et al*., 1996; cattle: Hudson and Mullord, 1977; Le Neindre and Garel, 1976; rabbits: González-Mariscal *et al*., 1998). In sheep and goats, it was initially thought that existence of a sensitive period pertained to the establishment of selective bonding to the lamb. However, the fact that anosmic ewes deprived of their lamb show a fading of maternal responsiveness similar to the intact (deprived) mothers indicates that the sensitive period concerns maternal responsiveness, as it does in the rat (Poindron and Le Neidre, 1980; Rosenblatt and Siegel, 1981).

The sensory cues, essential for the consolidation of maternal responsiveness have been investigated in rats and sheep by depriving mothers of some of the sensory stimulation provided by the young. In sheep and goats, the critical sensory modality for maintaining maternal responsiveness appears to be olfactory. For example, it is important that the mother has access to olfactory cues provided by licking their kid. About half of does prevented from licking their kid during first 4 h postpartum fail to show adequate maternal care when reunited with her young (Bordi *et al*., 1994; Romeyer *et al*., 1993). Additionally, the full access to olfactory cues through licking facilitates the establishment of maternal selectivity. Indeed, when selectively preventing the perception of stimuli from the lamb, postparturient ewes lose their responsiveness only if deprived of the neonate's olfactory cues (Poindron and Le Neindre, 1980). In fact, the single deprivation of olfactory stimulation provoked by placing the lamb in a smell-proof box leads to the fading of maternal behavior in a way similar to that caused by total separation (González-Mariscal and Poindron, 2002; Fig. 1). In contrast, prepartum anosmia does not provoke such effect (Baldwin and Shillito, 1974; Bouissou, 1968; Lévy *et al*., 1995b; Poindron, 1976a,b) and only maternal selectivity is affected. As a whole, this illustrates the possibility that compensation in the sensory regulation of maternal responsiveness during the sensitive period may occur, but only if maternal olfactory system is impaired and not if it is the perception of the olfactory cues that is impeded in an intact mother (González-Mariscal and Poindron, 2002).

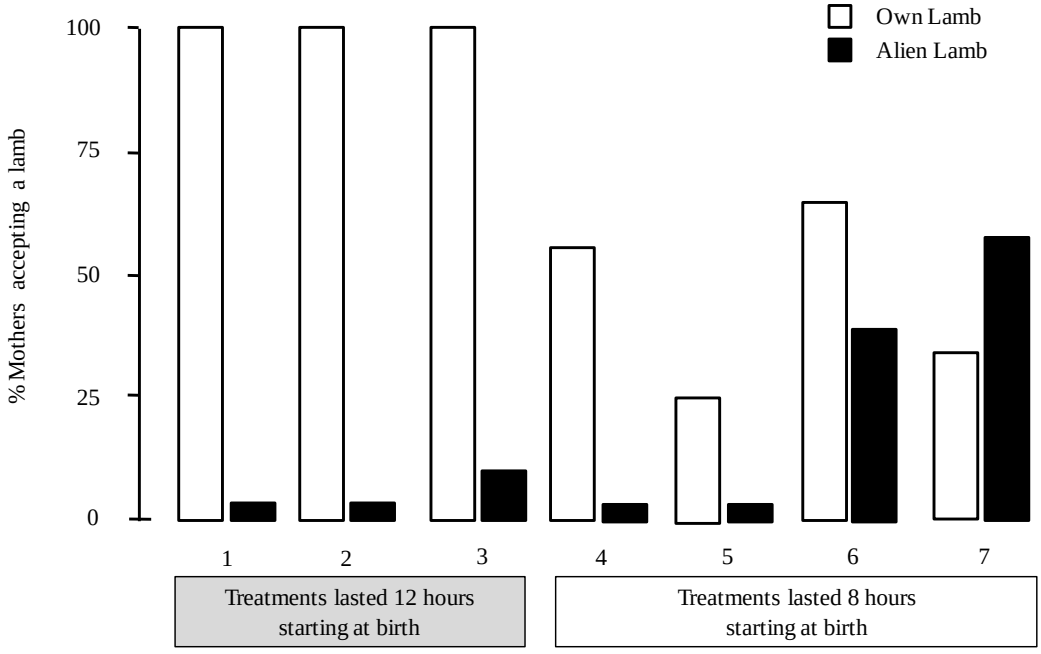

Figure 1. Percentage of mothers accepting their lamb or an alien one when a partial contact with own lamb is allowed in postparturient ewes. Groups were 1, full contact; 2, full contact except suckling; 3, lamb separated from dam by a 5cm thick double wire mesh; 4, lamb in a transparent smellproof box with ventilation toward the dam; 5, lamb in a transparent smell-proof box with ventilation away from the dam; 6, lamb in an opaque smell-proof box, with ventilation toward the dam; 7, ewe totally separated from her lamb. Visual and acoustic cues alone (group 5) did not allow maternal responsiveness to be maintained significantly better than when the mother was totally deprived of the lamb (group 7). Ewes with unrestricted access to olfactory cues from the lamb, even without direct physical contact (groups 3, 4 and 6), generally developed maternal selectivity (but note also group 5). Grey and white bars denote that treatments lasted 12 (groups 1, 2 and 3) and 8 (groups 4, 5, 6 and 7) hours, respectively starting at birth (Adapted from González-Mariscal and Poindron, 2002).

CONCLUSIONS AND PERPECTIVES

At the present, a wide body in the literature concerning to the characteristics of maternal behavior and their control mechanisms in sheep and goats has been generated. In both species, parturient females show of a series of behaviors that initiates with the prepartum isolation of the female from their coespecifics and that culminates with the successful exclusive nursing behavior toward their newborns during postpartum. Some studies underlie the role of the changes in peripheral circulating of both steroids hormones, progesterone and oestradiol. However, the sensory stimulation caused by fetus expulsion or by VCS induces an intracerebral OT release that is implicated in the onset of maternal responsiveness. Overall, estrogen and VCS induce a temporary state of maternal responsiveness that last for several hours, and interacting with the neonates allows its consolidation. While most of the studies on the characteristics and the control factors of maternal behavior in small ruminants have been conducted under experimental conditions, there is little literature concerning the possible complications on maternal behavior in animals maintained under natural grazing conditions, which could suffer an under nutrition. Because an inadequate maternal behavior at parturition as a result from under nutrition can be a common cause of neonatal mortality in flocks of sheep and goats; then, studying the effects of a short term nutritional supplementation before parturition on the mother-young interactions could help to apply some feeding strategies that reduce the productive lost in these flocks. Furthermore, contrary to a greater quantity of published studies on the onset of maternal behavior, mechanisms that contribute to their spontaneous disappearance in the mothers and the spontaneous weaning of the young in small ruminants are also little studied.

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