Animal (2014), **8:1**, pp 102–112 © The Animal Consortium 2013
doi:10.1017/S1751731113001614

animal

Maternal behaviour and lamb survival: from neuroendocrinology to practical application*

C. M. Dwyer†

Animal Behaviour and Welfare, Animal and Veterinary Science Research Group, SRUC, West Mains Road, Edinburgh EH9 3JG, Scotland

(Received 24 March 2013; Accepted 16 July 2013; First published online 8 October 2013)

Parental care promotes offspring survival and, for livestock species, this care is provided solely by the mother. Maternal behaviour in the sheep has been exceptionally well-studied compared with other species and many of the underpinning biological processes leading to the expression of maternal care are known. In this review the current state of play with regard to the biology of maternal care will be reviewed, and its application to provide practical solutions to reduce lamb mortality considered. For maternal care to be elicited at birth the ewe requires elevated circulating oestradiol in late gestation, which stimulates the expression of oxytocin receptors in both peripheral and central areas (particularly the hypothalamic and limbic areas of the brain). At birth stretching of the vaginocervical canal elicits a spinal reflex which triggers the release of oxytocin primarily from neurones within the paraventricular nucleus of the hypothalamus. Oxytocin release causes an increase in the neurotransmitters noradrenaline, acetylcholine, glutamate and γ-aminobutyric acid (GABA) in the olfactory bulb, and other brain regions important for maternal behaviour. Finally, sensory cues provided by the lamb, in particular the amniotic fluids surrounding it, lead to the expression of maternal behaviours (licking, low-pitched bleats, acceptance of the lamb at the udder and suckling). This allows the expression of the two facets of maternal behaviour in the ewe: nurturance of the young and maternal selectivity, whereby a specific olfactory memory for the ewes own lamb is formed and the expression of maternal care is restricted to this lamb. Variation in the expression of maternal care has been demonstrated in primiparous ewes compared with multiparous, in different sheep genotypes, with undernutrition, stress in pregnancy, following a difficult delivery, and may occur with variation in ewe temperament. An understanding of the importance of the timing of various events in late pregnancy and during parturition, as well as the factors that can disrupt these events, can help to design management activities to minimise risks to the successful onset of maternal behaviour. Management practices that work with the biology of the ewe will be the most successful in ensuring that maternal care is expressed, so improving the welfare of the ewe and lamb, and the profitability of the farm.

Keywords: maternal behaviour, oestradiol, oxytocin, neonatal survival, sheep

Implications

Our improved knowledge of the neurobiology governing the onset of maternal behaviour, and the importance of sensory stimuli from the neonate for maternal attachment, can offer practical guidance to improve offspring survival. In particular appropriate nutrition during pregnancy, management and sire selection to avoid difficult deliveries, allowing ewes the opportunity to lamb in a quiet and stress-free environment away from other ewes if they choose, and ensuring that ewes are exposed to amniotic fluids from the newborn lamb are important. Primiparous ewes are especially vulnerable to disturbance and need particular care to allow a bond to develop with the lamb.

Introduction

The function of maternal care is to promote improved offspring survival, by a range of strategies to provide the offspring with nutrition, thermoregulation, protection (both immunological and physical), comfort, and opportunities for social learning, particularly in higher animals. For mammalian livestock species there is a tendency to focus on the nutritional aspects of maternal care, which are vital for the early survival of the newborn through fuelling

* This paper is based on a presentation to the joint Annual Conference of the British Society of Animal Science, Animal Science Forum, and the Association for Veterinary Teaching and Research Work, held in Nottingham, UK from 24 to 25 April 2012.

† E-mail: cathy.dwyer@sruc.ac.uk

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press

thermoregulation, and providing immunological protection via colostrum intake. However, the psychological components and opportunities for social learning provided by maternal care are also very important, with the duration that offspring are dependent on their mother increasing with complexity of the social environment (e.g. Avital and Jablonka, 1994; Rosenblatt, 2003; Russell and Lummaa, 2009). Provision of opportunities for social learning may have been the driver for the evolution of maternal care, with other benefits co-evolving, as has been hypothesised, and suggests that we could pay closer attention to the non-nutritional benefits of maternal care in livestock husbandry.

The suite of behaviours and activities expressed by the mother to achieve the many benefits of maternal care vary with species-specific characteristics such as evolved social and reproductive strategy, litter size and offspring maturity at birth. This review will focus on maternal care in the sheep, as one of the most studied livestock species for these traits, particularly with respect to the neuroendocrine profile underpinning the onset of maternal care (e.g. Kendrick *et al*., 1997; Dwyer, 2008a). Lamb survival is dependent on the coordinated expression of behaviours of both ewe and lamb, but this review will be restricted to the behaviour of the ewe only, as the member of the partnership where we know most about the neuroendocrine basis of behaviour. The sheep is a seasonally breeding animal, which lives in a matriarchal social group and gives birth to typically one to two relatively large and precocious offspring that are able to follow their dam soon after birth. These evolved species-specific adaptations influence the behaviours expressed by the mother towards her newborn offspring: the ewe and lamb need to be able to identify one another and to rapidly develop an exclusive attachment. The costs of known non-offspring nursing are particularly high for mothers with small litters, especially if food is limited, and is not commonly observed in monotoccus mothers (Packer *et al*., 1992). Offspring may attempt to steal milk from ewes, and this is exacerbated in sheep flocks where there may be many young simultaneously. Thus the ewe that can rapidly identify her own offspring is able to limit her lactational effort largely to her own offspring, so improving the chances of its, and her own, survival. The dual components of maternal care (nurturing and recognition) are achieved by the immediate licking and grooming behaviour expressed by the ewe, which contributes to maternal learning of the olfactory signature of her own offspring (Kendrick *et al.,* 1997; Poindron *et al*., 2007), and cooperation with sucking attempts of the lamb, which promotes lamb attachment to its dam (Goursaud and Nowak, 1999). Maternal behaviour at birth is, therefore, characterised by high levels of licking and grooming (Lent, 1974; Alexander, 1988), accompanied by a specific maternal vocalisation (low-pitched bleating) and cooperation with lamb attempts to find the udder and suckle, and an absence of rejection or avoidance of the lamb. These behaviours progress to the development of an exclusive attachment to the lamb (termed maternal 'selectivity', Poindron *et al.,* 2007), recognition via all sensory modalities, increased maternal vigilance, maintenance of a close spatial proximity and frequent sucking interactions (e.g. Dwyer and Lawrence, 2005a). Following the successful establishment of maternal behaviour and the ewe-lamb bond the ewe will continue to express maternal behaviour throughout lactation, the quality of this subsequent care determined by the initial onset of maternal behaviour (Pickup and Dwyer, 2011). The purpose of this review is to consider the biological mechanisms whereby a ewe, which may have shown no interest in, or active avoidance of, a newborn lamb shortly before birth can show immediate and focused maternal attention after birth, even if she has never given birth before. The review will first consider current understanding about the neuroendocrine basis of maternal behaviour, then describe sources of individual variation in maternal care and their underlying biology. Finally the review will address how knowledge of these mechanisms can be utilised in a production setting to improve expression of these maternal behaviours and hence lamb survival.

The neurobiological basis for maternal behaviour

The onset of maternal behaviour at birth is critically dependent on the temporal sequence of events intimately associated with late pregnancy and parturition (illustrated in Figure 1). In brief, these are changes in the relative concentrations of oestradiol and progesterone in late gestation (specifically the decline in progesterone in the days before birth and an exponential rise in circulating oestradiol from the placenta (Kendrick and Keverne, 1991)), the stretching of the birth canal as the fetus is expelled from the uterus (vaginocervical stimulation, VCS) resulting in the central release of oxytocin from the paraventricular nucleus (PVN) of the hypothalamus (Keverne and Kendrick, 1992; Kendrick *et al.,* 1992a; Da Costa *et al*., 1996), and sensory cues provided by the newborn lamb, particularly emanating from the amniotic fluids in which it is soaked (Lévy *et al.,* 1983; Poindron *et al*., 2007, 2010).

Alone, neither maternal oestradiol nor VCS are effective in producing the full complement of maternal behaviours, but act in concert to bring about maternal responsiveness. Kendrick and Keverne (1991) demonstrated that when ewes were treated with oestradiol and progesterone, progesterone alone or saline and presented with a newborn lamb none of the animals showed maternal care, although there was a reduction in butting and withdrawal in ewes pre-treated with both progesterone and oestradiol. Following artificial VCS however, ewes treated with oestradiol, and particularly those treated with progesterone and oestradiol, showed licking and affiliative behaviours towards the lamb accompanied by low-pitched bleating. Ewes not pre-treated with the sex steroids continued to show aggressive responses and withdrawal towards the lamb after receiving VCS (Kendrick and Keverne, 1991).

The relative concentration of oestradiol and progesterone act as a primer for the onset of maternal behaviour and need the presence of oestrogen receptor-α (ER-α) to exert their

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press

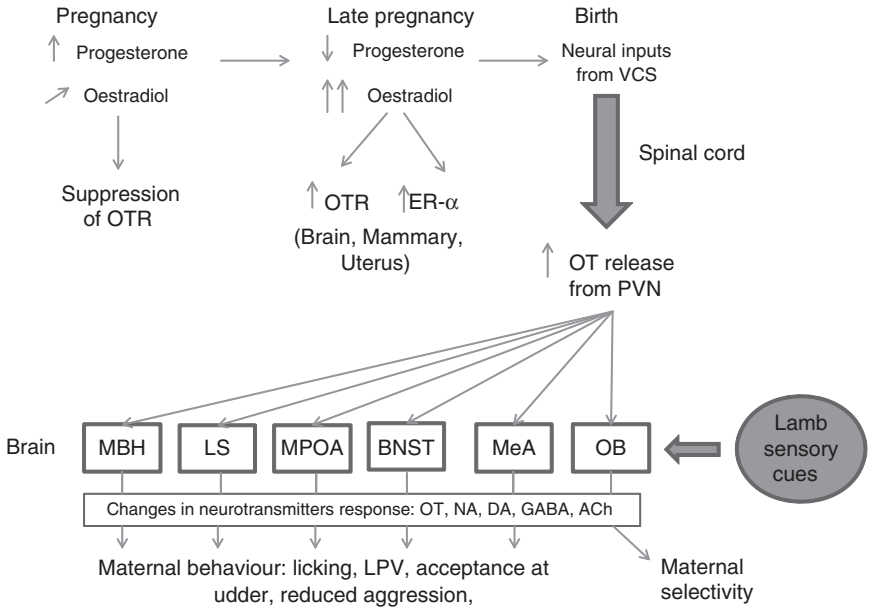


Figure 1 Schematic depicting the key physiological and neurological changes during pregnancy and birth associated with the onset of maternal behaviour. VCS = vaginocervical stimulation; OTR = oxytocin receptor; ER-α = oestrogen receptor-α; OT = oxytocin; PVN = paraventricular nucleus of the hypothalamus; MBH = mediobasal hypothalamus; LS = lateral septum; MPOA = medial pre-optic area; BNST = bed nucleus of the stria terminalis; MeA = medial amygdala; OB = olfactory bulb; NA = noradrenaline; DA = dopamine; GABA = γ-amino butyric acid; ACh = acetylcholine; LPV = low-pitched vocalisations.

effects (Young *et al.,* 1998). Binding of oestradiol to ER-α stimulates an increase in the expression of oxytocin receptors (OTR) in several key regions of the brain (e.g. medial preoptic area (MPOA), ventromedial hypothalamus, lateral septum, medial amygdala, bed nucleus of the stria terminalis (BNST), PVN; Broad *et al.,* 1999, Figure 1) associated with the expression of maternal behaviour. This up-regulation of OTR is inhibited by high relative concentrations of progesterone earlier in gestation (Broad *et al.,* 1993), thus it is only when there is an increase in oestradiol and a decrease in progesterone in late gestation that the ewe becomes prepared to express maternal care. The 'trigger' for the expression of maternal behaviour is provided by VCS at delivery such that the onset of maternal care is exquisitely timed to coincide with the birth of the lamb. VCS engenders the release of central oxytocin via a spinal reflex (known as the 'Ferguson Reflex'), terminating in the PVN of the hypothalamus (Da Costa *et al*., 1996, Figure 1). The importance of this reflex has been shown in studies where the peripheral input was prevented following spinal anaesthesia (Krehbiel *et al*., 1987) and onset of maternal behaviour was abolished. Maternal behaviour can be restored through the infusion of intracerebroventricular oxytocin (Lévy *et al*., 1992).

Parturition, and the accompanying increase in central oxytocin, elicits an increase in the neurotransmitters acetylcholine, noradrenaline, glutamate, GABA and dopamine in the olfactory bulb (Keverne *et al*., 1993; Lévy *et al*., 1993, 1995), and an increase in noradrenaline and dopamine in the BNST, MPOA and PVN (Kendrick *et al.,* 1992a; Da Costa *et al*., 1996). These brain regions are specifically associated with the nurturing and selectivity aspects of maternal care in the ewe.

The final cues in the sequence resulting in the successful expression of maternal behaviour are the behaviours and sensory information provided by the lamb. Initially the ewe is attracted not to the lamb but to the smell and taste of amniotic fluids, even though ewes are actively repulsed by these same cues only a day or so before parturition (Lévy *et al*., 1983; Arnould *et al*., 1991). During labour the ewe shows increasing interest in the amniotic fluids that have been spilt during the rupture of the amniotic sac (or indeed those of other lambing ewes), and this attraction is transferred to the newborn lamb whose birth coat is soaked in amniotic fluids. The importance of amniotic fluids for the onset of maternal care is shown by studies where the amniotic fluids have been removed from the newborn lamb by washing, which result in disturbances in the onset of maternal care, and may eliminate maternal care in inexperienced ewes (Lévy and Poindron, 1987; Poindron *et al.,* 2010). Likewise in ewes that have been rendered temporarily anosmic, maternal care, particularly of inexperienced animals, may be disrupted or prevented (Lévy *et al.,* 1983). Prevention of physical interaction between ewe and lambs for the first 4 h after birth (licking or nursing) reduces maternal acceptance in primiparous ewes, although not in multiparous ewes (Otal *et al*., 2009). These impairments were not seen in ewes only prevented from suckling their lambs, so emphasising the importance of olfactory information.

In addition to their role in the onset of maternal behaviour the olfactory cues provided by amniotic fluid also provide the basis of maternal specificity for her own lamb or 'selectivity' (Poindron *et al*., 2007). This is the process by which the ewe rapidly learns the olfactory signature of her own lamb, generally within 30 min of birth, and thereafter restricts her

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press

maternal care to her own offspring, repelling the attempts of other lambs to approach or suckle. The period of maternal learning is temporally related to the elevated release of oxytocin in the brain (Keverne and Kendrick, 1992; Kendrick *et al*., 1992a; Da Costa *et al*., 1996; Kendrick, 2000), and is accompanied by changes in neurotransmitter release profiles in the olfactory bulb when ewes are presented with their own or an alien lamb (Keverne *et al*., 1993; Lévy *et al*., 1995). This process is accompanied by a down-regulation of neurogenesis in the hippocampus and olfactory system, which may favour the retention of olfactory memories relating to offspring identity (Brus *et al*., 2010; Lévy *et al*., 2011). The reduction in neurogenesis is known to involve oestradiol (Lévy *et al*., 2011), further supporting a role for this hormone in organising maternal responses in the sheep.

Individual variation in maternal behaviour

When all the cues are present in the correct temporal sequence maternal behaviour and ewe-lamb bonding is elicited. However, there are several factors that are known to be associated with altered or absent expression of maternal behaviour. Impairments in maternal care can range from delayed onset of maternal behaviour, acceptance of only one of a pair of twins, or a complete absence of maternal responsiveness. Predispositions to these disturbances in maternal behaviour expression include maternal inexperience (specifically reduced maternal care in primiparous ewes; Dwyer and Lawrence, 2000), some maternal genotypes (Poindron *et al*., 1984; Le Neindre *et al*., 1998; Dwyer and Lawrence, 1998, 2000; Dwyer *et al*., 1998), maternal undernutrition in gestation (Dwyer *et al*., 2003), maternal psychological stress in gestation (Hild *et al*., 2011) and difficult delivery (Dwyer *et al*., 2003; Darwish and Ashmawy, 2011). The reason why these sources of variation in maternal behaviour have this influence can be at least partly related to their impact on the neurobiology underpinning the onset of maternal care.

Maternal experience

Ewes giving birth for the first time, as for many species, tend to give birth to smaller offspring, do not show as competent maternal care as more experienced ewes, and the mortality of their offspring is higher (Dwyer and Lawrence, 2005a). Although primiparous ewes show as much total grooming or licking and low-pitched bleating as more experienced ewes (Dwyer and Lawrence, 2000), they are slower to begin grooming their lambs, and show a higher frequency of behavioural disturbances such as aggression towards the lamb, withdrawal or lamb avoidance, and a lack of cooperation with lamb attempts to suck (Dwyer and Lawrence, 1998, 2005a). The data suggest that the primiparous ewes may be stimulated to express maternal behaviour but might be inhibited in their willingness to approach and interact with the lamb which represents a novel object and a potential source of fear. These behavioural disturbances are often short-lived, however, and the experience of interacting with and caring for the lamb is accompanied by a maturing of behavioural and physiological responses.

Primiparous ewes have been shown to have similar concentrations of circulating oestradiol in late gestation as multiparous animals (Dwyer and Smith, 2008). However, multiparous ewes have a higher density of ER-α in the hypothalamic and limbic regions of the brain (Meurisse *et al*., 2005) and are therefore more sensitive or reactive to similar circulating concentrations of oestradiol. Inactivation of MPOA in primiparous parturient ewes induces severe deficits in maternal behaviour which are much reduced in multiparous animals (Perrin *et al*., 2007), suggesting that primiparous ewes may rely more on the involvement of this area of the brain than multiparous ewes for the onset of maternal behaviour. Parturition increases release of the neurotransmitters acetylcholine, noradrenaline, glutamate and GABA in the olfactory bulb of multiparous but not primiparous ewes (Keverne *et al*., 1993; Lévy *et al*., 1993). Basal dopamine release, however, is greater in primiparous ewes compared with multiparous, but increases in response to parturition in both groups of ewe (Keverne *et al*., 1993). The greater sensitivity of multiparous ewes, mediated through their increased number of OTR and potentiated neurotransmitter responses, may explain why these animals are less disturbed in their behaviour than primiparous ewes when some of the olfactory cues eliciting maternal behaviour are manipulated (e.g. washing the newborn lamb or anosmia; Poindron *et al*., 2007).

Primiparous ewes have been shown, however, to develop selectivity at a similar rate to multiparous ewes (Keller *et al*., 2003). This means that the sensitive period for developing an olfactory recognition of their lamb may only be present for the first 30 to 60 min after birth. If fearfulness of the lamb, or a delayed ability to switch from an attraction to the spilt amniotic fluids to an attraction for the lamb, prevents the ewe from interacting with her lamb during this time window she may fail to establish selectivity with her own lamb. Lack of development of maternal recognition will then result in rejection of her own offspring, which is sometimes seen with primiparous ewes. In fact separation of the ewe and lamb at birth for 4 h is more detrimental to acceptance of the lamb in primiparous ewes compared with multiparous (Otal *et al*., 2009), suggesting that young ewes are more dependent on the maintenance of close contact with their lambs to be properly maternal than older ewes.

Genotype effects

Many studies, comparing several different breed combinations, have demonstrated breed differences in the expression of maternal behaviour, in terms of their ability to recognise their own offspring, willingness to remain at the birth site, lamb abandonment and differences in the expression of maternal affiliative and negative behaviours (Shillito-Walser, 1980; Alexander *et al*., 1983; Poindron *et al*., 1984; Le Neindre *et al*., 1998; Dwyer and Lawrence, 1998, 2000; Dwyer, 2008b; von Borstel *et al*., 2011). We have carried out a series of studies comparing Scottish Blackface (SBF) (a hill breed of sheep that is relatively unselected for production

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press

traits) to Suffolk ewes (a lowland breed intensively selected for growth characteristics). In these breeds, as is also true of other hill, upland and more primitive breeds which have been subjected to less human intervention, SBF ewes show higher levels of maternal care, in comparison to the Suffolk which, in common with other more intensively selected and reared animals, display greater variability in maternal behavior and express the poorest quality of maternal care (reviewed by Dwyer and Lawrence, 2005a; Dwyer, 2008b).

SBF ewes have higher circulating oestradiol concentrations in late gestation (Dwyer *et al*., 1999), and show a greater pre-partum surge of oestradiol (Dwyer *et al*., 2004), compared with Suffolk ewes. There is no consistent breed effect on plasma progesterone concentration, resulting in higher a oestradiol : progesterone ratio in SBF ewes in late gestation, which may lead to increased expression of OTR in SBF ewes. The elevated oestradiol concentration is positively correlated with the quantity of maternal grooming behaviour and frequency of low-pitched bleats (Dwyer *et al*., 1999, 2004). Basal oxytocin secretion to the periphery in late gestation, or at parturition, is not affected by ewe breed (Dwyer *et al*., 2004), although plasma oxytocin concentrations in the immediate post-partum period are elevated in SBF ewes in comparison to Suffolk ewes. This latter may, however, be explained by increased ewe-lamb contact and suckling which are also known to increase circulating oxytocin (Fuchs *et al*., 1987; Nelson and Panksepp, 1998). The effect of breed on central OTR numbers and neurotransmitter release has not been investigated.

Although still to be tested it can be hypothesised that higher circulating oestradiol in the late pregnant SBF ewe mediates an upregulation of OTR in the limbic and hypothalamic areas of the brain which results in an increased expression of maternal behaviour. Our preliminary data also suggests that Suffolk ewes show delayed development of maternal selectivity (Dwyer *et al*., unpublished): these ewes continue to express maternal care to both their own and alien lambs for a longer period than SBF ewes.

Maternal nutrition in pregnancy

Ewes undernourished in pregnancy have reduced udder weight and mammary development (Mellor and Murray, 1985; Mellor *et al*., 1987), delayed onset of lactation (Mellor *et al*., 1987), reduced colostrum yield and milk production (Mellor and Murray, 1985; Hall *et al*., 1992; O'Doherty and Crosby, 1996) and increased lamb mortality (Kleeman *et al*., 1993; Hinch *et al*., 1996; Rooke *et al*., 2010). These ewes also display behavioral impairments, taking longer to interact with their lambs (Thomson and Thomson, 1949), displaying more aggression to the lamb, spending less time grooming and more time eating after birth (Dwyer *et al*., 2003), and are more likely to desert their lambs (Putu *et al*., 1988; Lindsay *et al*., 1990), than well-fed ewes. In specific tests of the strength of attachment between ewe and lamb, undernourished ewes were less attached to their lambs than adequately fed ewes (Dwyer *et al*., 2003). Our recent unpublished work suggests these impacts on maternal behaviour in sheep are particularly pronounced when ewes are undernourished in late pregnancy.

The potential role of the relative concentrations of oestradiol and progesterone in mediating differences in maternal care is also supported by data from gestationally undernourished ewes, which show a poorer quality of maternal care at parturition and also have a reduced oestradiol to progesterone ratio in late gestation (Dwyer *et al*., 2003) in comparison to ewes fed adequately. In this case, however, the depressed ratio of oestradiol to progesterone derives from elevated progesterone concentrations in the undernourished ewes.

Difficult parturition

Ewes which experience a prolonged or difficult delivery are slower to begin grooming their lambs, show reduced grooming behaviour and fewer maternal (low-pitched) bleats, and are more likely to reject their lambs than ewes delivering after short or uncomplicated births (Dwyer *et al*., 2003; Darwish and Ashmawy, 2011). A prolonged or difficult birth is likely to be associated with pain and stress in the mother. Although not recorded in either of these studies, it is possible that a prolonged labour may lead to an increase in maternal circulating hormones (e.g. cortisol, vasopressin), as has been shown in goats and cattle (Hydbring *et al*., 1999). Elevated plasma cortisol at delivery has been shown to be negatively correlated with the expression of maternal grooming behaviour, although not with negative behaviours (Dwyer *et al*., 2004), which may account for some of the impact of a difficult birth on the expression of maternal behaviour. Further, if ewes are exhausted from a prolonged delivery, and are slow to stand and interact with their lambs, the sensitive period when they form a selective bond with their lamb may have passed, resulting in lamb rejection.

Ewe temperament

Temperament can be defined as the manner in which individuals react to novel or challenging situations that is repeatable over time (Bates *et al*., 1995). Most studies attempting to assess temperament and its potential relationship to maternal care in sheep have focused on fearfulness, and measured individual variation in behavioural reactivity to different challenge situations (e.g. arena test, isolation box, corridor test, etc., reviewed by Dodd *et al*., 2012). The most studied relationship with maternal behaviour comes from work where Merino ewes were tested in an isolation box and an arena test (with human presence) with locomotor and vocal activity being recorded (Blache and Ferguson, 2005). Animals were selected on these measures to produce lines of sheep that differed markedly in their response in the arena and isolation box tests. The lines have been described either as more active or less active on the basis of their activity in the tests (e.g. Beausoleil *et al*., 2008, 2012) or 'nervous' and 'calm' respectively in other studies (e.g. Bickell *et al*., 2009; Hawken *et al*., 2013). Analysis of the behaviour of these flocks in several test situations suggest that consistent behavioural differences exist with one line showing increased activity and vocalisation compared with the other

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press

in all test situations (Beausoleil *et al*., 2012). However, the more active sheep in some tests appeared more bold and less fearful than the less active sheep (Beausoleil *et al*., 2008), and other studies also show no between-flock difference in physiological responses in test situations that were not part of the selection paradigm (Hawken *et al*., 2013). The most conservative interpretation is that flock variation in activity in specific tests exists, although whether this is related to an emotional response or temperament trait in the animals is not clear.

Studies on maternal care using Merino ewes that were selected for behavioural activity to isolation and in an arena test, have suggested that less active ewes spend more time on the birth site (Lindsay *et al*., 1990) than more active ewes, and groom and bleat more frequently to their lambs (Murphy *et al*., 1994). Lamb mortality was also lower in the less active ewes compared with the more active animals. However, more recent studies with these ewe lines have shown few differences in maternal behaviour between flocks (Bickell *et al*., 2010, 2011) and no effect on the development of maternal selectivity (Bickell *et al*., 2009). There were also no differences in circulating oestradiol around parturition between the more or less active ewes (Bickell *et al*., 2011). In studies of non-selected sheep, a positive genetic correlation between activity in the isolation box and litter survival has been found (Plush *et al*., 2011) suggesting, contrary to the results of Murphy *et al.* (1994), that selection for increased activity in the isolation box would lead to improved lamb survival.

Ewes previously selected for their ability to rear lambs show behavioural responses, such as a closer approach distance, in an approach avoidance test, indicative of increased 'calmness' or a better ability to cope with acute stress (Kilgour and Szantar-Coddington, 1995; Hough *et al*., 2013) compared with unselected ewes or ewes with a lower rearing ability. Thus, although there appears to be some association between ewe temperament and maternal care in ewes the picture is not very clear, and how this is mediated is still unknown.

Maternal psychological stress in pregnancy

In rodents, maternal care (e.g. licking or grooming, arched-back nursing) is reduced in mothers that experienced psychological stress during pregnancy (Patin *et al*., 2002; Smith *et al*., 2004; Champagne and Meaney, 2006). The reduction in maternal care appears to be related to a stress-induced reduction in OTR density (Champagne and Meaney, 2006). In the sheep there is evidence for altered maternal behaviour following transport or social isolation in pregnancy (ewes showed a greater motivation to remain with lambs in the presence of humans if they had experienced isolation stress in pregnancy, but a lower motivation if they had been transported in pregnancy compared with untreated controls: Roussel *et al*., 2006), although the authors suggest that this may be more related to responses to humans than a direct impact on ewe-lamb behaviour. Another study in sheep suggests that primiparous ewes that had been handled in an unpredictable and negative manner in late pregnancy showed more grooming behaviour after birth than primiparous ewes which were gentled (Hild *et al*., 2011), unlike the responses seen in the rodent studies. The impact of stress in pregnancy on the expression of maternal behaviour in sheep, therefore, is still unclear, and whether this is mediated by similar pathways to those seen in rodents is still to be investigated.

Practical applications

Management of pregnant and parturient ewes

The foregoing sections have demonstrated how the onset of maternal behaviour is critically dependent on appropriate physiological changes in the ewe and the timely exposure to sensory cues from the lamb to be successfully elicited. Primiparous ewes are particularly sensitive to small disruptions in the temporal sequence of events and behavioural disturbances are common if these are not optimal. The ewe is also sensitive to management and husbandry conditions, particularly in late pregnancy, that can disturb or alter the physiological signals leading to maternal care. How can this understanding of the neuroendocrine mechanisms underpinning the onset of maternal behaviour be useful in practice?

An understanding of the importance of the timing of various events in late pregnancy and during parturition, as well as the factors that can disrupt these events can help to design management activities to minimise the risks to the onset of maternal behaviour. For example, avoiding nutritional or psychological stresses, particularly in the last part of gestation when hormonal changes are most important for the successful elicitation of maternal behaviour, will help to optimise the ability of the ewe to show adequate maternal care. Another key area is recognition of the critical importance of the initial postpartum period for the development of ewe selectivity for the lamb. Management activities or interventions during this period, as well as the potential influence of other ewes in highly stocked areas, that cause ewe-lamb separation or otherwise interfere with the olfactory cues from the lamb, can prevent maternal ewes from developing an olfactory recognition memory for her own lamb. Thus, although maternal behaviour has been elicited, the ewe is unable to develop the second facet of maternal care, maternal selectivity, and will not recognise her lamb as her own.

In open areas there is some evidence that ewes will separate from the flock at parturition (Alexander *et al*., 1990), as is seen in wild sheep species (reviewed by Dwyer and Lawrence, 2005a), which may minimise any possible disturbances to this important window for olfactory recognition. In housed situations, or where several ewes in various stages of parturition may be in close contact, ewes may swap or steal lambs from other ewes (e.g. Arnold and Morgan, 1975) as parturient ewes can be physiologically ready to show maternal care to newly born lambs, and have not yet become selective for their own offspring. In some cases ewes

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press

may steal lambs before delivering their own lamb, which may then be rejected, or attempt to mother both their own and the lambs of other ewes, which can increase lamb mortality (Arnold and Morgan, 1975). In studies where housed ewes were provided with cubicles, and opportunities to at least partially isolate themselves from other ewes at parturition, ewes chose to lamb in the cubicles and were more likely to remain with their lamb and less likely to experience interference from other ewes than animals lambing in the open pen (Gonyou and Stookey, 1983, 1985). Once the olfactory memory is established in the ewe, then short periods of ewe-lamb separation are not disruptive to the continued expression of maternal care (Lévy *et al*., 1991).

For primiparous ewes, where disturbance can cause a complete absence of maternal behaviour or an inability of the ewe to bond effectively to her young, appropriate management is critical. Young ewes need to be given adequate time for maternal behaviour to develop and for the transfer of attraction for amniotic fluids to the lamb to occur before attempting to move animals away from the birth site. For example, primiparous ewes will frequently show behavioural disturbances as the lamb stands and attempts to suck, such as moving away or pushing or butting the lamb, but will continue to lick the lamb while it lies still. As ewes become more accustomed to the presence of the lamb, and the recognition memory for her own lamb becomes established, maternal behaviour improves and negative behaviours towards the lamb wane (Dwyer and Lawrence, 1998). As primiparous ewes are particularly sensitive to the presence of amniotic fluid on the coats of their lambs for the elicitation of maternal behaviour (Lévy and Poindron, 1987; Poindron *et al*., 2010), removal or contamination of amniotic fluids of the ewes own lamb with those of other animals is a greater risk to successful maternal care in these animals than in multiparous ewes.

Genetic selection for improved maternal care

The relationship between temperament and maternal care is still unclear: evidence exists that selection for improved maternal rearing ability is associated with less fearful behaviour in the arena test (Kilgour and Szantar-Coddington, 1995; Cloete *et al*., 2010) compared with ewes with lower rearing ability. However the converse that selection using isolation box test activity will lead to improved maternal behaviour and lamb survival is less well supported (Bickell *et al*., 2009, 2010, 2011; Plush *et al*., 2011). Nevertheless, genotype impacts on maternal care have been well described, and there is substantial evidence that this may be mediated via alterations in the physiological processes, particularly circulating oestradiol, that underpin the onset of maternal care. There is more work to be done in this area, however it has the potential to offer new methods to select for improved maternal care in ewes. The reductions in maternal care associated with a difficult delivery also offer an opportunity to improve the expression of maternal care, first through management practices to reduce the incidence of difficult births. Second, birth difficulty is known to vary by breed (Dwyer and Lawrence, 2005b; Dwyer and Bünger, 2012) and has significant and moderate heritability (Matheson *et al*., 2012). This suggests that including ease of delivery in selection goals for sheep can improve the expression of maternal care, as well as behavioural development in the neonatal lamb (Dwyer, 2003) leading to improved survival.

Fostering

It is well known that, although practiced by many farmers (Ward *et al*., 2011), successful fostering of lambs is a difficult and sometimes unsuccessful process compared with polytocous species such as pigs or rodents. In these species, where bonding with individual animals in the litter does not occur, or only occurs at a later stage, fostered individuals can relatively easily be introduced and are reared with the dam's own offspring. Fostering in sheep, however, is a risk factor for increased lamb mortality (Binns *et al*., 2002), and may result in lambs that are rejected, sometimes violently, by the proposed foster mother. A variety of methods to foster lambs have been used including masking or matching the odour of the foster lamb to that of the ewes own lamb (e.g. use of various unguents, such as Neatsfoot oil, or jackets (Alexander *et al*., 1985; Price *et al*., 2003), use of birth fluids and cervical stimulation (Basiouni and Gonyou, 1988), restraining the ewe in stocks (Alexander and Bradley, 1985), applying the skin of a dead lamb to the foster lamb (Alexander *et al*., 1987) and experimental hormonal manipulations on non-pregnant ewes with (Kendrick *et al*., 1992b; Dwyer and Lawrence, 1997) or without VCS (Mellor *et al*., 1993). Of these, methods that use birth fluids or hormonal manipulations (although hormonal manipulations are unlikely to be practically or ethically possible on farm) with cervical stimulation, or use of a dead lamb skin, are the most successful in facilitating an immediate acceptance of the foster lamb by the ewe. Methods that transfer the odour of the ewes own lamb to the foster lamb were also successful, although often taking longer for the ewe to accept the new lamb (Alexander *et al*., 1985, 1989; Price *et al*., 2003), and achieved better and quicker success than restraint (Alexander and Bradley, 1985). Thus the foster methods that make best use of the biological processes that underpin the onset of maternal responsiveness and selectivity at birth have the best success in inducing a ewe to accept another lamb.

Future research areas

Maternal care in the ewe has been the best studied of livestock species, although there is still much that is not yet known. In addition and crucially for the subject of this review, this detailed knowledge of maternal behaviour accumulated over the last 20 or so years has not, yet, led to any marked decrease in lamb mortality. There remain several avenues of research that could still be pursued, spanning the basic biological responses to practical applications.

The onset of maternal behaviour and early interactions with the lamb is accompanied by a very dynamic phase of

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press

hormonal and behavioural change, leading to alterations in central neural transmitter release and neurogenesis (e.g. Kendrick *et al*., 1992a; Keverne *et al.,* 1993; Brus *et al*., 2010). However, the functional significance of these changes and how they may affect individual differences in maternal care and the development of maternal selectivity are still unknown. Further, the neurological basis of individual differences in expression of maternal care, and how environment factors which affect behavioural expression are mediated, are still to be completely unravelled. For example, although there is evidence supporting an organising role for circulating oestradiol in some differences in maternal care, this remains only correlational and whether oestradiol differences result in altered neuroendocrine processing (e.g. altered OTR numbers) is not known. In addition, although the role of olfactory information in the onset of maternal care is well established, whether other sensory information (e.g. vocal communication) also plays a role in influencing neuroendocrinological changes in the mother is not known.

In rodents, there is evidence that maternal care received by rat pups in the first week of life has a profound impact on the subsequent maternal care expressed by female offspring, which can be transmitted across generations (Champagne and Meaney, 2001). Maternal grooming and arched-back nursing (a specific nursing posture in the rat), expressed across the light–dark cycle (Pena and Champagne, 2013), result in alterations in the epigenome of the pup (Szyf *et al*., 2003; Weaver *et al*., 2004), and changed patterns of central oxytocin and steroid receptor expression (Pedersen and Boccia, 2002; Szyf *et al*., 2005; Pena and Champagne, 2013). Similar responses have also been seen in mice (Kikusui *et al*., 2005; Shoji and Kato, 2009). However, whether similar responses are seen in the sheep, a species where offspring are precocious and grooming occurs for a relatively short period after birth, are not known. There is evidence for altered lamb development following exposure to different levels of maternal care (Dwyer and Lawrence, 2000) but this did not include assessment of subsequent maternal behaviour.

There is also some evidence of prenatal impacts (undernutrition, stress) on subsequent maternal care expressed by the mother (described above), although these studies have generally not considered the maternal care expressed by the offspring. In pigs, however, there is evidence that prenatal exposure to stress results in an altered maternal phenotype in the offspring (Jarvis *et al*., 2006). In sheep, a species very often subjected to undernutrition in pregnancy, the potential role that this may have in shaping the subsequent behaviour of the mother and offspring, and its transmission to subsequent generations could be important in determining reproductive efficiency.

Genetic selection for increased maternal care has generally been achieved through selection for rearing ability or multiple rearing ability (Atkins, 1980; Cloete and Scholtz, 1998; Cloete *et al*., 2003). Historically also selection, through culling, for traits associated with survivability have resulted in the development of 'easycare' breeds, particularly in New Zealand (Fisher, 2003). Thus it is possible to alter maternal behaviour through genetic selection, and breed and line differences in maternal behaviour expression (described above) point to a genetic component to maternal behaviour. However, direct inclusion of measures of maternal behaviour in selection programmes are currently very difficult, as recording these traits accurately on large numbers of animals is virtually impossible. Several traits, including temperament, have been suggested as indirect measures that may be related to maternal behaviour. It is clear from the discussion above around the impact of ewe temperament on maternal behaviour and lamb survival, and even how temperament can be reliably measured, that this area would benefit from more research to define whether this could be a suitable proxy measure.

Finally, it is important to bear in mind that lamb survival depends fundamentally on the establishment of a bond between ewe and lamb, such that the lamb can obtain colostrum and milk from the dam, and the behaviour of both ewe and lamb contribute to lamb survival. Success in reducing lamb mortality must consider the behaviour of both partners in the interaction to achieve progress, the behaviour of either partner alone will not be sufficient to ensure survival. There has been significant recent progress in understanding the determinants of lamb neonatal behaviour (Cloete and Scholtz, 1998; Cloete *et al*., 2002; Dwyer, 2003; Dwyer and Morgan, 2006; Darwish *et al*., 2010). Further, practical ways to record lamb behaviour on farm, in some contexts, have been developed (Matheson *et al*., 2011) and shown to have moderate heritability (Matheson *et al*., 2012). However, we still know much less about the underlying neuroendocrinology governing individual variations in lamb behaviour compared with maternal behaviour, and how prenatal influences may alter expression of neonatal behaviours.

Conclusions

The ewe has been exceptionally well studied, compared with other livestock species, in terms of understanding the complex biological and environmental interactions that underpin the onset of maternal behaviour. In addition, ewes show marked selectivity for their own offspring and studies have unravelled the neurological pathways leading to the development of this olfactory recognition memory. Appropriate and timely expression of maternal behaviour in the ewe is a critical component in the survival and successful rearing of lambs, and so can have a direct impact on farm profitability. An improved understanding of the biological basis for the onset of maternal behaviour, and thus an appreciation of which events and critical time windows are most important for the ewe, will aid the development of appropriate management to facilitate the ability of the ewe to express these behaviours. Management practices that work with the biology of the ewe will be the most successful in ensuring that maternal care is expressed, so improving the welfare of the ewe and lamb, and the profitability of the farm.

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press

Acknowledgement

SRUC receives grant in aid from the Scottish Government. The author thanks the two anonymous referees for their valuable comments on an earlier version of this paper.

References

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

Alexander G and Bradley L 1985. Fostering in sheep. 4. Use of restraint. Applied Animal Behaviour Science 14, 355–364.

Alexander G, Stevens D and Bradley L 1985. Fostering in sheep. 1. Facilitation by use of textile lamb coats. Applied Animal Behaviour Science 14, 315–334.

Alexander G, Stevens D and Bradley L 1987. Fostering in sheep – fostering lambs onto ewes whose lambs have died soon after birth. Australian Journal of Experimental Agriculture 27, 765–769.

Alexander G, Stevens D and Bradley L 1989. Fostering in sheep – an exploratory comparison of several approaches. Australian Journal of Experimental Agriculture 29, 509–512.

Alexander G, Stevens D and Bradley L 1990. Distribution of field birth-sites of lambing ewes. Australian Journal of Experimental Agriculture 30, 759–767.

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

Arnold GW and Morgan PD 1975. Behaviour of the ewe and lamb at lambing and its relationship to lamb mortality. Applied Animal Ethology 2, 25–46.

Arnould C, Piketty V and Lévy F 1991. Behavior of ewes at parturition towards amniotic fluids of sheep, cows and goats. Applied Animal Behaviour Science 32, 191–196.

Atkins KD 1980. The comparative productivity of five breeds of ewe: 1. Lamb growth and survival. Australian Journal of Experimental Agriculture and Animal Husbandry 20, 272–279.

Avital E and Jablonka E 1994. Social learning and evolution of behaviour. Animal Behaviour 48, 1195–1199.

Basiouni GF and Gonyou HW 1988. Use of birth fluids and cervical stimulation in lamb fostering. Journal of Animal Science 66, 872–879.

Bates JE, Wachs TD and Vandenbos GR 1995. Trends in research on temperament. Psychiatric Services 46, 661–663.

Beausoleil NJ, Blache D, Stafford KJ, Mellor DJ and Noble ADL 2008. Exploring the basis of divergent selection for 'temperament' in domestic sheep. Applied Animal Behaviour Science 109, 261–274.

Beausoleil NJ, Blache D, Stafford KJ, Mellor DJ and Noble ADL 2012. Selection for temperament in sheep: domain-general and context-specific traits. Applied Animal Behaviour Science 139, 74–85.

Bickell SL, Nowak R, Poindron P, Ferguson D and Blache D 2010. Maternal behaviour at parturition in outdoor conditions differs only moderately between single-bearing ewes selected for their calm or nervous temperament. Animal Production Science 50, 675–682.

Bickell S, Poindron P, Nowak R, Ferguson D, Blackberry M and Blache D 2011. Maternal behaviour and peripartum levels of oestradiol and progesterone show little difference in Merino ewes selected for calm or nervous temperament under indoor housing conditions. Animal 4, 608–614.

Bickell SL, Nowak R, Poindron P, Sébé F, Chadwick A, Ferguson D and Blache D 2009. Temperament does not affect the overall establishment of mutual preference between the mother and her young in sheep measured in a choice test. Developmental Psychobiology 51, 429–438.

Binns SH, Cox IJ, Rizvi S and Green LE 2002. Risk factors for lamb mortality on UK sheep farms. Preventive Veterinary Medicine 52, 287–303.

Blache D and Ferguson D 2005. Increasing sheep meat production efficiency and animal welfare by selection for temperament – Part A. Final Report to Meat and Livestock Australia on Project SHGEN.025.

Broad KD, Kendrick KM, Sirinathsinghji DJS and Keverne EB 1993. Changes in oxytocin immunoreactivity and messenger RNA expression in the sheep brain during pregnancy, parturition and lactation and in response to oestrogen and progesterone. Journal of Neuroendocrinology 5, 435–444.

Broad KD, Lévy F, Evans G, Kimura T, Keverne EB and Kendrick KM 1999. Previous maternal experience potentiates the effect of parturition on oxytocin receptor mRNA expression in the paraventricular nucleus. European Journal of Neuroscience 11, 3725–3737.

Brus M, Meurisse M, Franceschini I, Keller M and Lévy F 2010. Evidence for cell proliferation in the sheep brain and its down-regulation by parturition and interactions with the young. Horomones and Behavior 58, 737–746.

Champagne F and Meaney MJ 2001. Like mother, like daughter: evidence for non-genomic transmission of parental behavior and stress responsivity. Progress in Brain Research 133, 287–302.

Champagne FA and Meaney MJ 2006. Stress during gestation alters postpartum maternal care and the development of the offspring in a rodent model. Biological Psychiatry 59, 1227–1235.

Cloete JJE, Cloete SWP and Hoffman LC 2010. Behaviour of Merino ewes divergently selected for multiple rearing ability in response to human beings. Proceedings of the 9th World Congress on Genetics applied to Livestock Production. Retrieved July 2013 from http://www.kongressband.de/wcgalp2010/assets/pdf/0703.pdf

Cloete SWP and Scholtz AJ 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merinos lines divergently selected for multiple rearing ability. Australian Journal of Experimental Agriculture 38, 801–811.

Cloete SWP, Scholtz AJ, Gilmour AR and Olivier JJ 2002. Genetic and environmental effects on lambing and neonatal behaviour of Dormer and SA Mutton Merino lambs. Livestock Production Science 78, 183–193.

Cloete SWP, van Wyk JB, Scholtz AJ and Gilmour AR 2003. Genetic and environmental parameters for lambing behaviour in Merino lines divergently selected for ewe multiple rearing ability. Proceedings of the New Zealand Society for Animal Production 63, 169–172.

Da Costa APC, Guevara-Guzman RG, Ohkura S, Goode JA and Kendrick KM 1996. The role of oxytocin release in the paraventricular nucleus in the control of maternal behaviour in the sheep. Journal of Neuroendocrinology 8, 163–177.

Darwish RA and 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.

Darwish RA, Abou-Ismail UA and El-Kholya SZ 2010. Differences in post-parturient behaviour, lamb performance and survival rate between purebred Egyptian Rahmani and its crossbred Finnish ewes. Small Ruminant Research 89, 57–61.

Dodd CL, Pitchford WS, Edwards JEH and Hazel SJ 2012. Measures of behavioural reactivity and their relationships with production traits in sheep: a review. Applied Animal Behaviour Science 140, 1–15.

Dwyer CM 2003. Behavioural development in the neonatal lamb: effect of maternal and birth-related factors. Theriogenology 59, 1027–1050.

Dwyer CM 2008a. 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 2008b. Genetic and physiological effects on maternal behavior and lamb survival. Journal of Animal Science 86, E246–E258.

Dwyer CM and Lawrence AB 1997. Induction of maternal behaviour in non-pregnant, hormone-primed ewes. Animal Science 65, 403–408.

Dwyer CM and Lawrence AB 1998. Variability in the in expression of maternal behaviour in primiparous sheep: effects of genotype and litter size. Applied Animal Behaviour Science 58, 311–330.

Dwyer CM and Lawrence AB 2000. Maternal behaviour in domestic sheep (*Ovis aries*): constancy and change with maternal experience. Behaviour 137, 1391–1413.

Dwyer CM and Lawrence AB 2005a. A review of the behavioural and physiological adaptations of extensively managed breeds of sheep that favour lamb survival. Applied Animal Behaviour Science 92, 235–260.

Dwyer CM and Lawrence AB 2005b. Frequency and cost of human intervention at lambing: an interbreed comparison. The Veterinary Record 157, 101–104.

Dwyer CM and Morgan CA 2006. Maintenance of body temperature in the neonatal lamb: effects of breed, birth weight and litter size. Journal of Animal Science 84, 1093–1101.

Dwyer CM and Smith LA 2008. Parity effects on maternal behaviour are not related to circulating oestradiol concentrations in two breeds of sheep. Physiology and Behavior 93, 148–154.

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press

Dwyer CM and Bünger L 2012. Factors affecting dystocia and offspring vigour in different sheep genotypes. Preventive Veterinary Medicine 103, 257–264.

Dwyer CM, Dingwall WA and Lawrence AB 1999. Physiological correlates of maternal-offspring behaviour in sheep: a factor analysis. Physiology and Behavior 67, 443–454.

Dwyer CM, Gilbert CL and Lawrence AB 2004. Pre-partum plasma estradiol and post-partum cortisol, but not oxytocin, are associated with individual differences in the expression of maternal behavior in sheep. Hormones and Behavior 46, 529–543.

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

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

Fisher MW 2003. New Zealand narratives of the benefits of reduced human intervention during lambing in extensive farming systems. Journal of Agricultural and Environmental Ethics 16, 77–90.

Fuchs AR, Ayromlooi J and Rasmussen AB 1987. Oxytocin response to conditioned and nonconditioned stimuli in lactating ewes. Biology of Reproduction 37, 301–305.

Gonyou HW and Stookey JM 1983. Use of lambing cubicles and the behaviour of ewes at parturition. Journal of Animal Science 56, 787–791.

Gonyou HW and Stookey JM 1985. Behavior of parturient ewes in group-lambing pens with and without cubicles. Applied Animal Behaviour Science 14, 163–171.

Goursaud AP and Nowak R 1999. Colostrum mediates the development of mother preference by newborn lambs. Physiology and Behavior 67, 49–56.

Hall DG, Holst PJ and Shutt DA 1992. The effect of nutritional supplements in late pregnancy on ewe colostrum production, plasma progesterone and IGF-1 concentrations. Australian Journal of Agricultural Research 43, 325–337.

Hawken PAR, Luckins N, Tilbrook A, Fiol C, Martin GB and Blache D 2013. Genetic selection for temperament affects behaviour and the secretion of adrenal and reproductive hormones in sheep subjected to stress. Stress 16, 130–142.

Hild S, Coulon M, Schroeer A, Andersen IL and Zanella AJ 2011. Gentle vs. aversive handling of pregnant ewes: I. Maternal cortisol and behaviour. Physiology and Behavior 104, 384–391.

Hinch GN, Lynch JJ, Nolan JV, Leng RA, Bindon BM and Piper LR 1996. Supplementation of high fecundity Border Leicester × Merino ewes with a high protein feed: its effect on lamb survival. Australian Journal of Experimental Agriculture 36, 129–136.

Hough D, Swart P and Cloete S 2013. Exploration of the hypothalamic-pituitary-adrenal axis to improve animal welfare by means of genetic selection: lessons from the South African Merino. Animals 3, 442–474.

Hydbring E, Madej A, MacDonald E, Drugge-Boholm C, Berglund B and Olsson K 1999. Hormonal changes during parturition in heifers and goats are related to the phases and severity of labour. Journal of Endocrinology 160, 75–85.

Jarvis S, Moinard C, Robson SK, Baxter E, Ormandy E, Douglas AJ, Seckl JR, Russell JA and Lawrence AB 2006. Programming the offspring of the pig by prenatal social stress: neuroendocrine activity and behaviour. Hormones and Behavior 49, 68–80.

Keller M, Meurisse M, Poindron P, Nowak R, Shayit M, Ferreira G and Lévy F 2003. Maternal experience influences the establishment of visual/auditory, but not of olfactory recognition of the newborn lamb by ewes at parturition. Developmental Psychobiology 43, 167–176.

Kendrick KM 2000. Oxytocin, motherhood and bonding. Experimental Physiology 85, 111S–124S.

Kendrick KM and 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, Lévy F and Keverne EB 1992a. Changes in the sensory processing of olfactory signals induced by birth in sheep. Science 256, 833–836.

Kendrick KM, da Costa AP, Hinton MR and Keverne EB 1992b. A simple method for fostering lambs using anestrous ewes with artificially induced lactation and maternal behaviour. Applied Animal Behaviour Science 34, 345–357.

Kendrick KM, da Costa APC, Broad KD, Ohkura S, Guevara R, Lévy F and Keverne EB 1997. Neural control of maternal behaviour and olfactory recognition of the young. Brain Research Bulletin 44, 383–395.

Keverne EB and Kendrick KM 1992. Oxytocin facilitation of maternal behaviour in sheep. Annals of the New York Academy of Sciences 652, 83–101.

Keverne EB, Lévy F, Guevara-Guzman R and Kendrick KM 1993. Influence of birth and maternal experience on olfactory bulb neurotransmitter release. Neuroscience 56, 557–565.

Kikusui T, Isaka Y and Mori Y 2005. Early weaning deprives mouse pups of maternal care and decreases their maternal behavior in adulthood. Behavioural Brain Research 162, 200–206.

Kilgour RJ and Szantar-Coddington MR 1995. Arena behavior of ewes selected for superior mothering ability differs from that of unselected ewes. Animal Reproduction Science 37, 133–141.

Kleeman DO, Walker SK, Walkley JRW, Ponzoni RW, Smith DH, Grimson RJ and Seamark RF 1993. Effect of nutrition during pregnancy on birth weight and lamb survival in FecB Booroola × South Australian Merino ewes. Animal Reproduction Science 31, 213–224.

Krehbiel D, Poindron P, Lévy F and Prud'homme MJ 1987. Peridural anesthesia disturbs maternal behaviour in primiparous and multiparous parturient ewes. Physiology and Behavior 40, 463–472.

Le Neindre P, Murphy PM, Boissy A, Purvis IW, Lindsay D, Orgeur P, Bouix J and Bibé B 1998. Genetics of maternal ability in cattle and sheep. Proceedings of the 6th World Congress of the Genetics of Livestock Production 27, 23–30.

Lent PC 1974. Mother-infant relationships in ungulates. In The behaviour of ungulates and its relationship to management, IUCN Publication No. 24 (ed. V Geist and F Walther), pp. 14–55. International Union for the Conservation of Nature, Morges, Switzerland.

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

Lévy F, Poindon P and 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.

Lévy F, Gheusi G and Keller M 2011. Plasticity of the parental brain: a case for neurogenesis. Journal of Neuroendocrinology 23, 984–993.

Lévy F, Kendrick KM, Keverne EB, Piketty V and Poindron P 1992. Intracerebral oxytocin is important for the onset of maternal behavior in inexperienced ewes delivered under peridural anesthesia. Behaviour Neuroscience 106, 427–432.

Lévy F, Guevara-Guzman R, Hinton MR, Kendrick KM and Keverne EB 1993. Effects of parturition and maternal experience on noradrenaline and acetylcholine release in the olfactory bulb of sheep. Behavioural Neuroscience 107, 662–668.

Lévy F, Kendrick KM, Goode JA, Guevara-Guzman R and Keverne EB 1995. Oxytocin and vasopression release in the olfactory bulb of parturient ewes – changes with maternal experience and effects on acetylcholine, gamma-aminobutyric acid, glutamate and noradrenaline release. Brain Research 669, 197–206.

Lévy F, Gervais R, Kinderman U, Litterio M, Poindron P and Porter R 1991. Effects of early postpartum separation on maternal selectivity and responsiveness in parturient ewes. Applied Animal Behaviour Science 31, 101–110.

Lindsay DR, Nowak R, Putu IG and McNeill D 1990. Behavioural interactions between the ewe and her young at parturition: a vital step for the lamb. In Reproductive physiology of Merino sheep – concepts and consequences (ed. CM Oldham, GB Martin and IW Purvis), pp. 191–205. University of Western Australia, Perth, Australia.

Matheson SM, Bünger L and Dwyer CM 2012. Genetic parameters for fitness and neonatal behavior traits in sheep. Behavior Genetics 42, 899–911.

Matheson SM, Rooke JA, McIlvaney KM, Ison S, Jack M, Bunger L, Ashworth CJ and Dwyer CM 2011. Development and validation of 'on-farm' behavioural scoring systems to assess birth assistance and lamb vigour. Animal 5, 776–783.

Mellor DJ and Murray L 1985. Effects of maternal nutrition on udder development during late pregnancy and on colostrum production in Scottish Blackface ewes with twin lambs. Research in Veterinary Science 39, 230–234.

Mellor DJ, Dingwall RA and King TJ 1993. Successful fostering of orphan lambs by non-pregnant ewes induced to lactate using exogenous hormone treatment. New Zealand Veterinary Journal 41, 200–204.

Mellor DJ, Flint DJ, Vernon RG and Forsyth IA 1987. Relationships between plasma hormone concentrations, udder development and the production of early mammary secretions in twin-bearing ewes on different planes of nutrition. Quarterly Journal of Experimental Physiology and Cognate Medical Sciences 72, 345–356.

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press

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

Murphy PM, Purvis IW, Lindsay DR, LeNeindre P, Orgeur P and Poindron P 1994. Measures of temperament are highly repeatable in Merino sheep and some are related to maternal behaviour. Proceedings of the Australian Society for Animal Production 20, 247–248.

Nelson EE and Panksepp J 1998. Brain substrates of infant-mother attachment: contributions of opioids, oxytocin, and norepinephrine. Neuroscience and Biobehavioural Reviews 22, 437–452.

O'Doherty JV and Crosby TF 1996. The effect of diet in late pregnancy on progesterone concentration and colostrum yield in ewes. Theriogenology 46, 233–241.

Otal J, Lévy F, Cornilleau F, Moussu C, Keller M and Poindron P 2009. Preventing physical interactions between parturient ewes and their neonate differentially impairs the development of maternal responsiveness and selectivity depending on maternal experience. Applied Animal Behaviour Science 120, 140–149.

Packer C, Lewis S and Pusey A 1992. A comparative analysis of non-offspring nursing. Animal Behaviour 43, 265–281.

Patin V, Lordi B, Vincent A, Thoumas JL, Vaudry H and Caston J 2002. Effects of prenatal stress on maternal behavior in the rat. Developmental Brain Research 139, 1–8.

Pedersen CA and Boccia ML 2002. Oxytocin links mothering received, mothering bestowed and adult stress responses. Stress 5, 259–267.

Pena CJ and Champagne FA 2013. Implications of temporal variation in maternal care for the prediction of neurobiological and behavioral outcomes in offspring. Behavioral Neuroscience 127, 33–46.

Perrin G, Meurisse M and Lévy F 2007. Inactivation of the medial preoptic area or the bed nucleus of the stria tenninalis differentially disrupts maternal behavior in sheep. Hormones and Behavior 52, 461–473.

Pickup HE and Dwyer CM 2011. Breed differences in the expression of maternal care at parturition persist throughout the lactation period in sheep. Applied Animal Behaviour Science 132, 33–41.

Plush KJ, Hebart ML, Brien FD and Hynd PI 2011. The genetics of temperament in Merino sheep and relationships with lamb survival. Applied Animal Behaviour Science 134, 130–136.

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

Poindron P, Le Neindre P, Lévy F and Keverne EB 1984. The physiological mechanisms of the acceptance of the newborn among sheep. Biology of Behaviour 9, 65–88.

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

Price EO, Dally MR and Hernandez L 2003. A note on the use of odor manipulation to facilitate the adoption of alien lambs by ewes bearing twins. Applied Animal Behaviour Science 81, 127–131.

Putu IG, Poindron P and Lindsay DR 1988. A high level of nutrition during late pregnancy improves subsequent maternal behaviour in Merino ewes. Proceedings of the Australian Society of Animal Production 17, 294–297.

Rooke JA, Houdijk JGM, McIlvaney KM, Ashworth CJ and Dwyer CM 2010. Differential effects of maternal nutrient restriction between days one and ninety of pregnancy on ewe and lamb performance and lamb parasitism of ewes in hill and lowland breeds. Journal of Animal Science 88, 3833–3842.

Rosenblatt JS 2003. Outline of the evolution of behavioral and nonbehavioral patterns of parental care among the vertebrates: critical characteristics of mammalian and avian parental behaviour. Scandinavian Journal of Psychology 44, 265–271.

Roussel S, Hemsworth PH, Leruste H, White C, Duvaux-Ponter C, Nowak R and Boissy A 2006. Repeated transport and isolation during pregnancy in ewes: effects on the reactivity to humans and to their offspring after lambing. Applied Animal Behaviour Science 97, 172–189.

Russell AF and Lummaa V 2009. Maternal effects in cooperative breeders: from hymenopterans to humans. Philosophical Transactions of the Royal Society B: Biological Sciences 364, 1143–1167.

Shillito-Walser E 1980. Maternal recognition and breed identity in lambs living in a mixed flock of Jacob, Clun Forest and Dalesbred sheep. Applied Animal Ethology 6, 221–231.

Shoji H and Kato K 2009. Maternal care affects the development of maternal behavior in inbred mice. Developmental Psychobiology 51, 345–357.

Smith JW, Seckl JR, Evans AT, Costall B and Smythe JW 2004. Gestational stress induces post-partum depression-like behaviour and alters maternal care in rats. Psychoneuroendocrinology 29, 227–244.

Szyf M, Weaver ICG, Champagne FA, Diorio J and Meaney MJ 2005. Maternal programming of steroid receptor expression and phenotype through DNA methylation in the rat. Frontiers in Neuroendocrinology 26, 139–162.

Szyf M, Weaver ICG, Cervoni N, D'Alessio AC, Champagne FA and Meaney MJ 2003. Transgenerational epigenomic imprinting by maternal behavior through DNA methylation and its reversal by histone deacetylase inhibitors. American Journal of Medical Genetics 122B, 13.

Thomson AM and Thomson W 1949. Lambing in relation to the diet of the pregnant ewe. British Journal of Nutrition 2, 290–305.

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

Ward SJ, Liste G and Tinarwo A 2011. Attitudes of UK sheep farmers towards fostering methods: A national survey. Small Ruminant Research 99, 87–92.

Weaver ICG, Cervoni N, Champagne FA, D'Alessio AC, Sharma S, Seckl JR, Dymov S, Szyf M and Meaney MJ 2004. Epigenetic programming by maternal behaviour. Nature Neuroscience 7, 847–854.

Young LJ, Wang ZX, Donaldson R and Rissman EF 1998. Estrogen receptor alpha is essential for the induction of oxytocin receptor by estrogen. Neuroreport 9, 933–936.

https://doi.org/10.1017/S1751731113001614 Published online by Cambridge University Press