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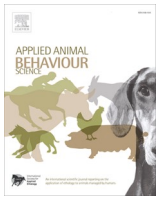

Mother-offspring bonding revisited: A blueprint for the future of beef cattle farming

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ABSTRACT

This review summarizes the status of the art of cow-calf relationships at birth and during lactation, including the physiological mechanisms throughout suckling/nursing and weaning which can impact on productive and reproductive parameters, social behaviour across the mother-offspring pairs, and the required positive cow-calf welfare approach in beef cattle. The time spent close to the calf after birth, latency to nurse, nursing time, grooming and vocalisations can be considered fair proxies of oxytocin release and maternal care during the neonatal period. Besides, maternal contact during the first days after parturition will be crucial to guarantee the adequate establishment of mother-offspring bonding and the correct social and emotional development of young calf in beef cattle. During lactation, restricted nursing systems have been demonstrated as cost-effective management alternatives to improve reproductive herd performance. As artificial weaning of calves is considered a significant stressor in the lives of beef cattle, the use of a fence-line or the two-step weaning have been proposed, although no clear benefits in reducing cow-calf distress have been found. Modelling the perspective from a productive to a welfare approach in a beef cattle system is required. The ability of cows and calves to engage in voluntary, self-generated and goal-directed behaviour must be considered in the design of tailored management practices that maintain the trade-off between animal performance, cow-calf interactions, and positive mental state. Likewise, social interactions may be considered as part of environmental optimization to provide cow-calf pairs with opportunities for positive experiences and improve cattle welfare. The Five Domains Model is proposed to develop welfare-orientated management strategies considering aspects such as maternal deprivation, behavioural stress and socio-emotional development in beef cattle. This holistic approach of mother-offspring bonding focused on nutrition (Domain 1), physical environment (Domain 2), health (Domain 3), behavioural interactions (Domain 4) and animal's mental state (Domain 5) will help to improve management decisions and cow-calf welfare state. Some management recommendations and opportunities for future studies to deeply enlarge the welfare perspective in the dyad are discussed.

1. Introduction

Nearly two-third of the world's cattle population around the world are reared in The American and Asian continents (mostly represented by their southern regions) (35.1 % and 30.6 %, respectively; FAO, 2024). In most of these areas, cow-calf systems are developed under extensive or semi-extensive grazing conditions with large variability of forage resources. Whatever the management system, optimal cow-calf pair relationship is the core to achieve the expected productive and reproductive performance at farm level.

The cattle herd has been traditionally referred as the "meat factory" or "engine room", as weaned calves will be the raw material for the following fattening period. Since nutrition and suckling are highly recognized as the most important factors influencing postpartum anoestrous interval (PPI) (Sanz et al., 2004), and consequently pregnancy rates, various management strategies were developed to maintain productive parameters. However, these business-as-usual management could have jeopardized the mother-offspring bonding. Most of the herds

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calve during spring, coinciding with the emergence of the summer pastures, and in some cases, a double calving season (autumn and spring) is carried out to achieve a greater number of calves through two periods in the year. Also, the "focus feed strategy", through supplementation or improved pastures, before or after parturition, ensures not only a good reproductive performance but also a healthy dam to nurse its recently born calf (Radunz et al., 2010; Claramunt et al., 2020). In fact, milk production is highly correlated with the nutritional status of the mother, being the main source of nutrition for the young, which also determines its development.

After parturition, the cow-calf bond must be established through a complex interaction of maternal behaviours with the offspring (Lidfors and Jensen, 1988; Lidfors et al., 1994). Generally, the cow isolates herself from the herd before calving. Immediately after calving the cow licks and sniffs the calf, possibly stimulating its activity, ingesting the foetal membranes, and helping the young to stand up and suckle (Nevard et al., 2023). These activities are crucial for fostering the cow-calf bond and promoting neonatal survival. In natural conditions, this bond is maintained until the calf is 6–12 months old (Newberry and Swanson, 2008). This great variability in the natural weaning time depends on nutritional and social determinants. Natural weaning is characterized by a gradual milk supply decrease accompanied by an increase in forage intake and a weakening in the social bond, with a consequent decrease in physical proximity and more independence of the young respect to the mother (Newberry and Swanson, 2008). Some authors indicate that the natural weaning age would not be earlier than 8–10 months (Schneider et al., 2021). However, under artificial conditions (commercial circumstances), weaning typically occurs between 6 and 8 months of age (Weary et al., 2008; Enríquez et al., 2011), or even earlier if the costs of pastures and other feedstuffs cannot be counterbalanced with weaning calf incomes. In commercial conditions, the abrupt separation between calves and mothers is generally used without considering the multiple stressing factors that this practice involves, such as loss of maternal contact, unfamiliar social and housing environments, and a new diet (Enríquez et al., 2010).

In order to enhance reproductive rates in beef herds, certain suckling restriction strategies have been applied during lactation. Management strategies such as reducing suckling frequency to one or two times per day (Sanz et al., 2003), using nose plates for two weeks (Quintans et al., 2010), completely separating the calf from 2 to 6 days (Shively and Williams, 1989; Quintans et al., 2004) or even permanent weaning at 2 months of age (early weaning; Parfet et al., 1986; Quintans et al., 2009) can improve the chances of the dam becoming pregnant, but also may alter social interactions and positive cow-calf welfare approach. However, much research lacks a positive animal welfare approach, including assessment of mental status. Accordingly, an animal welfare assessment should consider in the future the Five Domain model construct (Hemsworth et al., 2015; Mellor, 2017; Littlewood et al., 2023). In this holistic approach, the relationships between cow-calf pairs should focus on nutrition and physical environment (Domains 1 and 2) and functional states (health) (Domains 3), on the behavioural interactions with the environment, other animals and humans (Domain 4), and a fifth pillar that validates the rest based on the animal's mental state (Domain 5).

In the current review, cow-calf relationships at birth and during lactation, a variety of nursing systems, physiological mechanisms, productive and reproductive performances, and social behaviour and mental state across the mother-offspring pairs are evaluated, and some management recommendations and research gaps for future studies are discussed.

2. Material and methods

A systematic search of peer-reviewed publications was conducted with the Scopus® online database in October 2023. The main keywords were "cows" and "calves" and "beef" and "maternal behaviour", yielding a total 51 publications from 1985 to 2023. Additional searches were conducted by replacing "maternal behaviour" with "dam" or "mother" or "mother-young" and "behaviour" (71 publications), and with "nursing behaviour" or "suckling-mediated" (23 publications), and "affiliative behaviour" and "weaning" (6 publications). The outcomes were merged to gather a total of 100 records that met the following criteria: "cow-calf relationships at birth and during lactation", "breaking cow-calf bonding at weaning of calves" and "social skills as learned behaviours". Unless required to highlight some physiological or behavioural cues which are independent of genetic background, the manuscripts dealing with dairy cows and calves were not accounted for in this review, in alignment of objective with search techniques.

3. Cow-calf relationships at birth

During the last decades, many studies have analysed physiological mechanisms, nursing systems, productive and reproductive performances, or social behaviour across the mother-offspring pairs from calving throughout lactation. Just before calving, a slight separation from other adults normally occurs, even though there is not complete isolation from the herd. After calving, all cows lick their calves. The amount of licking between 0 and 30 min is significantly greater than that between 30 and 60 min after birth, and this is not correlated with subsequent licking behaviour during lactation (Lidfors and Jensen, 1988).

The interaction with the amniotic fluids soon after parturition may be used as an olfactory cue for the mother to recognize her offspring. In fact, maternal grooming is believed to be responsible of the stimulation of neonatal calf activity, facilitation of drying from maternal uterine fluids to reduce heat loss, as well as social bonding with the calf (Nevard et al., 2023). This behaviour also stimulates urination and defecation by the calf (Metz and Metz, 1986), which is key for meconium excretion soon after birth. In addition, maternal grooming during lactation decreases the quantities of bacteria on the calf's coat, which may contribute to maintaining the calf's body hygiene. Consequently, allowing the fulfilment of this behaviour and its full function might be important for calf production (Kohari et al., 2009).

The calf has a strong sucking reflex from its first few minutes of age, which is triggered when the young animals' oral mucosa is touched, developing into a chewing reflex as the calf gets older (FIBL, 2023). The latency to nurse in beef calves accounts for the time to stand for the first time plus the time to effectively reach the udder of dams, and it could range between 50 and 57 minutes (min) in outdoor conditions, being hardly affected by maternal nutrition during late pregnancy (Batista et al., 2020). The duration of the first suckling is significantly longer for heifer calves than for bull calves (Lidfors and Jensen, 1988). In cow-calf pairs requiring longer latency to nurse, this was reduced when a moderate volume of colostrum (1 L to 1.4 L) was fed at 60 min after birth, although the improvement in this variable could not be associated with an improved transfer of passive immunity to calves (kept at 70–100 g IgG/L at 24–36 h after birth) (Gamsjäger et al., 2021). In the latter study, the median latency to standing ranged from 100 to 131 min, while the median latency to nurse ranged from 162 to 222 min. In outdoor conditions, Cuttance et al. (2022) identified that risk factors for the hazard rate ratio for time to the first nursing event were time to standing (more than 78 min) and age of dam (less than 7 years of age). Suckling attempts without effective nursing represented 32.2 % of total encounters in first parity cow-calf pairs, which mostly failed to suckle as a result of rejection by the dam (65.3 % of the attempts) (Hogan et al., 2022). In that study, neonatal calves required three days to develop a consistent suckling pattern, being front teats sucked more frequently (65.3 % of the times), although in 67 % of nursing interactions the calves sucked on all four teats.

After only 24 hours (h) of interaction, cows could discriminate between her calf and similar alien calves, however, if cows were taken away at 24–96 h and re-joined with a different calf three days later, cows were unable to make a distinction between their own calves and alien calves, suggesting that 3-day separation would be enough to break down

the maternal bond (Kent and Kelly, 1987). Lidfors et al. (1994) described an interest by other herd members in a newborn calf which triggered aggressive behaviour by the dam, in an attempt to protect the calf health. In addition, the cows react more to alien male than female calves (Pérez-Torres et al., 2014). These studies evidence that maternal contact during the first days after parturition will be crucial to guarantee the adequate establishment of mother-offspring bonding.

4. Cow-calf relationships during lactation

In the first studies carried out on suckling-mediated anovulation and maternal behaviour, Silveira et al. (1993) found that enforced suckling by unrelated calves failed to attenuate the increase in luteinizing hormone (LH) pulse frequency and luteal activity, and it did not increase the frequency of oxytocin release following suckling, whereas suckling-induced release of prolactin was not modified (Silveira et al., 1993). In the same study, these authors evidenced that the cumulative frequency of cows exhibiting luteal activity did not differ between those nursing an alien calf or submitted to a temporal calf removal for 6 days (72.7 and 75.0 % on day 10, respectively), but it was lower in their counterparts nursing their own calf (38.0 %). However, this result could not be related to the recorded maternal behaviour (distinguishing between maternal and non-maternal aggression). The mother-offspring bond, in terms of maternal protective behaviour to their own or alien calves, was evaluated for 120 days postpartum in Zebu cows, showing that at 30 days postpartum 90 % of the cows responded to the stimulus of calves being handled, 40 % reacted exclusively to alien calves, and 50 % responded to their own or alien calves (Pérez-Torres et al., 2014). As postpartum increased, proportion of cows responding to calf manipulation and intensity of the reaction declined, only 20 % cows responding at 120 days postpartum. Interestingly, protective behaviour of the mother observed in this study was not influenced by cow temperament. In another study, evaluating maternal protective behaviour during earmarking of their calves in a large set of cows (n=390) during seven consecutive years, protective behaviour score could not correlate with weaning weights or average daily gain (ADG) of calves (Hoppe et al., 2008). The time a cow and calf stayed in the vicinity of each other is significantly longer for heifer calves, but they generally have a lighter weaning weight (Lidfors and Jensen, 1988). Olfaction and vision are equally effective in permitting calf identification, but the elimination of both senses prevents calf identification and the negative effects of suckling on LH secretion (Griffith and Williams, 1996). Thereby, cows appear to compensate effectively for the loss of either vision or olfaction by using the remaining sense to achieve calf identification.

In the 80 s and 90 s, several experiments were conducted to evaluate the role of maternal olfaction, sight, ovarian and udder function on calf suckling behaviour and reproductive hormone secretion. Although they were a scaffold for the current understanding of maternal physiology, most of them involved approaches that were a challenge to animal welfare, and are no longer being applied in the current scientific animal models. These studies proved that endogenous opioids participated in the regulation of PPI (Malven et al., 1986), and that mammary somatosensory pathways were not fully responsible for the inhibition of LH secretion and delay of PPI when cows nurse their own calves (Williams et al., 1993). The ability of naloxone (an opioid antagonist) to increase LH in ovariectomized non-suckled cows indicated that opioid inhibition of LH secretion was not entirely dependent on the ovary and suckling (Rund et al., 1989), thereby, visual and olfactory cues may also be involved in suckling-mediated PPI. Other works suggested that when the udder was not stimulated by the calf the PPI was resumed earlier both in mastectomized (Viker et al., 1993) and restricted-nursing cows (Lamb et al., 1999). Likewise, serum cortisol, oxytocin and prolactin were found to increase when own calves attempt to suckle mastectomized dams (Stevenson et al., 1994). However, neither estradiol priming in ovariectomized heifers nor estradiol plus progesterone in intact heifers resulted in an induction of maternal behaviours following genital stimulation (release of oxytocin) and presentation of a neonate wetted with amniotic fluid (Williams et al., 2001).

The correlations between maternal saliva oxytocin, cortisol, heart rate and eye temperature with maternal behaviours during the first three days after calving are generally low (Geburt et al., 2015). A summary of physiological pathways mediating maternal behaviour in cattle revised in the literature is shown in Table 1. Neonatal Holstein dairy calves separated from their dams at birth underwent a systemic stress response through a surge of pro-inflammatory cytokines, whereas Limousin-Friesian beef calves reared by dams exhibited early signs of humoral immune development with observed increases in the expression genes coding for immunoglobulin receptors, which was not evident in Holstein or Charolais-Limousin calves by 7 days of age (Surlis et al., 2018).

Faecal glucocorticoid concentrations in dams during the first three days postpartum were not affected by a reduction of calf access (restricted to once or twice 30-min daily periods) or parity, but they were greater during the first 12 h postpartum than subsequently (Álvarez-Rodríguez et al., 2010a). However, temporary separation of Zebu calves for 72 h at 1 month of age increased blood cortisol concentrations of calf at definitive weaning four months later more than those induced by restricted suckling for 30 min/day, which highlights a long-term negative effect of early separation from the dam (Pérez-Torres et al., 2021).

Factors interfering with mother-newborn imprinting may be inexperience, poor physical condition, number of newborns per parturition, dystocia at parturition leading to exhaustion and prolonged pain, and weak neonates (Orihuela et al., 2021). Epidural anesthesia blocks the release of oxytocin and markedly reduces licking behaviours following parturition in primiparous cows but does not result ultimately in rejection of the calf (Williams et al., 2001).

Restricting maternal dietary protein before conception may result in subsequent increased blood flow to the fetus-placental unit enabling enhanced nutrient supply, resulting in increased birth weight of calves and increased dam standing time after parturition (Miguel-Pacheco et al., 2019). A modification of maternal nutritional status and endocrine signals (mainly circulating Insulin-like growth Factor-I) via herbage allowance management (4 vs. 2.5 kg of dry matter/kg of live-weight, LW), which increases both energy and protein status postpartum, can result in a differential maternal behaviour by reducing cow–calf physical distance during grazing access, which could contribute to improving milk yield and cow-calf productive performance responses (Claramunt et al., 2020).

The extended PPI is a significant cause of poor reproductive performance in beef cattle. Previous studies have shown that suckling significantly delays the resumption of ovarian activity after calving, when nutrient intake and body reserves are not limiting factors (Wettemann et al., 2003; Sanz et al., 2004). Under moderate nutritional conditions, the length of PPI can range from 45 to 120 days, being the longest period observed in suckler cows nursing continuously. Various methods have been applied to reduce suckling-meditated anovulation, such as the restricted suckling (reducing mother-calf encounters). Álvarez-Rodríguez et al. (2010b) found that once-daily suckling (for 30 min) from the day after calving reduced the PPI compared with ad libitum suckling (56 vs. 87 days) when suckler cattle were fed at maintenance on Spanish mountain areas, but this practice had no effect when these cattle were slightly underfed during early and mid-lactation (PPI: 74 days) (Álvarez-Rodríguez et al., 2009a).

Furthermore, cow-calf pairs may function as a cohesive unit, where factors such as nutrition, cow and calf performance, suckling or breed interact among them and influence each other. For example, cows with good body condition score (BCS), based on adipose tissue and muscle reserves, were suckled less frequently by their calves and maintained future reproductive efficiency, as measured by PPI, compared with cows with lower BCS when managed on improved pastures in Australia (Kour et al., 2021). This study found that, at 4 months of age, calves suckled

Table 1
Summary of physiological pathways mediating maternal behaviour in cattle.

Communication cue	Hormone/ neurotransmitter	Brain region	Positive feed-back streams	References
Fetal ACTH and cortisol	Oxytocin	Hypothalamus-Neurohypophysis (paraventricular and supraoptic nucleus).	Dam estrogens: Nest building, myometrium contraction (uterotonic) at parturition	(Mota-Rojas et al., 2023)
Tactile, Olfactory, Auditory, Visual		Limbic system (amygdala, vomeronasal organ and olfactory bulb) and the nucleus accumbens.	Suckling and butting, sniffing offspring perianal region and head, licking and grooming: Imprinting after birth, maternal care, social cognition, and affiliative behaviour (including nursing non-filial offspring), facilitation of milk ejection.	(Mota-Rojas et al., 2023)
			Imprinting process: Vocalization (bidirectional between the mother and her offspring); odor molecules.	(Orihuela et al., 2021)
			Stimulation of glucagon release and thereby, mobilisation of glucose.	(Uvnäs-Moberg et al., 2001)
	Prolactin	Adenohypophysis (Medial preoptic area)	Suckling and butting: Milk synthesis, maternal care, prevention of postpartum anxiety	(Mota-Rojas et al., 2023)
	Arginine-vasopressin	Hypothalamus-Neurohypophysis	Activation of dopaminergic system: stress-related (protection/fear/aggression), and social behaviours	(Mota-Rojas et al., 2021; Mota-Rojas et al., 2023)
	Dopamine	Nucleus accumbens and prefrontal cortex	Motivation, approach, interaction, Inhibit rejection/ fear	(Coria-Avila et al., 2022)
	Norephinephrine	Locus coeruleus	Olfactory learning, nest building	(Nevard et al., 2023)
	Serotonin	Raphe nuclei	Maternal care	(Nevard et al., 2023)
	Luteinizing hormone	Hypothalamus-Adenohypophysis	Ovulation of the dominant follicle	(Griffith and Williams, 1996)
	Opioid neuropeptides (methionine-enkephalin, β-endorphin, dynorphin)	Hypophyseal neurointermediate lobe	Reduction of LH secretion	(Malven et al., 1986)
	Opioid peptides	Basolateral amygdala	Inhibit rejection/fear	(Coria-Avila et al., 2022)

less frequently (8.2 times/24 h) than at 1 month of age (9.8 times/24 h), and had longer suckling durations at 4 months (9.3 min/bout) than at 1 month (8.3 min/bout). Although this pattern did not affect calf ADG, it was negatively associated with cow ADG (correlation coefficient=-0.54). Sanz et al. (2003) found that suckling frequency did not affect changes in dams' weight and BCS during lactation in Brown Swiss (Centre Europe dual-purpose breed) and Pirenaica cows (local Spanish beef breed) nursing twice a day or ad libitum. However, under similar nutritional conditions, Pirenaica cows showed a higher rate of weight gain, lower milk yield and lower calf ADG during lactation compared with Brown Swiss cows, regardless of suckling frequency. Free access of calves to dams did not affect PPI in Pirenaica cows, however, it markedly delayed the resumption of PPI in Brown Swiss cows (31.8 vs. 82.7 days, for restricted and ad libitum, respectively). The previous authors suggested that higher milk yield beef breeds could be more susceptible to the suppressor effect of ad libitum nursing on PPI compared with low milk production breeds, although genetic differences may not appear to be mediated by differences in energy balance or in ovarian follicular dynamics. In a subsequent study, when evaluating mother-offspring behaviour at weeks 3, 8 and 13 of lactation, Parda de Montaña cows (ancient Brown Swiss selected nowadays for beef purposes) allowed more allonursing by foster calves when kept in group pens the whole day (until 10.7 min per day) while Pirenaica cows performed more agonistic encounters to own or alien calves in once-daily restricted nursing systems (3.7 vs. 0.9 times per nursing session) (Álvarez-Rodríguez et al., 2010b). In that experiment, postpartum first ovulation occurred at a similar time after calving between breeds (70 vs. 73 days in Parda and Pirenaica, respectively), although it was shorter in once-daily restricted suckling for 30 min than in ad libitum nursing (54 vs. 89 days). In addition, the fulfilment of nutritional requirements when calves remained ad libitum with their dams was accomplished with approximately 1 h of nursing per day, regardless of breed. Despite some contrasting aspects, in general suckling restriction can be a useful strategy with benefits on reproductive rates in beef cattle herds.

Nursing an alien calf (allonursing) or suckling an alien dam (allosuckling) are maternal behaviours observed to some extent in beef cattle during lactation. Víchová and Bartoš (2005) observed in cow-calf pairs from birth until 203 days of lactation that 27 % of sucking attempts and 19 % of suckling bouts were non-filial. Two different views are considered for non-filial cow-calf contacts. On the one hand, allonursing may reflect social benefit (increase social status when nursing offspring of dominant females) or may facilitate milk evacuation to avoid inflammation in dams. On the other hand, allosuckling may reflect compensation for nutritional or immunological deficiency (Mota-Rojas et al., 2021).

To better understand conflicting results in the literature, several aspects related to nursing-suckling behaviour may be revisited. One suggestion made by some authors is that restricting calf access without cow-calf contact between suckling periods only after day 30 postpartum was even more useful in shortening the PPI than restricted suckling from the onset of lactation (Stagg et al., 1998). Suckling restriction to twice-daily 30 minutes periods at day 21 postpartum was able to trigger the first dominant follicle ovulation (42.9 vs. 62.0 days postpartum), but only in cows with sufficient BCS (≥2.5 on a 1–5 scale), perhaps through improved, insulin-mediated, metabolic status (Sinclair et al., 2002). In a further study, additional visual or olfactory isolation of calves by dams between twice-daily suckling periods did not seem to be necessary to induce anovulation, as the length of nursing and the PPI did not differ between restricted nursing with or without fence contact (Álvarez-Rodríguez et al., 2009b).

Some studies from South America, developed under grazing conditions, have described that temporary suckling restriction (using nose plates for 14 days or calf completely removed) in multiparous cows significantly decreased milk production (in low BCS cows) and PPI, and increased percentage of cycling cows (presence of corpus luteum) at day 94 postpartum compared to ad libitum suckling cows (68 %, 57 % and 21 %, for nose plate, completely removed or ad libitum suckling) (Quintans et al., 2010). This study highlighted that temporary suckling restriction with or without the presence of the calf may be an excellent management tool to increase the reproductive performance of cows in moderate body condition, but the trade-off effects on cow-calf welfare were not evaluated. In that case, calves' LW at weaning was conditioned by the suckling management (150, 147 and 159 kg LW for nose plate, completely removed or ad libitum suckling), although in another study

under similar experimental conditions, the dam milk yield and calf LW did not differ between the temporary nose plate and ad libitum suckling groups (Hötzel et al., 2012). Another possible handicap resulting from temporary calf removal during 4–6 days at 61 days of lactation may be that, although a high proportion of beef cows reach subsequent ovulation, the restoration of normal-length oestrous cycles may not be achieved (Quintans et al., 2004).

Variety in productive and reproductive performances obtained in nursing systems studies evidence the complex cow-calf relationships, which may be conditioned by cow body condition at the beginning of the experiments, cow-calf diets during lactation, genetic potential for milk yield, the prenatal environment, and behavioural and emotional aspects. Based on literature results, the mechanisms underlying the reproductive response to suckling managements are not yet well understood. The study of affiliative behaviours and positive relationships within the Five Domains model offers an opportunity to gain further knowledge regarding welfare compromise and enhancement (Hampton et al., 2023). In Domain 2, which focuses on the productive environment, animals that adapt to changes in their environment are more likely to survive and reproduce compared to other members of their species. In this line, protective maternal behaviour might affect some reproductive variables in Zebu cows (Enríquez et al., 2021). Although the authors did not observe any differences in ovarian activity between protective and non-protective dams, cows with no postpartum follicular presence reacted to approaching calves (correlation coefficient =-0.39) and the cows displaying more intensity of reaction toward approaching calves were those that did not display oestrous behaviour (correlation coefficient =-0.46), underlying the complex interactions between mother-offspring bonding, including temperament, with productive and reproductive performances in beef cattle.

5. Breaking cow-calf bonding at weaning of calves

Some efforts have been made to quantify the decrease in productivity and the stress generated in the calf and cow when weaning is applied, and alternative weaning methods have been evaluated to minimize negative impacts. The use of nose plates for different periods (Haley et al., 2005; Enríquez et al., 2010), the separation of the mother-young through a fence line (Price et al., 2003), the use of an experienced social facilitator with weaned calves are some examples (Nickles et al., 2021). However, some conflicting results have been reported regarding these weaning strategies. For example, Price et al. (2003) reported the benefits of weaning through a fence line in ADG of the calves, but they observed confused results in variables regarding calf behaviour (time eating, lying, walking and vocalizations). On the other hand, Haley et al. (2005) previously reported that weaned calves in two stages (nose plates) showed less distress than calves abruptly separated from their mothers, but no benefit in calf ADG was observed. Enríquez et al. (2010) reported no clear benefits in reducing calf stress with the two weaning alternatives evaluated (fence line or nose plates) compared to abrupt weaning. Finally, Nickles et al. (2021) reported that it was unlikely that a social facilitator cow could decrease the distance and time spent walking by calves enough to improve calf LW after weaning. The afore-mentioned studies aimed mostly at evaluating herd productivity, with less attention paid to the wellbeing of calves and mothers. This represents an opportunity for future studies to deeply enlarge the welfare perspective in the dyad.

From a productive point of view, early weaning of calves at 73 days of age has been shown to have a positive impact on dam reproductive parameters (Quintans et al., 2009) and calf LW at the age of a normal weaning would have occurred, which could be interpreted as improved welfare. At the field level, early calf weaning is considered a very useful tool to boost suckler cow performance, particularly in primiparous cows, who have elevated energy demands until they reach 5 years of age and complete their own growth (Cano et al., 2016). It is important to consider whether the wellbeing of the primiparous dam is more important than that of the calf, as both early and conventional weaning are considered to be significant stressors in the lives of beef cattle. These stressors can have direct impacts on the short-and long-term health and performance of the mother-offspring pairs. Early weaning of calves at 71 days of age led to a more intense behavioural change to cow-calf separation in multiparous compared with primiparous cows, showing increased pacing parallel to the fence and vocalizations. However, parity did not affect hematological parameters (total protein, albumin, neutrophil/basophil ratio) around early weaning (Ungerfeld et al., 2011). This study evidenced the greater behavioural response to early weaning in multiparous cows, regardless of physiological status, which should be considered during the early weaning or regrouping manipulations, in order to adapt these managements to each parity category.

The use of nose flaps at a maximum for one week in order to avoid injuries has also been suggested under European framework (Schneider et al., 2021), combined with fence-line weaning, or pen partition (preventing suckling), to enable visual and physical contact of calf and cow which facilitates final separation as an intermediate step. Haley et al. (2005) also proposed that the use of anti-suckling devices, such as nose plates for 7–14 days, could minimize the stress response of cow-calf pairs, because these devices separate the end of access to the udder and milk intake from the physical separation from the dam. Weaning the calves in two steps clearly reduced the behavioural stress response observed in abruptly weaned cows (Ungerfeld et al., 2015), which included the decrease in grazing and lying, and the increase in pacing, walking and vocalizing. The same effect was observed when the calf was weaned shortly after birth, when the bond between the cow and calf is still very strong (Ungerfeld et al., 2016). The two-step weaning method at 5–6 months of age could distributed the behavioural stress response of the calves between the two stages compared with abrupt weaning (Enríquez et al., 2010), while both methods display similar calf ADG before and after separation (Haley et al., 2005). The calf wellbeing benefits of two-step weaning with nose flaps would be greater for calves that have worn nose flaps from 71 to 84 days of age (during the breeding of their dams), compared with those fitted with them at 189 days of age (Hötzel et al., 2012). This weaning alternative also reduced the dam LW loss associated with weaning (Ungerfeld et al., 2015). Yet, some studies have described irritations of the nasal septum caused by the nose plates for 7 days, attaining lower calf LW (Lambertz et al., 2015) or similar calf LW (Freeman et al., 2021) compared with conventional weaning, suggesting the need for future studies of the design and the fitted period of the nose plate use. In this study, humoral stress indicators (cortisol and haptoglobin) in steers abruptly weaned at 7 months of age were not improved by 7-day placement of nose plates or by delaying weaning 49 days later. In addition, nose plates reduced the calf activity and vocalizations after weaning. Based on physiological markers, these authors concluded that, when weaning was accomplished in the absence of other stressors such as co-mingling and transport, it was not so stressful as it was perceived to be according to animal behaviour.

The adaptation of calves to weaning could also be facilitated by mother deprivation during the suckling period (24, 48 or 72 h at 25 and 45 days of lactation), since these calves showed fewer behavioural distress signs, diminished cortisol response and higher LW during the first days after weaning (Pérez et al., 2017). However, the potential negative impact on calf welfare caused by emotional stress as a result of maternal restriction was not considered in that study. Another common method of weaning is to move calves from pasture to a feedlot pen that is out of sight, smell, and hearing range of the dams, or to separate calves and cows into adjacent pastures with the aid of a fence-line for a certain period (Price et al., 2003), which reduces stress caused by separation by allowing them to socialize while preventing nursing. In that study, fence-line contact with cows at weaning minimized calf losses in ADG in the days following separation. In a subsequent work, Enríquez et al. (2010) compared the effects of alternative weaning methods (fence-line and nose plates) with the abrupt weaning on the behaviour of beef calves, reporting a greater ADG in fence-line than in nose plate calves.

Although fence-line calves vocalized more than the rest of calves, no clear benefits in reducing weaning distress in calves were found for the alternative weaning methods compared to abrupt weaning.

According to Orihuela and Galina (2019), separated calves should be grouped based on body size, with familiar members to discourage aggressive encounters, reduce distress and promote a social buffering effect. Additionally, calves should be offered creep feed starter rations and/or forage some weeks before separation or as soon as possible after separation to get them familiar with solid food. This familiarization can be aided by other calves that are already eating. Lisboa-Valente et al. (2012) recommended supplying creep feed to the calves during the 3–4 months before weaning to improve LW at weaning and ADG, since this practice had no effect on suckling time or frequency, or dam performance, milk yield and behaviour. Creep feeding is also extremely important in temporal weaned calves with nose plates, as this practice consistently promotes an increase in ADG during the period of temporal weaning and increases the final weaning weight of calves (Santa Cruz et al., 2022). To assure adaptation to subsequent feedlot conditions, a minimum mean creep feed intake may be reached before weaning. Accordingly, a target of 1 kg/calf/day during a 180-day lactation period may be recommended.

6. Social skills as learned behaviours

When domesticated cattle rear their young, they exhibit maternal care behaviours similar to those observed in wild ungulates (von Keyserlingk and Weary, 2007). Maternal behaviour in cattle is defined by some authors as the care of the calf by the cow, which includes strong social interactions, milk provision, nursing, and protection from danger or predation (Nevard et al., 2023). Nevertheless, close proximity is also of great importance for social and behavioural reasons, with potential transgenerational effects. During the first few months of life, the mother is the primary social contact for the newborn (Zilkha et al., 2016). The mother provides the offspring important information about the physical and social environment, feeding and care (Mora-Medina et al., 2018). A summary of the Five Domains Model at fostering mother-offspring bonding and promoting neonatal survival, adapted from Mellor (2017), is shown in Fig. 1. A mother who has formed a bond with her offspring will overtly express maternal behaviour, including suckling, and may show negative behavioural responses such as increased vocalizations and locomotor activity when separated from her young, as has it mentioned in previous sections. These responses tend to decrease when the mother cow is reunited with her calf (Solano et al., 2007; Sirovnik et al., 2020). Similarly, the bonded offspring will express affiliative behaviour towards the mother and will show marked distress when separated from her (Sirovnik et al., 2020).

Altered imprinted bonds may reduce the probability of survival in newborns and impair their behavioural development into adulthood (Galef and Laland, 2005). For example, animals raised in isolation from social groups may display increased aggression due to a lack of necessary information or social stimuli, such as maternal deprivation during the early stages. This can result in an inability to react to or interact with conspecifics in situations requiring prior knowledge (Laland, 1994; Langmore, 1998; Price and Wallach, 1999) and behavioural reactivity to stressful situations. Therefore, the quality of maternal contact may also affect the intensity of their future gregariousness as adults and their relationships with conspecifics (Damián et al., 2018a, 2018b). Calves reared (at least partially) in the presence of their mothers during the sensitive period showed a wider range of social behaviours, were more attentive to their social environment and initiated social play with an unfamiliar peer more often than those isolated from their mothers early in life and reared with other calves (Waiblinger et al., 2020).

The impact of the early complexity of the social environment on the neonatal social ontogeny varies across species. It is widely accepted that domestic animals construct responses to their environment based on experience and integration of several environmental features, including social partners. This ability to perceive the environment is not fully developed at birth but improves and varies throughout the animal's life (Veissier et al., 1998). The social relationships of an animal may change over time. During the neonatal period, the young animal primarily focuses its attention on its dam. As it integrates into the matriarchal group, it gradually expands its social environment. For instance, under semi-natural conditions, calves experience a complex social environment and engage in social interactions with other conspecifics of different ages and sexes, in addition to their dam (Kiley-Worthington and de la Plain, 1983).

Young ruminants that are reared without their mothers often exhibit abnormal oral behaviour, such as non-nutritive sucking activity (Toinon et al., 2022). Furthermore, separation from the mother can affect the social and nonsocial development of young animals because learning that occurs during the sensitive period has a long-lasting influence on the development of the individual's social and emotional behaviour (Knudsen, 2004). Wagner et al. (2012) and Buchli et al. (2017) found that calves and cows reared without their mothers had lower social skills

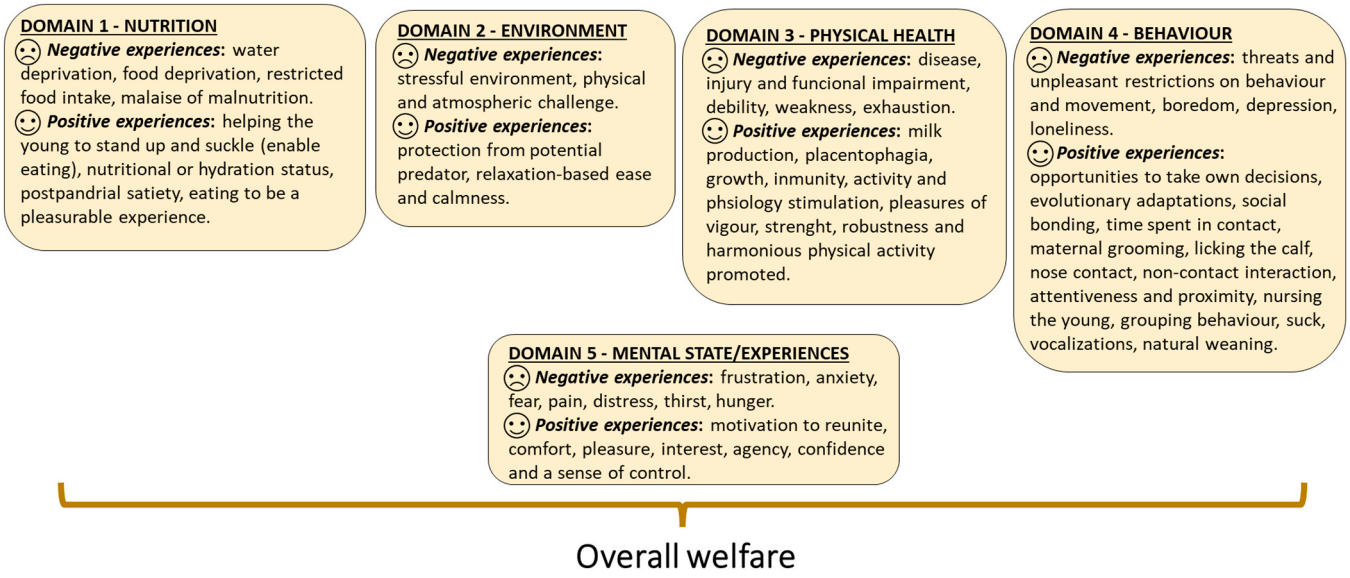

Fig. 1. The Five Domains Model at fostering mother-offspring bonding and promoting neonatal survival (adapted from Mellor, 2017).

than those reared with their mothers. This suggests that maternal deprivation can have long-lasting impacts on the social behaviour of adult ruminants. Preferential relationships between individual cows within a herd have been reported. However, less is known about the ontogeny of preferential relationships between calves and subsequent bonding behaviour. Preliminary results support individual differences in the sociality of beef calves prior to weaning, but how these may be associated with different behavioural states remains to be elucidated (Robbins et al., 2019).

The social development of young mammals can be influenced by their rearing systems, which may have long-term effects on their social behaviour and welfare. In 2014, Daros et al. (2014) provided the first evidence of a pessimistic judgement bias and a low mood in dairy calves following a conventional separation from the dam. Furthermore, the traditional individual housing for weaned dairy calves has been associated with evidence of behavioural and developmental harm, social housing improving feed intake and weight gains (Lorenz et al., 2021). In their first post-weaning grazing experience, calves were able to imitate grazing behaviour of their dams, selecting grasses throughout pasture use, and improving their welfare and performance, compared to calves separated at birth (Nicolao et al., 2020). These evidences about the impact of maternal deprivation on social development in domestic cattle are particularly important given that early separation from the dam only a few days after birth is a common farming practice in conventional dairy systems, and help to understand the current public objection to these dairy industry practices.

Yadav et al. (2009) found that multiparous mothers spent more time licking their calves than primiparous mothers, indicating a higher degree of maternal care expressed by more experienced mothers. Further research is needed to understand how to provide primiparous cows with more control over their experience during the transition period. Furthermore, it is crucial to examine social cognition during this period, including the possible impact of social support in alleviating stressors (Proudfoot and Huzzey, 2022).

Research on the effects of maternal deprivation on social ontogeny in domestic cattle is limited. Descriptive information on suckling behaviour is of practical value in assessing maternal effects on calf performance (Paranhos da Costa et al., 2006). Maternal deprivation, behavioural stress and socio-emotional development are all affected by weaning and separation, which can be a stressful experience for both mother and calf (Acevedo et al., 2005), as some afore-mentioned studies described. Research has provided valuable insights into the range of social and environmental stressors experienced by cows and calves during this process, but the need for social reorganization following the removal of adults from the group has received less attention. Changing the physical environment may affect the animals' ability to recognize group members, which may lead to social stress, so further studies should consider the effect of social disruption on the overall response of beef cattle to weaning. This can be done by comparing the response to weaning in groups that are challenged with a social separation and others that remain in their social group, or by exposing them to the new environmental features they will find after weaning, such as new social partners (Enríquez et al., 2011).

7. Research gaps for future research

The evaluation of maternal behaviour in beef cattle systems shows a huge variation in experimental conditions. Efforts are needed to standardize behavioural definitions and recording schedules across studies to enable the development of welfare-orientated management strategies. In addition, most of the studies placed more emphasis on calves' behaviour with respect to mothers' one. Restricted nursing and two-step weaning are cost-effective management practices that have been extensively researched and mostly proven to enhance beef performance. However, the economic trade-off between nutrition, milk yield, reproductive performance, cow-calf weight gains, mother-offspring bonds and emotional cues yet to be fully determined. Furthermore, contemporary society expects ethical treatment of animals. Therefore, the separation of a mother and her calf during lactation and at weaning should be considered in agreement with minimum stress on the animals. Since weaning is required to organize the herd and to increase productive performance, it is necessary to generate more information integrating wellbeing and productive aspects in the dyad at this time gap. A palatable creep feeding for calves, which eventually may be coupled with a once daily suckling restriction, may ease a more natural weaning.

Maternal behaviour studies are challenging in extensive systems, where remote assessment of behaviours through precision livestock devices may be required to evaluate maternal investment, especially in primiparous cows with unknown maternal care. This trait could be characterized by the time spent by a cow near its calf, and it could be compared with the time spent in nursing (Kour et al., 2021; Nevard et al., 2023). Besides, a combination of behavioural and physiological markers may be required to reflect maternal bonding and weaning response. Yet distress during handling of animals should be avoided, key dam behaviours reflecting oxytocin release, such as grooming and vocalizing, as well as determination of glucocorticoids in body fluids (especially feces or hair) of cows and calves could be minimally invasive approaches to evaluate whether the farm management practices permit expressing optimum mother-offspring relationships and welfare status.

Modern approaches to animal welfare science aim to provide animals with opportunities for positive experiences. In certain scenarios, animals experiencing significantly negative mental states, such as those reared in isolated and barren environments that do not provide opportunities for social and exploratory behaviours, may be unable to respond to inappropriate housing conditions despite enrichment. Therefore, social interactions may be considered as part of environmental optimization, which could be a more nuanced term rather than environmental enrichment of cow-calf systems.

In order to improve welfare, a better understanding of the underlying welfare trade-offs should be developed to target management strategies. Accordingly, the concept of agency, which refers to an animal's ability to engage in voluntary, self-generated and goal-directed behaviour that is motivated to perform, may be gathered. Assessing opportunities for animals to exercise agency and experience positive affective engagement involves considering their ability to choose, control and face challenges. In order to determine the significance of choice opportunities, the meaningfulness of options and the ability to choose across the lifespan for animals to achieve positive outcomes, it is essential that animal welfare science identifies which aspects of these factors are of paramount importance. Furthermore, it is crucial to ascertain how these opportunities can be integrated into best management practices.

In conclusion, maternal contact during the first days after parturition will be essential to guarantee the adequate establishment of mother-offspring bonding and the correct social development of young calf in beef cattle. Suckling restriction during lactation can be an excellent management tool to increase reproductive performance in cows in moderate body condition. Some alternatives to abrupt weaning, as the use of a fence-line or the two-step weaning, have been revised, although no clear benefits in reducing cow-calf distress have been found. Therefore, the ability of cows and calves to engage in voluntary, self-generated and goal-directed behaviour must be considered in the design of tailored management practices that maintain the trade-off between animal performance, cow-calf interactions, and positive mental state (Fig. 2). The Five Domains Model is proposed to develop welfare-orientated management strategies considering aspects such as maternal deprivation, behavioural stress and socio-emotional development in beef cattle.

As a final consideration, all these lessons learned about maternal bonding in beef cattle, particularly successful restricted nursing practices, may also be useful for dairy systems seeking to introduce calf nursing during lactation.

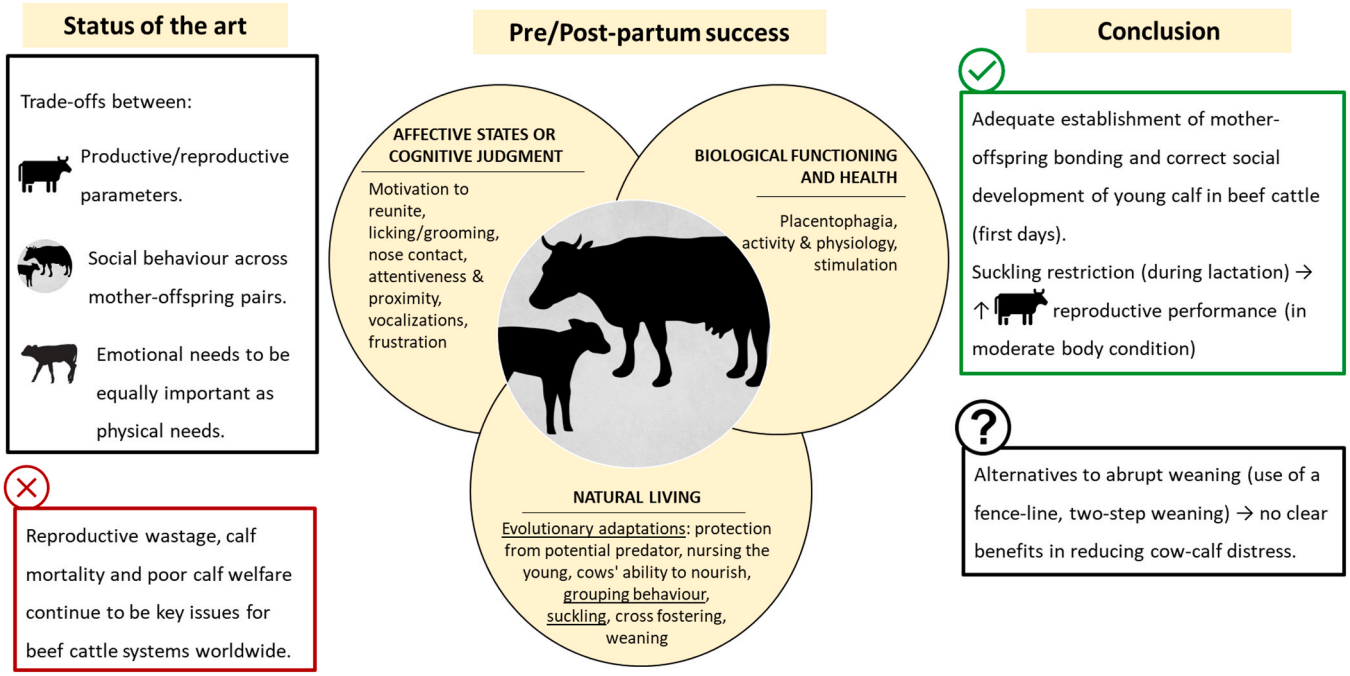

Fig. 2. Mother-offspring bonding revisited: a blueprint for the future of beef cattle farming.

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CRediT authorship contribution statement

Albina Sanz: Writing – review & editing, Writing – original draft, Resources, Methodology, Funding acquisition. **Isabel Blanco-Penedo:** Writing – review & editing, Writing – original draft, Resources, Methodology. **Graciela Quintans:** Writing – review & editing, Writing – original draft, Resources, Methodology, Funding acquisition. **Javier Álvarez-Rodríguez:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Acevedo, N., Hernández, C., Orihuela, A., Lidfors, L.M., Berg, C., 2005. Effect of restricted suckling or temporal weaning on some physiological and behavioural stress parameters in Zebu cattle (Bos indicus). Asian-Aust. J. Anim. Sci. 18 (8), 1176–1181. https://doi.org/10.5713/ajas.2005.1176.

Álvarez-Rodríguez, J., Palacio, J., Sanz, A., 2010a. Effects of nursing frequency and parity on the productive, metabolic and reproductive parameters of beef cows. Liv. Sci. 129, 111–121. https://doi.org/10.1016/j.livsci.2010.01.013.

Álvarez-Rodríguez, J., Palacio, J., Casasús, I., Revilla, R., Sanz, A., 2009a. Performance and nursing behaviour of beef cows with different types of calf management. Animal 3, 871–878. https://doi.org/10.1017/S175173110900408X.

Álvarez-Rodríguez, J., Palacio, J., Casasús, I., Sanz, A., 2010b. Does breed affect nursing and reproductive behaviour in beef cattle? Can. J. Anim. Sci. 90, 137–143. https://doi.org/10.4141/CJAS09033.

Álvarez-Rodríguez, J., Sanz, A., 2009b. Physiological and behavioural responses of cows from two beef breeds submitted to different suckling strategies. Appl. Anim. Behav. Sci. 120, 39–48. https://doi.org/10.1016/j.applanim.2009.05.004.

Batista, C., Velazco, J.I., Baldi, F., Banchero, G., Quintans, G., 2020. Effect of two energy levels during the last third of gestation of beef cows on characteristics of the placenta and offspring at birth. Arch. Latinoam. Prod. Anim. 28 (1-2), 9–18. ⟨https://ojs.alpa.uy/index.php/ojs_files/article/view/2781⟩.

Buchli, C., Raselli, A., Bruckmaier, R., Hillmann, E., 2017. Contact with cows during the young age increases social competence and lowers the cardiac stress reaction in dairy calves. Appl. Anim. Behav. Sci. 187, 1–7. https://doi.org/10.1016/j.applanim.2016.12.002.

Cano, G., Blanco, M., Casasús, I., Cortés-Lacruz, X., Villalba, D., 2016. Comparison of B-splines and non-linear functions to describe growth patterns and predict mature weight of female beef cattle. Anim. Prod. Sci. 56, 1787. https://doi.org/10.1071/AN15089.

Claramunt, M., Meikle, A., Soca, P., 2020. Metabolic hormones, grazing behaviour, offspring physical distance and productive response of beef cow grazing at two herbage allowances. Animal 14, 1520–1528. https://doi.org/10.1017/S1751731119003021.

Coria-Avila, G.A., Herrera-Covarrubias, D., García, L.I., Toledo, R., Hernández, M.E., Paredes-Ramos, P., Corona-Morales, A.A., Manzo, J., 2022. Neurobiology of maternal behavior in nonhuman mammals: acceptance, recognition, motivation, and rejection. Animals 12, 3589. https://doi.org/10.3390/ani12243589.

Cuttance, E.L., Mason, W.A., McDermott, J., Laven, R.A., 2022. Suckling behavior of calves in seasonally calving pasture-based dairy systems, and possible environmental and management factors affecting suckling behaviors. J. Dairy Sci. 105 (7), 6094–6110. https://doi.org/10.3168/jds.2021-21324.

Damián, J.P., Beracochea, F., Machado, S., Hötzel, M.J., Banchero, G., Ungerfeld, R., 2018a. Growing without a mother results in poorer sexual behaviour in adult rams. Animal 12, 98–105. https://doi.org/10.1017/S1751731117001574.

Damián, J.P., Hötzel, M.J., Banchero, G., Ungerfeld, R., 2018b. Growing without a mother during rearing affects the response to stressors in rams. Appl. Anim. Behav. Sci. 209, 36–40. https://doi.org/10.1016/j.applanim.2018.08.022.

Daros, R.R., Costa, J.H.C., Von Keyserlingk, M.A.G., Hötzel, M.J., Weary, D.M., 2014. Separation from the dam causes negative judgement bias in dairy calves. PLoS ONE 9 (5), e98429. https://doi.org/10.1371/journal.pone.0098429.

Enríquez, D., Hötzel, M.J., Ungerfeld, R., 2011. Minimising the stress of weaning of beef calves: a review. Acta Vet. Scand. 53, 28. https://doi.org/10.1186/1751-0147-53-28.

Enríquez, M.F., Pérez-Torres, L., Orihuela, A., Rubio, I., Corro, M., Galina, C.S., 2021. Relationship between protective maternal behavior and some reproductive variables

in zebu-type cows. J. Anim. Behav. Biometeorol. 9 (2), 2124. https://doi.org/10.31893/jabb.21024.
Enríquez, D.H., Ungerfeld, R., Quintans, G., Guidoni, A.L., Hötzel, M.J., 2010. The effects of alternative weaning methods on behaviour in beef calves. Liv. Sci. 128, 20–27. https://doi.org/10.1016/j.livsci.2009.10.007.
FIBL, 2023. Cow-reared calf husbandry in dairy farming. Housing Systems for species-specific rearing with mother cows and nurse cows. No. 1660 Tech. Guide 36. https://doi.org/10.5281/zenodo.7970064.
Food and Agriculture Organization (FAO) of the United Nations, 2024. FAOSTAT statistical database. Rome.
Freeman, S., Poore, M., Pickworth, C., Alley, M., 2021. Influence of weaning strategy on behavior, humoral indicators of stress, growth, and carcass characteristics. Transl. Anim. Sci. 5 (1), 16. https://doi.org/10.1093/tas/txaa231.
Galef, B.G., Laland, K.N., 2005. Social learning in animals: empirical studies and theoretical models. BioScience 55, 489–499. https://doi.org/10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2.
Gamsjäger, L., Haines, D.M., Pajor, E.A., Lévy, M., Windeyer, M.C., 2021. Impact of volume, immunoglobulin G concentration, and feeding method of colostrum product on neonatal nursing behavior and transfer of passive immunity in beef calves. Animal 15 (9), 100345. https://doi.org/10.1016/j.animal.2021.100345.
Geburt, K., Friedrich, M., Piechotta, M., Gauly, M., König von Borstel, U., 2015. Validity of physiological biomarkers for maternal behavior in cows - a comparison of beef and dairy cattle. Physiol. Behav. 139, 361–368. https://doi.org/10.1016/j.physbeh.2014.10.030.
Griffith, M.K., Williams, G.L., 1996. Roles of maternal vision and olfaction in suckling-mediated inhibition of luteinizing hormone secretion, expression of maternal selectivity, and lactational performance of beef cows. Biol. Reprod. 54, 761–768. https://doi.org/10.1095/biolreprod54.4.761.
Haley, D.B., Bailey, D.W., Stookey, J.M., 2005. The effects of weaning beef calves in two stages on their behavior and growth rate. J. Anim. Sci. 83, 2205–2214. https://doi.org/10.2527/2005.8392205x.
Hampton, J.O., Hemsworth, L.M., Hemsworth, P.H., Hyndman, T.H., Sandøe, P., 2023. Rethinking the utility of the Five Domains model. e62 Anim. Welf. 32, 1–10. https://doi.org/10.1017/awf.2023.84.
Hemsworth, P.H., Mellor, D.J., Cronin, G.M., Tilbrook, A.J., 2015. Scientific assessment of animal welfare. N. Z. Vet. J. 63, 24–30. https://doi.org/10.1080/00480169.2014.966167.
Hogan, L.A., McGowan, M.R., Johnston, S.D., Lisle, A.T., Schooley, K., 2022. Suckling behaviour of beef calves during the first five days postpartum. Ruminants 2 (3), 321–340. https://doi.org/10.3390/ruminants2030022.
Hoppe, S., Brandt, H.R., Erhardt, G., Gauly, M., 2008. Maternal protective behaviour of German Angus and Simmental beef cattle after parturition and its relation to production traits. Appl. Anim. Behav. Sci. 114, 297–306. https://doi.org/10.1016/j.applanim.2008.04.008.
Hötzel, M.J., Quintans, G., Ungerfeld, R., 2012. Behaviour response to two-step weaning is diminished in beef calves previously submitted to temporary weaning with nose flaps. Liv. Sci. 149, 88–95. https://doi.org/10.1016/j.livsci.2012.06.029.
Kent, J.P., Kelly, E.P., 1987. The effect of cow-calf separation on the maternal behaviour of the Cow (Bos taurus). Appl. Anim. Behav. Sci. 17, 370. https://doi.org/10.1016/0168-1591(87)90165-1.
Kiley-Worthington, M., de la Plain, S., 1983. The cow's world. In: The Behaviour of Beef Suckler Cattle (Bos taurus). Tierhaltung / Animal Management, vol 14. Birkhäuser, Basel. https://doi.org/10.1007/978-3-0348-6782-5_2.
Knudsen, E.I., 2004. Sensitive periods in the development of the brain and behavior. J. Cogn. Neurosci. 16, 1412–1425. https://doi.org/10.1162/0898929042304796.
Kohari, D., Sato, S., Nakai, Y., 2009. Does the maternal grooming of cattle clean bacteria from the coat of calves? Behav. Proc. 80, 202–204. https://doi.org/10.1016/j.beproc.2008.11.003.
Kour, H., Corbet, N.J., Patison, K.P., Swain, D.L., 2021. Changes in the suckling behaviour of beef calves at 1 month and 4 months of age and effect on cow production variables. Appl. Anim. Behav. Sci. 236, 1–7. https://doi.org/10.1016/j.applanim.2021.105219.
Laland, K.N., 1994. On the evolutionary consequences of sexual imprinting. Evolution 48, 477–489. https://doi.org/10.1111/j.1558-5646.1994.tb01325.x.
Lamb, G.C., Miller, B.L., Lynch, J.M., Thompson, K.E., Heldt, J.S., Loest, C.A., Grieger, D. M., Stevenson, J.S., 1999. Twice daily suckling but not milking with calf presence prolongs postpartum anovulation. J. Anim. Sci. 77, 2207–2218. https://doi.org/10.2527/1999.7782207x.
Lambertz, C., Bowen, P.R., Erhardt, G., Gauly, M., 2015. Effects of weaning beef cattle in two stages or by abrupt separation on nasal abrasions, behaviour, and weight gain. Anim. Prod. Sci. 55, 786–792. https://doi.org/10.1071/AN14097.
Langmore, N.E., 1998. Functions of duet and solo songs of female birds. Trends Ecol. Evol. 13, 136–140. https://doi.org/10.1016/S0169-5347(97)01241-X.
Lidfors, L., Jensen, P., 1988. Behaviour of free-ranging beef cows and calves. Appl. Anim. Behav. Sci. 20, 237–247. https://doi.org/10.1016/0168-1591(88)90049-4.
Lidfors, L.M., Moran, D., Jung, J., Jensen, P., Castren, H., 1994. Behaviour at calving and choice of calving place in cattle kept in different environments. Appl. Anim. Behav. Sci. 42, 11–28. https://doi.org/10.1016/0168-1591(94)90003-5.
Lisboa-Valente, É.E.L., Fonseca, M., Detmann, E., Campos-Valadares de Filho, S., Vieira-Barros, L., Francisco de Paula, N., Lopes, S.A., Majeste de Almeida, D., Soares-Martins, L., 2012. Effect of calves' supplementation on performance, nutritional and behavioral characteristics of their dams. Trop. Anim. Health Prod. 45, 487–495. https://doi.org/10.1007/s11250-012-0245-7.
Littlewood, K.E., Heslop, M.V., Cobb, M.L., 2023. The agency domain and behavioral interactions: assessing positive animal welfare using the Five Domains Model. Front. Vet. Sci. 10, 1284869 https://doi.org/10.3389/fvets.2023.1284869.
Lorenz, I., 2021. Calf health from birth to weaning - an update. Ir. Vet. J. 74 (1), 5. https://doi.org/10.1186/s13620-021-00185-3.
Malven, P.V., Parfet, J.R., Gregg, D.W., Allrich, R.D., Moss, G.E., 1986. Relationships among concentrations of four opioid neuropeptides and luteinizing hormone-releasing hormone in neural tissues of beef cows following early weaning. J. Anim. Sci. 62 (3), 723–733. https://doi.org/10.2527/jas1986.623723x.
Mellor, D.J., 2017. Operational details of the five domains model and its key applications to the assessment and management of animal welfare. Animals 7 (8), 60. https://doi.org/10.3390/ani7080060.
Metz, J., Metz, J.H.M., 1986. Maternal influence on defecation and urination in the newborn calf. Appl. Anim. Behav. Sci. 16, 325–333. https://doi.org/10.1016/0168-1591(86)90004-3.
Miguel-Pacheco, G.G., Perry, V.E.A., Hernandez-Medrano, J.H., Wapenaar, W., Keisler, D.H., Voigt, J.P., 2019. Low protein intake during the preconception period in beef heifers affects offspring and maternal behaviour. Appl. Anim. Behav. Sci. 215, 1–6. https://doi.org/10.1016/j.applanim.2019.04.003.
Mora-Medina, P., Orihuela, A., Arch-Tirado, E., Vázquez, C., Mota-Rojas, D., 2018. Metabolic changes during brief periods of ewe–lamb separation at different ages. Anim. Prod. Sci. 58, 1297–1306. https://doi.org/10.1071/AN16221.
Mota-Rojas, D., Marcet-Rius, M., Domínguez-Oliva, A., Martínez-Burnes, J., Lezama-García, K., Hernández-Ávalos, I., Rodríguez-González, D., Bienboire-Frosini, C., 2023. The role of oxytocin in domestic animal's maternal care: Parturition, bonding, and lactation. Animals 13, 1207. https://doi.org/10.3390/ani13071207.
Mota-Rojas, D., Marcet-Rius, M., Freitas-de-Melo, A., Muns, R., Mora-Medina, P., Domínguez-Oliva, A., Orihuela, A., 2021. Allonursing in wild and farm Animals: biological and physiological foundations and explanatory hypotheses. Animals 11, 3092. https://doi.org/10.3390/ani11113092.
Nevard, R.P., Pant, S.D., Broster, J.C., Norman, S.T., Stephen, C.P., 2023. Maternal behavior in beef cattle: The physiology, assessment and future directions—a review. Vet. Sci. 10 (1), 10. https://doi.org/10.3390/vetsci10010010.
Newberry, R.C., Swanson, J.C., 2008. Implications of breaking mother-young social bonds. Appl. Anim. Behav. Sci. 110, 3–23. https://doi.org/10.1016/j.applanim.2007.03.021.
Nickles, K.R., Relling, A.E., Moraes, L.E., Parker, A.J., 2021. The effect of a social facilitator cow on the distance walked and time spent walking by abruptly weaned beef calves. Anim. Prod. Sci. 61, 596–601. https://doi.org/10.1071/AN20434.
Nicolao, A., Coppa, M., Bouchon, M., Sturaro, E., Pomiès, D., Martin, B., Koczura, M., 2020. Early-life dam-calf contact and grazing experience influence post-weaning behavior and herbage selection of dairy calves in the short term. Front. Vet. Sci. 7, 600949 https://doi.org/10.3389/fvets.2020.600949.
Orihuela, A., Galina, C.S., 2019. Effects of separation of cows and calves on reproductive performance and animal welfare in tropical beef cattle. Animals 9, 223.
Orihuela, A., Mota-Rojas, D., Strappini, A., Serrapica, F., Braghieri, A., Mora-Medina, P., Napolitano, F., 2021. Neurophysiological mechanisms of cow–calf bonding in buffalo and other farm animals. Animals 11, 1968. https://doi.org/10.3390/ani11071968.
Paranhos da Costa, M.J.R., Albuquerque, L.G., Eler, J.P., Augusto II de Vasconcelos Silva, J., 2006. Suckling behaviour of Nelore, Gir and Caracu calves and their crosses. Appl. Anim. Behav. Sci. 101, 276–287. https://doi.org/10.1016/j.applanim.2006.02.006.
Parfet, J.R., Marvin, C.A., Allrich, R.D., Diekman, M.A., Moss, G.E., 1986. Anterior pituitary concentrations of gonadotropins, GnRH-receptors and ovarian characteristics following early weaning in beef cows. J. Anim. Sci. 62 (3), 717–722. https://doi.org/10.2527/jas1986.623717x.
Pérez, L.I., Orihuela, A., Galina, C.S., Rubio, I., Corro, M., Cohen, A., Hernández, A., 2017. Effect of different periods of maternal deprivation on behavioral and cortisol responses at weaning and subsequent growth rate in zebu (Bos indicus) type cattle. Liv. Sci. 197, 17–21. https://doi.org/10.1016/j.livsci.2016.12.006.
Pérez-Torres, L., Orihuela, A., Corro, M., Rubio, I., Cohen, A., Galina, C.S., 2014. Maternal protective behavior of zebu type cattle (Bos indicus) and its association with temperament. J. Anim. Sci. 92 (10), 4694–4700. https://doi.org/10.2527/jas.2013-7394.
Pérez-Torres, L., Ortiz, P., Martínez, J.F., Orihuela, A., Rubio, I., Corro, M., Galina, C.S., Ungerfeld, R., 2021. Short-and long-term effects of temporary early cow–calf separation or restricted suckling on well-being and performance in zebu cattle. Animal 15 (2), 100132. https://doi.org/10.1016/j.animal.2020.100132.
Price, E.O., Harris, J.E., Borgwardt, R.E., Sween, M.L., Connor, J.M., 2003. Fenceline contact of beef calves with their dams at weaning reduces the negative effects of separation on behavior and growth rate. J. Anim. Sci. 81, 116–121. https://doi.org/10.2527/2003.811116x.
Price, E.O., Wallach, S.J.R., 1999. Physical isolation of hand-reared Hereford bulls increases their aggressiveness toward humans. Appl. Anim. Behav. Sci. 27, 263–267. https://doi.org/10.1016/0168-1591(90)90061-H.
Proudfoot, K.L., Huzzey, J.M., 2022. A first time for everything: the influence of parity on the behavior of transition dairy cows. JDS Commun. 3, 467–471. https://doi.org/10.3168/jdsc.2022-0290.
Quintans, G., Banchero, G., Carriquiry, M., Lpez-Mazz, C., Baldi, F., 2010. Effect of body condition and suckling restriction with and without presence of the calf on cow and calf performance. Anim. Prod. Sci. 50, 931–938. https://doi.org/10.1071/AN10021.
Quintans, G., Vazquez, A.I., Weigel, K.A., 2009. Effect of suckling restriction with nose plates and premature weaning on postpartum anestrous interval in primiparous cows under range conditions. Anim. Rep. Sci. 116, 10–18. https://doi.org/10.1016/j.anireprosci.2008.12.007.
Quintans, G., Viñoles, C., Sinclair, K.D., 2004. Follicular growth and ovulation in postpartum beef cows following calf removal and GnRH treatment. Anim. Rep. Sci. 80, 5–14. https://doi.org/10.1016/S0378-4320(03)00154-4.

Radunz, A.E., Fluharty, F.L., Day, M.L., Zerby, H.N., Loerch, S.C., 2010. Prepartum dietary energy source fed to beef cows: I. Effects on pre- and postpartum cow performance. J. Anim. Sci. 88, 2717–2728. https://doi.org/10.2527/jas.2009-2744.

Robbins, J.A., Roberts, C., Weary, D.M., Franks, B., von Keyserlingk, M.A.G., 2019. Factors influencing public support for dairy tie stall housing in the U.S. PLoS One 14, e0216544. https://doi.org/10.1371/journal.pone.0216544.

Rund, L.A., Leshin, L.S., Thompson, F.N., Rampacek, G.B., Kiser, T.E., 1989. Influence of the ovary and suckling on luteinizing hormone response to naloxone in postpartum beef cows. J. Anim. Sci. 67 (6), 1527–1531. https://doi.org/10.2527/jas1989.6761527x.

Santa Cruz, R.S., Barbieri, I., Olmos, V.M., Montossi, F., Viñoles, C., 2022. Effect of temporary weaning and creep feeding on calf growth and the reproductive efficiency of their Hereford dams. Anim. Biosci. 35 (10), 1524–1534. https://doi.org/10.5713/ab.21.0384.

Sanz, A., Bernúes, A., Villalba, D., Casasús, I., Revilla, R., 2004. Influence of management and nutrition on post-partum interval in Brown Swiss and Pirenaica cows. Liv. Prod. Sci. 86, 179–191. https://doi.org/10.1016/S0378-4320(03)00116-7.

Sanz, A., Casasús, I., Villalba, D., Revilla, R., 2003. Effects of suckling frequency and breed on productive performance, follicular dynamics and post-partum interval in beef cows. Anim. Rep. Sci. 79, 57–69. https://doi.org/10.1016/S0378-4320(03)00116-7.

Schneider, C., Bieber, A., Neff, A.S., Ivemeyer, S., 2021. Separation and weaning of calves reared in cow-calf contact systems (ProYoungStock - Practice abstract). Available in: ⟨https://orgprints.org/id/eprint/42549/⟩.

Shively, T.E., Williams, G.L., 1989. Patterns of luteinizing hormone release and ovulation frequency in suckled anestrous beef cows following varying intervals of temporary weaning. Dom. Anim. Endocrinol. 6, 379–387. https://doi.org/10.1016/0739-7240(89)90032-5.

Silveira, P.A., Spoon, R.A., Ryan, D.P., Williams, G.L., 1993. Evidence for maternal behavior as a requisite link in suckling-mediated anovulation in cows. Biol. Reprod. 49, 1338–1346. https://doi.org/10.1095/biolreprod49.6.1338.

Sinclair, K.D., Molle, G., Revilla, R., Roche, J.F., Quintans, G., Marongiu, L., Sanz, A., Mackey, D.R., Diskin, M.G., 2002. Ovulation of the first dominant follicle arising after Day 21 post partum in suckling beef cows. Anim. Sci. 75, 115–126. https://doi.org/10.1017/S1357729800052899.

Sirovnik, J., Barth, K., de Oliveira, D., Ferneborg, S., Haskell, M.J., Hillmann, E., Jensen, M.B., Mejdell, C.M., Napolitano, F., Vaarst, M., Verwer, C.M., Waiblinger, S., Zipp, K.A., Johnsen, J.F., 2020. Methodological terminology and definitions for research and discussion of cow-calf contact systems. J. Dairy Res. 87 (S1) https://doi.org/10.1017/S0022029920000564.

Solano, J., Orihuela, A., Galina, C.S., Aguirre, V., 2007. A note on behavioral responses to brief cow-calf separation and reunion in cattle (Bos indicus). J. Vet. Behav. 2, 10–14. https://doi.org/10.1016/j.jveb.2006.12.002.

Stagg, K., Spicer, L.J., Sreenan, J.M., Roche, J.F., Diskin, M.G., 1998. Effect of calf isolation on follicular wave dynamics, gonadotropin and metabolic hormone changes, and interval to first ovulation in beef cows fed either of two energy levels postpartum. Biol. Reprod. 59, 777–783. https://doi.org/10.1095/biolreprod59.4.777.

Stevenson, J.S., Knoppel, E.L., Minton, J.E., Salfen, B.E., Garverick, H.A., 1994. Estrus, ovulation, luteinizing hormone, and suckling-induced hormones in mastectomized cows with and without unrestricted presence of the calf. J. Anim. Sci. 72, 690–699. https://doi.org/10.2527/1994.723690x.

Surlis, C., Earley, B., McGee, M., Keogh, K., Cormican, P., Blackshields, G., Tiernan, K., Dunn, A., Morrison, S., Arguello, A., Waters, S.M., 2018. Blood immune transcriptome analysis of artificially fed dairy calves and naturally suckled beef calves from birth to 7 days of age. Sci. Rep. 8 (1), 15461 https://doi.org/10.1038/s41598-018-33627-0.

Toinon, C., Waiblinger, S., Rault, J.L., 2022. Maternal deprivation affects goat kids' social behavior before and after weaning. Dev. Psychobiol. 64, e22269 https://doi.org/10.1002/dev.22269.

Ungerfeld, R., Hötzel, M.J., Quintans, G., 2015. Changes in behaviour, milk production and bodyweight in beef cows subjected to two-step or abrupt weaning. Anim. Prod. Sci. 55, 1281–1288.

Ungerfeld, R., Hötzel, M.J., Scarsi, A., Quintans, G., 2011. Behavioral and physiological changes in early-weaned multiparous and primiparous beef cows. Animal 5 (8), 1270–1275. https://doi.org/10.1017/S1751731111000334.

Ungerfeld, R., Quintans, G., Hötzel, M.J., 2016. Minimizing cows' stress when calves were early weaned using the two-step method with nose flaps. Animal 10, 1871–1876. https://doi.org/10.1017/S1751731116000793.

Uvnäs-Moberg, K., Johansson, B., Lupoli, B., Svennersten-Sjaunja, K., 2001. Oxytocin facilitates behavioural, metabolic and physiological adaptations during lactation. Appl. Anim. Behav. Sci. 72 (3), 225–234. https://doi.org/10.1016/S0168-1591(01)00112-5.

Veissier, I., Boissy, A., Nowak, R., Orgeur, P., Poindron, P., 1998. Ontogeny of social awareness in domestic herbivores. Appl. Anim. Behav. Sci. 57, 233–245. https://doi.org/10.1016/S0168-1591(98)00099-9.

Víchová, J., Bartoš, L., 2005. Allosuckling in cattle: gain or compensation? Appl. Anim. Behav. Sci. 94 (3–4), 223–235. https://doi.org/10.1016/j.applanim.2005.02.015.

Viker, S.D., Larson, R.L., Kiracofe, G.H., Stewart, R.E., Stevenson, J.S., 1993. Prolonged postpartum anovulation in mastectomized cows requires tactile stimulation by the calf. J. Anim. Sci. 71, 999–1003. https://doi.org/10.2527/1993.714999x.

von Keyserlingk, M.A.G., Weary, D.M., 2007. Maternal behavior in cattle. Horm. Behav. 52, 106–113. https://doi.org/10.1016/j.yhbeh.2007.03.015.

Wagner, K., Barth, K., Palme, R., Futschik, A., Waiblinger, S., 2012. Integration into the dairy cow herd: Long-term effects of mother contact during the first twelve weeks of life. Appl. Anim. Behav. Sci. 141 (3-4), 117129 https://doi.org/10.1016/j.applanim.2012.08.011.

Waiblinger, S., Wagner, K., Hillmann, E., Barth, K., 2020. Play and social behaviour of calves with or without access to their dam and other cows. J. Dairy Res. 87 (S1), 144–147. https://doi.org/10.1017/S0022029920000540.

Weary, D.M., Jasper, J., Hotzel, M.J., 2008. Understanding weaning distress. Appl. Anim. Behav. Sci. 110, 24–41. https://doi.org/10.1016/j.applanim.2007.03.025.

Wettemann, R.P., Lents, C.A., Ciccioli, N.H., White, F.J., Rubio, I., 2003. Nutritional- and suckling-mediated anovulation in beef cows. J. Anim. Sci. 81 (E suppl. 2), E48–E59. https://doi.org/10.2527/2003.8114_suppl_2E48x.

Williams, G., Gazal, O., Leshin, L., Stanko, R., Anderson, L., 2001. Physiological regulation of maternal behavior in heifers: Roles of genital stimulation, intracerebral oxytocin release, and ovarian steroids. Biol. Reprod. 65, 295–300. https://doi.org/10.1095/biolreprod65.1.295.

Williams, G.L., McVey, W.R., Hunter, J.F., 1993. Mammary somatosensory pathways are not required for suckling-mediated inhibition of luteinizing hormone secretion and delay of ovulation in cows. Biol. Reprod, 49, 1328–1337. https://doi.org/10.1095/biolreprod49.6.1328.

Yadav, A.K., Pramanik, P.S., Kashyap, S.S., 2009. Dam-calf interactions in Murrah buffaloes up to six hours post-parturition. Indian J. Anim. Prod. Manag. 25, 78–80.

Zilkha, N., Sofer, Y., Beny, Y., Kimchi, T., 2016. From classic ethology to modern neuroethology: overcoming the three biases in social behavior research. Curr. Opin. Neurobiol. 38, 96–108. https://doi.org/10.1016/j.conb.2016.04.014.