

Relationships between cow-calf sensory cues and the postpartum interval in suckler cows - Relaciones entre vínculos sensoriales vaca-ternero y duración del anestro post-parto en vacas nodrizas

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Abstract

At present, it is known that the suppressive influence of suckling on reproduction is independent of the neurosensory pathways from the teat or the udder; and that the maternal-offspring bond is the essential component of the prolonged postpartum anoestrus induced by suckling in beef cows. It has been shown that olfaction and vision are equally effective in allowing the calf identification by its dam, and that abolition of both senses attenuate the negative effects of suckling on luteinizing hormone (LH) secretion. This review indicates that the net effects of suckling or pseudo-suckling on the central regulation of tonic LH release are determined by the ability of the dam to identify the calf as its own or as unrelated. The use of several nursing systems (i.e. early weaning, temporary weaning and restricted suckling) to achieve early post-partum ovarian cyclicity are discussed. The management practices that limit suckling must also avoid close cow-calf association to reduce long postpartum intervals to first ovulation.

Keywords: Beef cattle | suckling | anoestrus | post-partum physiology

Resumen

En la actualidad, se sabe que la influencia supresiva del amamantamiento sobre la reproducción es independiente de las vías neurosensoriales del pezón o la ubre, y que el vínculo maternal vaca-ternero es el componente esencial de un prolongado anestro postparto inducido por la crianza en vacas nodrizas. Se ha

demostrado que el olfato y la vista son igualmente eficaces en la identificación de la vaca sobre el ternero, y que la abolición de ambos sentidos atenúa los efectos negativos del amamantamiento sobre la secreción de hormona luteinizante (LH). Esta revisión indica que los efectos netos del amamantamiento o pseudo-amamantamiento sobre la regulación central de liberación tónica de LH son determinados por la capacidad de la madre de identificar a su cría como propia o como ajena. Se discute la utilidad de diversos sistemas de crianza como el destete precoz, el destete temporal y el amamantamiento diario restringido para acortar el período de inactividad cíclica ovárica postparto. Las prácticas de manejo que limitan el amamantamiento deberían asimismo limitar la asociación próxima entre vaca y ternero para reducir la duración del anestro postparto.

Palabras clave: vacuno de carne | amamantamiento | anestro | fisiología del post-parto

1. Introduction

The target calving interval of suckler beef cattle have to be around 1 year and taking into account that pregnancy is an event of invariable duration (275-285 days), postpartum intervals to first ovulation (PPI) should not exceed 85 days. Following parturition, the restoration of pituitary luteinizing hormone (LH) stores occurs paralleled by concomitant increases in releasable pools of LH, which appear to peak between 2 and 4 week after calving (reviewed by Williams, 1990). Nevertheless, extended periods of acyclicity often follow. Suckling is a major effect delaying the resumption of post-partum ovarian cyclicity when nutrient intake and body reserves are not limiting factors (reviewed by Short et al., 1990; Williams, 1990; Wettemann et al., 2003).

The inhibition of episodic LH release provoked by suckling may be influenced by the secretion of hypothalamic opioid peptid β -endorphin, in response to the suckling stimulus (Malven *et al.*, 1986; Boland *et al.*, 1990). Concentrations of endogenous opioid peptides in neural tissue are affected by suckling, and it has been observed that short-term administration of opioid antagonists increase LH secretion in suckled anoestrous cows (Williams and Griffith, 1995).

The aim of this review is to describe the main sensory cues between cow-calf pair (tact, vision, olfaction and hearing) to aid designing management strategies that allow optimising reproductive performance in suckler beef cattle.

2. Sensory cues

2.1. Tact through nursing frequency

If calves are permanently weaned at birth, PPI of cows is markedly reduced relative to suckled counterparts. In an attempt to separate the effects of energy demands from lactation, presence of mammary tissue and suckling, Short *et al.* (1972) compared the postpartum intervals of suckled, non-suckled and non-suckled mastectomized cows. The suckled cows in their experiment had a PPI to first oestrus of 65 vs. 25 ($P > 0.05$) and 12 ($P < 0.01$) days for the non-suckled and non-suckled mastectomized cows, respectively. By adjusting nutrient intake to maintain constant live-weight among groups, these authors concluded that both suckling and the presence of mammary tissue without suckling could delay postpartum oestrus independent of lactation energy demands. Wettemann *et al.* (1978) provided data from range cows that support this concept and concluded that suckling intensity increased PPI, with no differences ($P > 0.05$) across natural (67.0 ± 6.4 d; $n=12$) and foster (63.12 ± 9.2 d; $n=9$) calves but greater when cow raised two calves 94.6 ± 11.5 d; $n=11$; $P < 0.05$).

Neural connections from the mammary gland have been implicated as primary relays for signals that originate with the calf and that theoretically suppress function of the LH pulse generator. However, until recently, little effort has been made to define the time course of events leading to diminished gonadotropin release or the specific sensory cues required to produce it.

Williams *et al.* (1987) initially reasoned that if the suckling process evokes a specific response from the central nervous system that alters the control of tonic LH release, an artificial stimulus such as hand milking should elicit a similar response and this should not be dependent on lactation. However, both of these hypotheses proved false, at least within a 24-h period. In the same study, these authors examined the ability of various related cues to cause acute and chronic effects on gonadotropin release and oestrus by testing the effects of suckling (negative control), non-suckling (positive control), milking eight times daily (on the basis of a previous work where calves suckled these times during a 24-h period under confinement conditions), presence of a nuzzled calf, and a combination of milking eight times daily and calf presence. They observed that cows in all but the suckled group exhibited the typical weaning response with regard to tonic LH secretion, although behavioural oestrus was not uniformly associated with these apparent ovulations.

Results of these studies confirmed a requirement for specific somatosensory input from the suckling calf in order to inhibit gonadotropin release. Further studies revealed that somatosensory effects of suckling apparently cannot be blocked by placing latex "mask" over the teats and udder of the cow and even the chronic presence of the mask and its manipulation by the calf actually may enhance the inhibiting effects of suckling on resumption of cyclicity (McVey and Williams, 1991). In this regard, mastectomized cows maintained with their natural calves with unlimited interaction exhibited anovulatory periods similar to suckled-intact cows (Viker *et al.*, 1989) and to milked cows maintained with muzzled calves with unlimited oral access to the inguinal region (MacMillan, 1983). Williams (1990) approached to this question by testing the hypothesis that the teat of the cow contains somatosensory pathways capable of modulating hypothalamic-hypophyseal function via neural input to the hypothalamus or higher brain centres. Perhaps these putative receptors distinguish between the somatosensory input of suckling vs. that of manual milk removal. In turn, only the suckling offspring could elicit a response capable of impinging fully on neural centres controlling gonadotropin secretion. If this hypothesis was correct, neural pathways that control milk ejection reflex must be different from those that suppress gonadotropin secretion. These ascending arcs must relay their message by causing release of specific neurotransmitters within a currently undefined hierarchy of neurons that eventually modulate hypothalamic function. The chronic presence of this stimulus may increase the sensitivity of hypothalamic neurons, such as those involving the opioid peptides, to estradiol negative feedback. This in turn would enhance opioid or adrenergic tone (via norepinephrine) and decrease spontaneous firing of the pulse generator. In this hypothetical model, multiunit electrical activity may be suppressed, GnRH remains sequestered and pituitary LH release is inhibited.

In order to study the role of mammary somatosensory pathways in suckling-mediated anovulation, Williams *et al.* (2001) conducted a serial of experiments to evaluate endocrine, lactation and reproductive features of an experimental animal model employing complete neural disconnection of the udder in beef cows and then to utilize the validated model. Crossbred beef cows were randomly assigned to suckled/sham-operated control, weaned (calf removed)/sham-operated control, and suckled/mammary-denervated groups between days 14 and 18 post-calving. Additional cows were divided into weaned or suckled unoperated control groups. Complete mammary anaesthesia was attained in all denervated cows but sensory perception was not affected in sham-operated controls. Although acute sham-surgery attenuated weaning-induced increases in LH pulse and ovulation frequency, normal responses to weaning

were observed in unoperated controls as well as in sham-operated controls 1 year later. Finally, denervated-suckled cows that had been denervated before conception exhibited LH secretion patterns and mean PPI was similar to those of intact-suckled cows. In contrast, the intact-weaned group responded within 2 weeks postcalving with an increased frequency of LH pulses, and PPI were shortened compared to the other groups. The conclusion was that suckling-mediated anovulation is not dependent upon mammary somatosensory cues.

In addition, suckling frequency and duration is associated with suckling-mediated anovulation. However, in two studies where cows nursed calves from 2 to 23 times daily for the first 6 weeks old, variation in suckling frequency by single calves was unrelated to rebreeding activity in the dam (Williams *et al.*, 1984b; Day *et al.*, 1987). Table 1 summarizes the suckling behaviour observed in several studies performed in a broad rank of environments, breeds and calf managements.

Table 1. Suckling behaviour in beef cattle

Breed/purpos (suckling frequency)	Calf age (days)	Calf feeding	Calf management	Suckling Bouts (times/day)	Suckling duration per bout (min)	Suckling duration (min/day)	Source
Beef (AS) ¹	0-180	Milk and pasture	Range	4.6 (0-30 d) ² 4.8 (60-90 d) 3.0 (150-180 d)	ND ³	38.8 (0-30 d) 55.9 (60-90 d) 30.7 (150-180 d)	Drewry <i>et al.</i> (1969)
Beef (AS)	0-100	Milk	Confinement	Rank 4.4-5.5	Rank 8.5-11.4	Rank 45.9-53.4	Lewandrowski <i>et al.</i> (1983)
Beef (AS)	3-53	Milk	Confinement	12.5 (d 3-11), 8.5 (d 17-39), 7.5 (d 45-53).	8 (d 3-11), 9 (d 17-53).	100 (d 3-11), 76.5 (d 17-39), 67.5 (d 45-53).	Williams <i>et al.</i> (1984b)
Beef (AS)	0-120	Milk and pasture	Range	5.0 (rank 1 to 11) (0-120 d)	ND	46 (rank 11 to 99) (d 0-120)	Odde <i>et al.</i> (1985)
Dairy (AS)	Day 45	Milk	Confinement	4.3 (3 calves) 3.7 (1 calf)	12.2 (3 calves) 7.8 (1 calf)	50.4 (3 calves) 29.3 (1 calf)	Pérez <i>et al.</i> (1985)
Beef (AS)	52-167 (Exp. 1), 17-80 (Exp. 2).	Milk and pasture.	Range	8.6 (d 52), 4.5 (d 167) (Exp.1); 11.3 (d 17), 3.8 (d 80) (Exp. 2).	8.7 (d 52-167) (Exp. 1), 8.4 (d 17-80) (Exp. 2).	64 (d 52), 44 (d 167) (Exp. 1), 80 (d 17), 42 (d 80) (Exp. 2).	Day <i>et al.</i> (1987)
Beef (AS)	0-180	Milk and pasture	Range	4.3	9.9 (0-180 d)	ND	Lidfors <i>et al.</i> (1988)

Beef (AS)	1-123	Milk and pasture	Range	ND	14 (d 1) 12 (d 7 and 65) 10 (d 123)	ND	Lidfors <i>et al.</i> (1994)
Zebu and crossbred (dual purpose, RS) ⁴	0-180	Milk, pasture and concentrate	Range	3.8 (Zebu), 3.2 (crossbred)	2.8 (Zebu), 2.3 (crossbred)	23.6 (Zebu), 18.8 (crossbred)	Das <i>et al.</i> (2001)
Crossbred <i>B.taurus</i> x <i>B.indicus</i> (dual purpose, RS)	0-100	Milk, pasture and concentrate (Exp. 1) Milk and pasture (Exp. 2)	Range	3.4 (Exp. 1) 2.0 (Exp. 2)	ND	20.8 (Exp. 1) 32.3 (Exp. 2)	Pérez-Hernández <i>et al.</i> (2002)
Dairy (AS)	5-45	Milk and pasture	Range	Rank 4-5	ND	Rank 29-32	Zimmermann <i>et al.</i> (2003)

2.1.1. Nursing systems

Some of different management strategies to address long PPI in suckler cattle are (modified from Galina *et al.*, 2001):

- a) Early weaning a few days postpartum, or weaning at 3-5 months;
- b) Partial weaning for 24, 48, 72 or 96 h (followed or not by induction of ovulation and oestrus synchronization);
- c) Restricted suckling once- or twice-daily for 30-60 min, or overnight;
- d) Delayed suckling for 6 to 8 h after milking (dual purpose cows).

Under natural conditions, most cows only allow their own calves to suckle (Lewandrowski *et al.*, 1983). Therefore, it is possible that only cow's own calf can attenuate gonadotropin release (Williams and Griffith, 1995). Nonetheless, as explained before, when a cow adopts an additional calf, PPI is extended markedly (Wettemann *et al.*, 1978). Williams and Griffith (1995) tested the hypothesis that exteroceptive cues responsible for the suppression of LH secretion are specifically attributable to the dam's own calf and, therefore, are a product of the maternal offspring bond. The latter authors found that removal of natural calves from cows resulted in the expected increases in serum LH concentrations and pulse frequency within 48 h, and suckling by unrelated calves every 6h for 4 days did not prevent these increases. However, suckling by cow's own calf at 6 h intervals maintained the suppressed pattern of LH release typical of suckled anovulatory females. Moreover, the onset of luteal activity in weaned and unrelated-suckled groups were nearly identical, both of

them being markedly reduced compared with cows suckling their own calves.

Early weaning can be a valuable tool to reduce PPI (Bellows *et al.*, 1974), but the economics favour its use only under adverse conditions due to the high cost and intensive labour associated with early-weaned calves (Williams, 1990; Blanco *et al.*, 2005).

Partial weaning is normally used when it is followed by induction of ovulation and oestrus synchronization. The success of this practice *per se* is dependent on the postpartum stage and duration of calf removal, obtaining better results with 72 h than with 48 h, but even further time (96 h) is needed according to Shively and Williams (1987) to provoke ovulation in acyclic cows. Other authors found no improvement in reproductive performances with this calf management (Wright *et al.* 1987; Bonavera *et al.*, 1990).

Several studies (Acosta *et al.*, 1983; Shively and Williams, 1989; Short *et al.*, 1990; Williams, 1990; Zalesky *et al.*, 1990; Lamb *et al.*, 1999) have found that **restricted suckling** twice-daily is not enough to reduce PPI, and only once-daily suckling is useful as a calf management strategy to improve reproductive performance. However, in cows with moderate condition (around 2.5 on a 1-5 scale), restricted suckling twice a day has advanced the resumption of ovarian cyclicity (Revilla, 1997; Sanz *et al.*, 2001), but this practice has no effect when cows suffer negative energy balance in early lactation (Sanz *et al.*, 2006). The behavioural trends of the previous study revealed as well that the number of licks from cows to calves was significantly higher in cows suckling once- than twice-daily (55.5 ± 16.1 vs. 22.5 ± 4.8) to the detriment of licking their-selves (0.1 ± 0.1 vs. 2.7 ± 0.8), although both suckling systems allowed raising calves without impairing the maternal bond (Alvarez *et al.*, 2006).

Other factors may contribute to the inhibitory effects of suckling on postpartum reproduction, and time of suckling during the solar day has been proposed as one of those factors. Two reports using *Bos Taurus* cattle in South Africa have indicated that calves were less likely to suckle from 22:00 h to dawn (2.2% of suckling events observed) during the period when ovulation and anoestrus were ending (Stewart *et al.*, 1993a), and that nighttime suckling maintained the anovulatory state longer than daytime suckling (22 vs. 57% of cows cycling at 30 days post-partum, Stewart *et al.*, 1993b). Nevertheless, Gazal *et al.* (1999) found in *Bos indicus* x *Bos taurus* cows that although mean number of suckling bouts per 24 h was greater for the *ad libitum* suckled group than either night- or day-suckled groups (5.9 ± 0.4 vs. 3.8 ± 0.1 and 3.9 ± 0.3 , respectively),

suckling episodes were not confined to a particular period during the 24-h period, occurring at a periodicity of 4 to 6 h, and PPI did not differ among groups. These results questioned the previous conclusions in *Bos Taurus* in which eliminating nighttime suckling reduces PPI.

Therefore, the suckling systems discussed previously, which alter the frequency and duration of nursing, may be conditioned by the physical contact that allows recognition between dam and young. Calves maintained with mastectomized cows exhibited chronic "pseudo-suckling", which was defined as positioning by the calf in the reverse parallel or perpendicular position, bunting, oral manipulation of skin of the leg or flank, and characteristic head to tail contact between cow and calf. If cow-calf interaction is restricted mechanically (Williams *et al.*, 1987) or spatially (Viker *et al.*, 1993; Stevenson *et al.*, 1994), eliminating direct oral contact with the inguinal region, the anovulatory state is not maintained. Hence, the direct oral contact with the inguinal region and, therefore, the mere perception of being suckled may be sufficient for prolonging the period of anovulation (Williams and Griffith, 1995).

Hoffman *et al.* (1996) provided evidence that the presence of a nonsuckling calf prolongs the PPI of its dam, but not to the same extent as a continuously present calf allowed *ad libitum* suckling. Extended PPI in cows with presence of a nonsuckling calf indicated that calf presence without suckling is a factor that limits the onset of ovarian cyclicity in suckled cows. Release of cortisol is independent of suckling, because the return of a nonsuckling calf (without suckling) increased cortisol.

The afore-mentioned effects of suckling stimulus on the resumption of cyclicity interact with cow's nutritional status (Warren *et al.*, 1988; Schillo, 1992; Browning *et al.*, 1994; Jolly *et al.*, 1995; Sanz *et al.*, 2004a; Sanz *et al.*, 2004b), and may be more marked in dual purpose and/or crossbred than in hardy breeds (Marongiu *et al.*, 2002; Sanz *et al.*, 2003; Sanz *et al.*, 2005). Moreover, PPI is generally longer in *Bos indicus* compared to *Bos Taurus* (Chenoweth, 1994).

2.2. Vision, olfaction and hearing

The role of vision and olfaction in suckling-mediated inhibition of LH secretion has been broadly investigated in cattle (Williams and Griffith, 1995; Griffith and Williams, 1996; Williams *et al.*, 1996). Olfaction plays a critical role in the development of maternal selectivity, with a minimum time required for sensitization of 5 min,

with up to 5 h of effect in the absence of the calf (Hudson and Mullord, 1977).

However, cows rendered anosmic after the maternal bond has been established, recognized their calves visually, allowed them to suckle and continued to exhibit an inhibited pattern of LH secretion in a suckled environment (Griffith and Williams, 1994).

Neither blindness nor anosmia in cows nursing their own calves caused disinhibition of gonadotropin secretion (Griffith and Williams, 1996). In this study, at 3 weeks after calving cows were separated from their calves and allowed to be suckled by their own calf or an unrelated calf every 6 h for 6 days. Blind, olfactory-intact cows recognized their calves by smell, and anosmic, sighted cows recognized their calves by sight. Cows that were both blind and anosmic, and were forced to suckle unrelated calves, exhibited increases in pulse frequency of LH for 6 days. When both senses were abolished, cows could not identify the calf as their own or as unrelated, behaving as cows with weaned calves and having the typical increase in LH secretion. Both weaning (total absence of calf-related stimuli) and suckling by an unrelated calf results in a rapid escape from the inhibitory influence previously maintained by the cow's own calf. Thus, the maternal-offspring bond is essential for the suckling-induced anovulation, and cows can use both olfactory and visual cues to identify own and unrelated offspring.

A sequence of estrogen priming, genital stimulation (oxytocinergic effect) and olfaction may be the primary communication link that drives the full establishment of maternal behavioural responses in the sheep, and although no data are available, it is assumed that similar events characterize the development of maternal behaviour in cows (Williams and Griffith, 1995). Le Neindre (1984) proposed from a behavioural point of view that cows recognize their young through olfactory and visual cues, while calves first use visual and hearing cues, discriminating dam's moos from unrelated ones (Barfield *et al.*, 1994).

In sheep, the recognition through olfaction is believed to be based upon the offsprings' individual olfactory signature that emanates from their body coat, specifically from the anal region. Many of the odours from the anal region of most animals have been associated with pheromones that are specifically detected by the vomeronasal organ and that influence a variety of reproductive activities from sexual maturation to maternal behaviour (reviewed by Booth, 2006).

In cattle, maximum maternal responsiveness is critical at parturition, when there is an increased opioid effect (Williams and Griffith, 1995),

which is maintained during early lactation in suckled beef cows, suppressing LH secretion (Malven *et al.*, 1986; Whisnant *et al.*, 1986). Although no relationship between intra-cerebral oxytocin release and suckling-induced inhibition of gonadotropin secretion has been found in cattle, there is an inverse relationship between factors facilitating maternal behaviour and factors modulating gonadotropin secretion (Silveira *et al.*, 1993).

Suckling stimulates peripheral oxytocin release and increases opioid tone in cattle; however, cows forced to suckle unrelated calves showed reduced frequency of peripheral oxytocin release and rapid resumption of pulsatile LH secretion, relative to cows suckling their own calves. Hence, suckling by unrelated calf might not maintain a hypothalamic opioid tone that can inhibit neuronal stimulation of GnRH secretory neurons (Williams and Griffith, 1995). These authors hypothesized that there is a close linkage between physiological variables that modulate maternal behaviour, opioidergic tone, and the LH pulse generator during suckling-mediated anovulation in cows.

In summary, the suppressive influence of suckling is independent of the neurosensory pathways within the teat or the udder (Williams *et al.*, 1984a; Cutshaw *et al.*, 1991; McVey and Williams, 1991; Viker *et al.*, 1993; Williams *et al.*, 1993), and that the maternal-offspring bond is the essential component of the prolonged postpartum anoestrus induced by suckling in beef cows (Silveira *et al.*, 1993; Lamb *et al.*, 1997). It has been shown that olfaction and vision are equally effective in allowing the calf identification by its dam (Griffith and Williams, 1996), and abolition of both senses attenuate the negative effects of suckling on LH secretion (Stagg *et al.*, 1998). Although partial weaning provokes an increase in pulsatile LH frequency (Shively and Williams, 1987), several authors question its usefulness to induce ovarian cyclicity in postpartum cows, unless at the same time progestogen-based treatments are applied (Troxel *et al.*, 1980; Walters *et al.*, 1982; Smith *et al.*, 1983; Williams *et al.*, 1987).

The management practices that limit suckling must also limit close cow-calf association to reduce deep postpartum anoestrus. Bearing in mind that pre- and post-partum nutrition are primary factors determining the interval to first post-partum ovulation (Stagg *et al.*, 1998; Sanz *et al.*, 2004a), the suckling strategy may exert the greatest effect on cows with an intermediate body condition score at calving (2.5 on a 1-5 scale) and meeting maintenance requirements throughout lactation. Moreover, in case that restricted suckling at short intervals (once- or twice-daily for 30-60 min) needs to be applied, the isolation from visual and olfaction cues between cow-calf pair may improve reproductive performance of beef herds.

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