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Suckling and reproduction in dairy buffalo: A review

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ABSTRACT

Following parturition, a longer period of anovulation and anestrus occurs in suckled buffalo. Delayed onset of ovarian activity is attributed to different factors, viz. suckling, nutrition, season, parity, body condition score (BCS) and milk yield. This causes serious economic constraints in the efficiency of milk production. Even though uterine involution begins soon after parturition, failure of follicular development is primarily due to apparent lack of luteinizing hormone (LH). Resumption of LH pulsality is limited by the depletion of anterior pituitary LH stores during early postpartum period (calving to 20 days postpartum), while it is suppressed during days 20 through 35 postpartum due to suckling. Endocrine regulation of this behavior and its relationship with hypothalamic gonadotropin releasing hormone (GnRH) secretion has been facilitated using techniques that assess the functioning of pituitary gland in response to GnRH challenges exogenously. Based on the economic importance of buffalo as an integral part of livestock agriculture in Asia, a model of suckling-induced postpartum acyclicity has been discussed.

Key words: Buffalo, Luteinizing hormone, Postpartum anestrus, Reproductive performance, Suckling

The main aim of buffalo calf operations is to obtain one calf per buffalo per year (Usmani *et al.* 1990). Therefore, after the gestation period of approximately 310 days, buffalo have to conceive within 85–115 days after calving. Resumption of cyclicity is delayed during early postpartum period. Factors, viz. suckling, nutrition, season, body weight, milk yield, breed and parity, contribute to a delay in the onset of ovarian activity (Qureshi *et al.* 1999, Nanda and Kumar 2000, Vijh *et al.* 2008). Suckling mediated acyclicity remains as one of the foremost problems associated with buffalo management in developing countries (Tiwari *et al.* 1995, Hassan *et al.* 2000, Jha 2002). It is an exteroceptive stimulus that governs the reproductive cycle in females (McNeilly 1988). Biological impact of suckling in farm species vary from total blockage of ovulation in dairy animals to little or no effect on breeding ewe resulting in low reproductive efficiency and leading to huge economic losses to the dairy industry (Foster 1988, Arya and Madan 2001b, Birthal and Jha 2005). Although, cow holds an intermediate position within this ranking, buffalo than cow, having the merits of higher milk fat percentage, better feed conversion efficiency, resistance to diseases, adaptability to harsh conditions and high economic importance (Nanda *et al.* 2003) in this part of the world, exhibit relatively poor reproductive efficiency during early postpartum period, and thus, commands extraordinary attention as a model to study the influence of suckling on female reproduction. In this article, postpartum acyclicity and/or subsequent resumption of cyclicity in postpartum buffalo, with focus on suckled buffalo is reviewed.

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Current managemental practices

In the developing countries, 99% of the dairy buffaloes are owned by marginal to medium scale land holding farmers and are merely used as a source of extra income; and they manage them under backyard system. They are fed green berseem, wheat straw, paddy straw, etc. supplemented with grazing and/or fodder by the cut-and-carry-system and concentrate to meet their maintenance, production and reproduction requirements and are used as multi-purpose animals. Suckling of dairy buffalo is a common practice in rural areas for milk letdown (Banerjee 2002, Verma 2005) and calf feeding (Sastry and Thomas 2005). The frequency of suckling ranges from 6–8 times a day (Hogberg 2003) after which hand milking is done twice a day. Buffalo calves are generally weaned at 2–3 months of age (Abdalla 2003).

Postpartum anestrus in buffalo with comparison to cow

Hormonal control of postpartum ovarian activity: A continuous hypophysiotropic signal is required for the maintenance of ovarian activity in female animals after parturition. In the early eighties, the concept was well provided in the primates, humans and cattle (Pohl *et al.* 1983, Williams *et al.* 1996). Inadequate evidence in buffalo suggests that pulsatile LH secretion is a prerequisite for resumption of normal cyclicity during early postpartum period (EL-Wishy 2007b). LH is an essential intrinsic property of hypothalamic GnRH neurons (Vazquez-Martinez *et al.* 2001). Regulation of GnRH secretion into the adenohypophysis involves a close coordination of hypothalamus, pituitary and gonads. During the late pregnancy and up to early postpartum period, the hypothalamic-hypophyseal-ovarian axis is under continuous negative feedback effect of gonadal hormones, thereby reducing its sensitivity to protein hormones (FSH and LH) and hence delays the onset of ovarian activity (Usmani *et al.* 1985, El-Wishy 2007a). This results in suppression of FSH release and depletion of LH stores in anterior pituitary (Palta and Madan 1995, Palta and Madan 1996). The available information indicated that although FSH release is suppressed, depletion of releasable pituitary LH stores appeared to be a critical factor for resumption of cyclicity postpartum (Chauhan and Singh 1979, Abul-Ela *et al.* 1988, Singh *et al.* 2007). So the follicles fail to ovulate and undergo atresia due to apparent lack of LH release (Spicer *et al.* 1986, Kang and Brar 2003, El-Wishy 2007b).

Luteinizing hormone suppression during early postpartum period: The LH concentrations remain either fairly constant (Leung *et al.* 1986, Kamonpatana 1984) or increase through days 2–20 in buffalo (Palta and Madan 1995, Palta and Madan 1996) and days 10 through 15 in cow (Moss *et al.* 1985, Nett *et al.* 1988) postpartum. While the pituitary estradiol–17-ß levels were reported to increase through days 15 postpartum in cow (Nett *et al.* 1988), slightly longer period (days 18 postpartum) in buffalo was also reported by Tiwari *et al.* (1995). This indicated suppression of LH pulsality during early postpartum period not influenced due to lack of estradiol–17-ß concentrations. Both in cow (95%) as well as buffalo ($\geq$ 90%), the LH stores are greatly reduced at calving (Galhotra *et al.* 1981) due to depletion of anterior pituitary LH stores during late gestation (Palta and Madan 1996, Nett *et al.* 1987). The LH concentrations gradually increase through days 20–35 postpartum (Palta and Madan 1995) in buffaloes compared to days 20 through 30 in cow (Labhsetwar *et al.* 1964, Lamming *et al.* 1981, Moss *et al.* 1985, Nett *et al.* 1988). So LH release is diminished in late pregnancy (Irvin *et al.* 1981, Jaeger *et al.* 1987, Palta and Madan 1996), remains low during early postpartum period (Galhotra *et al.* 1981) and gradually increase with time postpartum (Palta and Madan 1995). Therefore, Nett *et al.* (1987), Nett *et al.* (1988), Palta and Madan (1995), Palta and Madan (1996) reported that suppression of LH release is primarily due to depletion of LH stores in anterior pituitary in both the species during early postpartum period, although the release is early in cow. Secretion of LH is a pre-requisite for augmentation of ovarian activity during early postpartum period (Singh *et al.* 2005b). Early release of LH in cow than buffalo resulted in early onset of cyclicity in the former (Dobson and Kamonpatana 1986). Ali *et al.* (1980) observed longer postpartum interval to first estrus in buffalo (87.0±11.0 days) compared to cow (62.5±4.9 days).

Factors influencing postpartum ovarian activity in buffalo

Prolonged postpartum acyclicity and anestrum are major sources of economic loss to buffalo breeders in terms of annual calf crop production and milk yield. Delayed onset of ovarian activity during early postpartum period is attributed to various factors including suckling, nutrition, body weight, milk yield, parity, season etc.

Suckling: The postpartum ovarian activity is greatly influenced by suckling both in dairy and swamp buffalo. In dairy buffalo, ovulation induced early in weaned (40.0±6.0 days) than suckled buffalo (56.0±9.0 days, Barkawi 1993). Suckled buffalo took significantly ($P < 0.05$) longer period to exhibit their first postpartum estrus (71.7±11.1 days) compared to their non-suckled counterparts (Arya and Madan 2001b). Similar observations in other studies (El-Fouly *et al.* 1976, Singh *et al.* 2005b) indicated prolonged postpartum anestrus in suckled buffalo. For optimum reproduction, a buffalo is expected to show its first estrus by 60 days postpartum (Chauhan *et al.* 1977). Delayed onset of reproductive cyclicity prolonged the conception time (Singh *et al.* 2005a). Arya and Madan (2001b) reported longer conception interval in suckled (98.0±17.5 days) than weaned buffalo (70.3±9.6 days). Furthermore, the frequency, intensity or duration of suckling has been considered to influence the length of postpartum anoestrus. Exaggerated stimuli delay the occurrence of first postpartum estrus in most mammals including cow (McNeilly 1988). Additional 2–3 suckles per day are required to lengthen the postpartum anoestrus in bovine (Williams 1990). More studies are clearly required on the regulatory role of suckling frequency and intensity on the postpartum rebreeding in buffalo.

Similarly in swamp buffalo, the onset of first postpartum estrus is significantly prolonged in suckled than in weaned ones (Wang and Chou 1985). Early initiation of cyclicity in weaned buffalo is consistent with other reports (Jainudeen *et al.* 1984, Wongsrikeao *et al.* 1990). The basic mechanism by which suckling lengthens postpartum ovarian activity will be reviewed later in this manuscript.

Body weight and body condition score: The energy status of animals is generally reflected by their body weight and BCS (Ruegg *et al.* 1992). Body weight and BCS are important predictors of potential reproductive efficiency. Loss of body weight during the early postpartum period is an indication of negative energy balance in buffaloes (Bhalaru *et al.* 1981, Lubis and Fletcher 1987). Therefore, adequate nutrition and management are recommended during the last trimester of pregnancy to enhance body weight recovery immediately after calving (Prakash *et al.* 1990). Ali and El-Sheikh (1983) reduced the length of acyclic periods through early ovulation in buffalo weighing > 400 kg (104 days) than weighing < 400 kg (206 days).

Similarly, BCS at parturition influenced the duration of anestrus periods. Ribeiro *et al.* (1997) reported that a score of 3.5 at calving is required to improve reproductive performance of buffalo. Thin buffalo (63 days) compared to moderate body condition (47 days) took longer time for their first postpartum ovulation (thin = 1 and obese = 5, Hegazi *et al.* 1994b). Similar observations were reported by Baruselli *et al.* (2001). Wongsrikeao *et al.* (1990) indicated that swamp buffalo having a BCS of ≤ 2.8 during the early postpartum period had reduced ovarian activity. A BCS of 3–3.75 is must for optimum reproduction (Charnetzki 1999).

Season: Season of the year affects the reproductive efficiency in buffalo especially in the Indian subcontinent where extreme climates are seen. The reproductive performance of dairy buffalo reaches a nadir during hot months (April-June) when most buffalo (80%) have quiescent ovaries (Nanda *et al.* 2003). Prolonged postpartum acyclicity was observed in buffalo calved during summer (62.0±6.0 days) than those during winter (50.0±6.0 days) thereby, enhancing the reproductive performance in the later (Qureshi *et al.* 1998). Seasonal variation corresponds with temperature extremes, green fodder availability and/or quality and photoperiodism.

Effect of heat stress: High ambient temperatures contribute to lower reproductive potential of buffalo (Singh *et al.* 2000). Singh and Nanda (1993) reported a significantly delayed ovarian activity in buffalo calved from February to May (116–148 days) compared to rest of the year (38–64 days) after calving. Results of other studies (Borghese *et al.* 1993, El-Fouly *et al.* 1977) are consistent to that of previous one (acyclic periods of 76.0±15.0 days in summer calvers compared to 25.0±4.0 days for autumn calvers). Keeping buffalo cool by wallowing, water sprinklers or shade improved the conception rates (80% vs 13%) (Roy *et al.* 1968, Srivastava *et al.* 1978, Nanda *et al.* 2003). Thus, extreme hot weather hampered the early onset of ovarian activity.

Nutrition: Optimum nutrition is vital to enhance reproductive efficiency in buffalo. Most buffalo cease ovarian activity during hot summers due to poor nutrition (Kaur and Arora 1984). Negative energy balance reduces the availability of glucose and increases mobilization of body reserves (Grimard *et al.* 1995). Perera (1999) reported, feeding balanced ration to buffalo improved fertility in summer. Feeding of low plane than high plane of energy during the pre-partum period reduced pituitary gonadotropin content, delayed resumption of LH pulsality and prolonged the anestrous periods (75 vs 66 days, Hegazi *et al.* 1994a). The quality of feed governs profitable buffalo breeding. El-Keraby *et al.* (1981) reduced acyclic periods in buffalo fed succulent green fodder (29.0±1.0 days) than dry fodder (34.0±2.0 days). Lack of green fodder availability round the year limits the reproductive performance of buffalo. Therefore, adequate feeding strategies need to be formulated to exploit round the year potential. Regular supplementation of urea molasses multi-nutrient blocks (UMMB) for 60 days before calving enhanced early onset of postpartum estrus as well as improved pregnancy rates in anoestrus non-pregnant buffalo (40% more) and also increased milk production (8% more, Nanda *et al.* 2003). Inadequate nutrition aggravates the effect of suckling, thereby affecting postpartum reproduction in buffalo.

Photoperiodicity: The onset of ovarian activity is inversely related to the duration of day light exposure. Singh *et al.* (2000) reported that fewer buffaloes (26–31%) exhibit estrus under long day length. The pineal gland secretes melatonin that is sensitive to photoperiodism. Administering 18 mg melatonin once daily induced estrus in buffalo (Hassan *et al.* 2000). Hence, reduced sexual activity coincides with increasing day length.

Although, the overall response of seasonal breeding patterns seemed to have significant impact on acyclic and anestrus periods (Shah *et al.* 1989, Suthar and Kavani 1992, El-Wishy 2007b), it is necessary to determine the role of management practices, relative humidity, milk yield and suckling, other than season that might contribute to reduced buffalo reproduction.

Parity: A controversial debate has been observed between the relationship of parity and interval to first postpartum ovulation. Until late seventies, El-Fouly *et al.* (1976), Porwal *et al.* (1981) observed a nonsignificant impact of parity on the post partum ovarian activity. Ali and El-Sheikh (1983), Devaraj and Janakiraman (1986) and Barkawi (1984) reported enhanced post partum reproductive performance in pleuriparous buffalo than primiparous buffalo due to high LH pulse and frequency in the former attained through proper growth and maturity. A high percentage of corpora lutea were palpable in old buffalo compared to their young counterparts (80 vs 68%) during the early post partum period (Devanathan *et al.* 1987). Chaudhry *et al.* (1987) demonstrated early onset of post partum cyclicity in pleuriparous (27 days) than that in primiparous buffaloes (39 days). Again in the nineties, Suthar and Kavani (1992) reported, parity did not seem to influence the reproductive performance in buffalo. The controversy still persists due to wide variation between parities and acyclic periods in different studies.

Milk yield: Reproductive performance is compromised through delayed ovarian activity and reduced conception rates by the demands of high milk yield. Increased milk production is associated with delayed involution of uterus resulting in protraction of interval to first post partum estrus with significant correlation between the 2 traits (Reddy *et al.* 1986). El-Azab *et al.* (1984) reported that buffalo having high milk yield (> 8.0 kg/day) than with low milk yield (< 8.0 kg/day) had longer acyclic periods (107.0±36.0 vs 77.0±30.0 days). In other studies as well, significant correlation was found between total milk production and interval to first ovulation (El-Fouly *et al.* 1976, Qureshi *et al.* 1999). Selection for milk yield increased blood concentrations of prolactin, and decreased insulin, a hormone antagonistic to lactation and important for normal follicular development. These endocrine changes promote high milk yield but may potentially be detrimental to other physiological functions, such as reproduction (Nebel and McGilliard 1993).

Other factors: Several minor factors like individual genetic variation, stress, dystocia, uterine infections, non-descript breeds, involution of uterus, diseases and twin birth influence the post partum reproductive performance (Ali and El-Sheikh 1983, Usmani *et al.* 2001, Ghuman *et al.* 2002). Usmani *et al.* (2001) delayed involution of uterus in buffalo with uterine infections (46.0±5.0 days) than in normal cases (36.0±7.0 days). Retention of fetal membranes, abortions and uterine prolapse contribute to a delay in uterine involution by 5–14 days compared to normal animals (Chauhan *et al.* 1977). Early involution is associated with early onset of ovarian activity (Perera *et al.* 1987). Once ovarian activity resumes, conception occurs rapidly. Significant correlations of r = 0.45 in Nagpuri (Pargaonkar and Kaikini 1974) and r = 0.70 in Murrah buffaloes (Roy and Luktuke 1962) were reported between uterine involution and service periods.

Follicular development during post-partum period

The development of follicles is negligible on the day of parturition but increases progressively at days 15 through 35 post partum (Agrawal *et al.* 1979, Singh *et al.* 1979). Baruselli *et al.* (1997) reported a smaller diameter of ovulatory follicle (1.3±0.1 cm) during first 15 days than during late post partum (1.6±0.2 cm). The formation and maturation of graafian follicle during early post partum period could be inhibited due to depletion of anterior pituitary LH stores (Dobson and Kamonopatana 1986). While Singh *et al.* (1979) did not find any impact of season on resumption of follicular activity, Capitan and Takkar (1988) opined that follicular development is definitely dependent upon seasonal variation. They found that buffalo, which calved during winter resumed early follicular development (29.4 days) than those calved in summer (34.1 days). Effect of heat stress in delaying the follicular activity could be implicated (Nanda *et al.* 2003). Resumption of follicular activity has also been delayed due to carry over effect of pregnancy (Usmani *et al.* 1990). Singh *et al.* (1979) reported decreased follicular activity in ipsilateral ovary (21%) compared to contralateral (40%) to the gravid horn. This could be attributed to a difference in blood flow from uterine horn due to early involution of gravid horn (El-Wishy 2007a). Usmani *et al.* (1990) observed early follicular development in weaned (22.3 days) than suckled buffalo (30.2 days). Suckling stimulus delays the maturation of follicle and results in poor follicular development (Tiwari and Pathak 1995). A profound effect of suckling in delaying the follicular activity could be through suppression of LH release.

Current understanding of suckling as regulator of post partum rebreeding in buffalo

During early post partum period there is depletion of LH stores from anterior pituitary since the receptors for LH are not present (Palta and Madan 1995) and is not influenced by suckling. Therefore, even complete weaning could not initiate LH release immediately after parturition. Once the LH stores are replenished around 20 days post partum in dairy buffalo (Palta and Madan 1995) and days 30 in swamp buffalo (El-Wishy 2007a), absence of LH pulses becomes dependent on suckling (Singh *et al.* 1979, Usmani *et al.* 1985, Table 1). Maximum pituitary stores and releasable pools of LH occur between days 15–35 after calving due to formation of LH receptors (Honnapagol *et al.* 1993). Complete weaning than suckling at 25–35 days post partum increased follicular

Table 1. LH and FSH concentrations (ng/ml) during various stages in suckled and weaned buffalo

Stage	LH		FSH		Source
	Suckled	Weaned	Suckled	Weaned	
10 days pre-calving	0.34±0.3	0.4±0.1	N. D.	N. D.	(Kamonpatana 1984)
At 3 days post partum	0.9±0.1[a]	0.9±0.2	31.1±2.8[a]	24.7±4.0	(Arya and Madan 2001a)
3 to 20 days post partum	0.9±0.2[a]	1.3±0.03	35.5±2.3[a]	32.7±1.7	(Palta and Madan 1995, Arya and Madan 2001a)
20 to 35 days post partum	1.4±0.1[b]	2.2±0.1	32.4±4.5[b]	30.1±3.5	(Palta and Madan 1995, Arya and Madan 2001a)
35 to 90 days post partum	1.5±0.2[b]	1.3±0.2	35.7±1.5[b]	38.3±1.5	(Palta and Madan 1995, Arya and Madan 2001a)
GnRH induced gonadotropin release	14.3±2.7	26.2±4.3	41.9±11.1	40.5±7.5	(Arya and Madan 2001a, Singh *et al.* 2006)

[a] Depletion of LH stores from anterior pituitary (suckling independent)

[b] Depletion of LH stores during the period of suckling dependency

N. D. Not Detected

receptor concentrations for LH (Singh *et al.* 2006) and FSH (Arya and Madan 2001a) followed by ovulation within few days (Razdan *et al.* 1981) and shortened the duration of post partum anestrus in buffalo. Usmani *et al.* (1990) observed longer anestrus intervals in suckled (61.0±3.0 days) than weaned buffalo (42.0±4.0 days). These observations suggested that suckling decreased LH release in the anterior pituitary during the post partum period (15–35 days) and reduced the reproductive performance in buffalo.

Suckling induced LH suppression: The hypothalamic GnRH content in suckled and non-suckled buffalo do not alter between days 25–35 post partum but exogenous GnRH induced LH release is definitely suppressed in the former (Singh *et al.* 2006). Therefore, after replenishment of anterior pituitary stores, suckling suppressed pituitary LH release by inhibiting GnRH discharges from hypothalamus. Sharma and Nanda (1994) demonstrated that the sensitivity of hypothalamus to the negative feedback effect of gonadal steroids is increased through suckling stimulus resulting in tonic inhibition of LH. As the post partum interval increases, the hypothalamus becomes less sensitive to suckling stimulus by evading from the negative feedback effect of ovarian steroids (Tiwari *et al.* 1995).

Effect of suckling on pituitary gonadotropins and gonadal steroids

Luteinizing hormone: Suppression of LH release is the most notable feature associated with anestrus. Arya and Madan (2001a) observed nonsignificant changes in the basal LH levels during the early post partum period between weaned (0.9±0.2 to 1.3±0.2 ng/ml) and suckled (0.9±0.1 to 1.5±0.2 ng/ml) buffaloes. The concentration of bioactive LH increased during the days 20 through 35 post partum than at calving (Palta and Madan 1995). Singh *et al.* (2006) reported that total LH release in response to exogenous GnRH was significantly higher in non-suckled (26.2±4.3 ng/ml) than that in suckled buffalo (14.3±2.7 ng/ml). Limited studies in buffalo revealed that endogenous periodic LH concentrations were suppressed due to *ad lib.* suckling (Perera *et al.* 1992).

Follicle stimulating hormone: In dairy buffalo, studies have been conducted to study the variations in FSH levels due to weaning. The mean FSH levels in suckled (35.7±1.5 ng/ml) and weaned (38.3±1.5 ng/ml) Murrah buffaloes did not differ significantly during early post partum period although values for suckled animals were low (Arya and Madan 2001a). Palta and Madan (1995) observed a similar response on pituitary responsiveness to exogenous GnRH induced FSH release at days 2 through 35 post partum. FSH did not appear to be a limiting factor in the resumption of cyclicity yet a threshold level is required below, which the ovarian activity might be suppressed. Clearly, a further delineation of the mechanism by which suckling influences FSH release in buffalo is required.

Prolactin: Arya and Madan (2001c) reported mean prolactin levels before and after milking as 150.6±31.4 ng/ml and 234.6±36.3 ng/ml in suckled and 118.3±26.8 and 323.0±43.2 ng/ml in weaned buffalo, respectively, up to 90 days post partum. Post milking values showed a 6–fold increase in the prolactin levels in weaned compared to suckled buffalo, suggesting that milking rather suckling is a more potent stimuli for prolactin release. The milk yield was however, not affected by suckling and/or milking stimuli. The role of suckling on prolactin release in buffalo still requires elucidation.

Estrogen: Significantly higher concentrations of estradiol–17-ß in weaned buffalo (117.5 pg/ml) than in their suckled counterparts (85.3 pg/ml) were reported by Tiwari *et al.* (1995) immediately after parturition. A similar but nonsignificant trend was also observed by Arya and Madan (2001b) in suckled (16.8±3.7 pg/ml) compared to non-suckled buffalo (18.4±5.5 pg/ml). Thereafter, the estrogen levels fluctuated till the commencement of ovarian cyclicity (days 18 in non-suckled and days 40 in suckled buffalo). The continuous presence of suckling stimulus influenced the functional aspects of ovary in the postpartum period.

Progesterone: During early post partum period, low progesterone values (0.4 ng/ml for suckled and 0.5 ng/ml for weaned buffaloes) were reported by Tiwari *et al.* (1995). While suckling did not seem to influence the progesterone profiles, decrease in progesterone concentration potentiates a rise in LH levels (Hafez *et al.* 2000) and regulates the hypothalamo-pituitary-ovarian axis from anestrus to cyclicity.

Testosterone: The average testosterone concentrations for suckled and non-suckled Surti buffalo were 0.62 ng/ml and 0.79 ng/ml respectively (Tiwari *et al.* 1993). The levels were comparatively higher to that reported for Murrah buffalo (Singh and Madan 1985). This variation in testosterone content could merely be a breed difference. Higher concentrations of testosterone in non-suckled buffaloes reflect better development of follicle due to its role in manifestation of estrus (Shemesh and Hansal 1974).

Current model on suckling induced acyclicity in buffalo

The buffalo mammary gland is primarily supplied through inguinal nerve (Dyce *et al.* 1996). Sensory stimulation of teat through suckling lead to production of distinct reflexes through spinal tract. In post partum buffalo, perikarya of GnRH producing cells are localized in pre-optic area (POA) whereas perikarya of cells containing endogenous opioid peptides (pro-opiomelanocortin) are found in the media basal hypothalamus (MBH) where pro-opiomelanocortin (POMC) gene is expressed (Sharma and Nanda 1994). POMC perikarya in the MBH (few of which have estradiol receptors) project axons to the POA, synapse directly with GnRH cells and inhibit the release of GnRH neurons from POA (Leshin *et al.* 1988). The chronic presence of suckling stimulus increases POMC mRNA levels in the MBH as well as

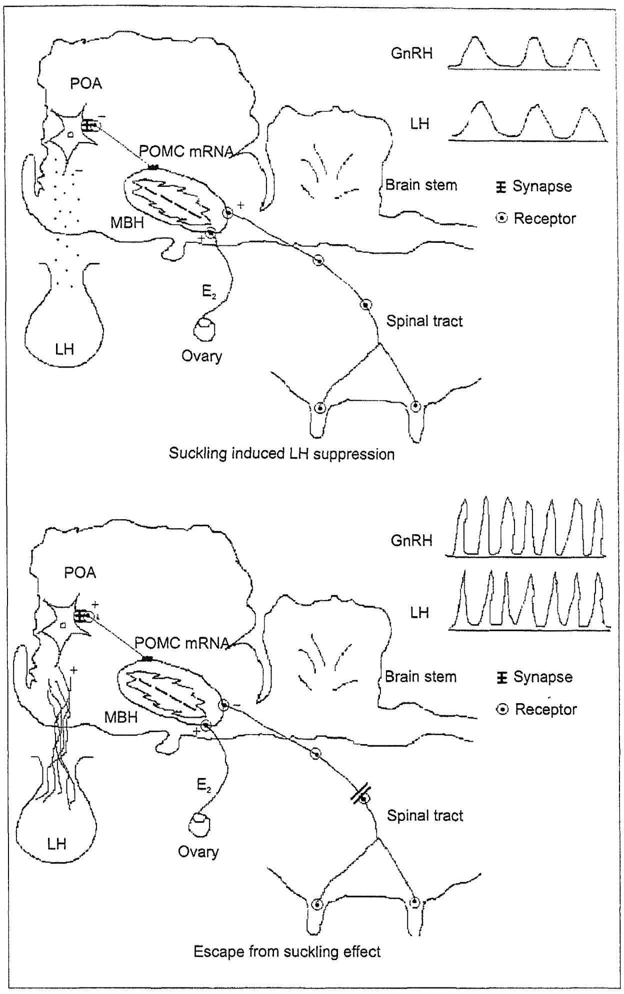

Fig. 1. Schematic representation of suckling induced acyclicity in buffalo. The star shaped object represents a GnRH neuron; the round shaped object with serrations represents POMC mRNA. Abbreviations represent the following: Pro-opiomelanocortin (POMC), media basal hypothalamus (MBH), pre-optic area (POA), Estradiol 17-b (E_2).

sensitivity of endogenous opioid peptides (pro-opiomelanocortin) to the negative feedback effect of estradiol and sequestered the GnRH discharges from POA resulting in suppression of LH release. The POMC and gonadal steroids operate in parallel to suppress LH release (Sharma and Nanda 1994). While POMC appear to reduce the amount of LH per pulse, steroid hormone decreases the frequency of LH pulse and hence, delays in the onset of cyclicity (Fig. 1).

Possible effects of suckling on calf health and lactation length

Effect on calf survival and growth rate: Suckling is encouraged in buffalo to enhance calf survival rate (Dobson and Kamonpatana 1986). The health and growth rate of buffalo calves are likely to be better if they are fed whole milk rather than milk substitutes and/or milk replacers. Whole milk compared to milk replacers, is nutritionally appropriate and has more specific protective properties (Bourne 1977). It contains antibodies and non-specific agents that coat the mucosal surface of gut. These antibodies provide passive immunity to the calf from various infectious diseases (Ryle and Orskov 1990). Low mortality rate in suckled (5.2%) compared to bucket fed buffalo calves (12.3%) was reported in a study by Ugarte and Preston (1972). Milk fed through bucket resulted in less availability of these antibodies and cell types to coat the gut mucosa as they remain attached to the surface of bucket, thereby increasing the mortality rate in the later. Further, the live weight gain was more (0.5 to 0.9 kg/day) in suckled calves than those fed milk replacers (0.35 to 0.5 kg/day). A similar, rather slower growth rate was observed (Maree *et al.* 1974, Usmani and Inskeep 1989) up to late post partum period. Adequate feeding and good management practices could be correlated for better growth rate in the previous study. Suckling is encouraged to enhance calf survival and growth rate, but unfortunately this practice also attenuates the neuroendocrine signals required for post partum resumption of ovarian activity (Nanda *et al.* 2003). Although, limited suckling enhances the onset of ovarian activity in buffalo but protocols still require refinement (Usmani *et al.* 1985).

Effect on lactation performances: Sastry and Tripathi (1998) observed longer lactation lengths for suckled buffalo (306 days) than for weaned buffalo (283 days). A longer lactation in buffalo suckling their own calf compared to weaned ones have been reported previously (Knowles and Edwards 1983) suggesting that the lactation length may be influenced by the strength of the bond between the dam and calf. A more rapid evacuation of udder of buffalo cow suckling their calf through increased oxytocin production might reduce the involution of udder epithelial cells in late lactation (Gorman and Swanson 1967). More studies on maternal offspring relationship including roles for lactation yield are needed.

Manipulation of suckling stimulus to enhance reproductive efficiency

Alterations in suckling regimes: Wongsrikeao *et al.* (1990) reported that limited and/or restricted over *ad lib.* suckling reduced the onset of first estrus (75.0±8.0 days, 78.0±7.0 days vs 92.0±10.0 days, respectively). Different suckling regimes, viz. limited suckling, limited suckling and suckling limited to twice daily, were used to hasten first post partum ovulation in buffalo. The first post partum ovulation significantly prolonged in *ad lib.* suckled (82.0±11.0 days) compared to restricted suckled buffalo (69.0±10.0 days) and enhanced the reproductive efficiency in the latter (Nordin and Jainudeen 1991).

Early weaning: Early weaning can be a valuable tool, but the economics favour its use only under adverse conditions due to high cost associated with intensive labour. Jainudeen *et al.* (1984) reported that early weaning (30 days) initiated early resumption of cyclicity (42.0±8.0 days vs 55.0±10.0 days) thereby reducing the post partum interval to first estrus and improving the reproductive performance of buffalo.

Bull-cow interactions: Continuous exposure of buffalo cow to a fertile bull is likely to detect more estrous buffalo before 70–90 days post partum to achieve annual calving interval (El-Wardani *et al.* 1998). Abdalla (2003) reported that full time rather than limited exposure reduced the interval from calving to first estrus in suckled buffalo (39 days vs 59 days). Presence of male along with other management factors seemed to contrast the effect of suckling stimulus through early resumption of ovarian activity.

Temporary calf removal: Temporary calf removal for 72 h resumed cyclicity about 19 days earlier in weaned compared to suckled animals (Usmani *et al.* 1990). Post partum interval to resumption of follicular development, first rise in milk progesterone and first palpable corpus luteum were longer for suckled buffalo.

Endocrine therapy: One therapeutic approach for overcoming delayed ovarian activity in suckled buffalo was achieved through administration of GnRH or its analogues (Arya and Madan 2001a). Shah *et al.* (1990) improved the pregnancy rates in buffaloes through use of GnRH (100 µg) at 14 days post partum. Calving to conception interval significantly ($P < 0.05$) decreased in treated buffaloes (62.1±13.6 days) compared to control animals (77.7±11.4 days). Other studies have directed the use of prostaglandin treatment to enhance post partum reproduction in buffaloes. Most buffaloes (88%) express estrus after administration of prostaglandin (Sahasrabudhe and Pandit 1997). Although the conception rates improved by prostaglandin treatment (Rao and Rao 1979, Chauhan *et al.* 1982, Rao and Rao 1988, Chohan, 1998), the relationship between prostaglandin secretion and hypothalamic-hypopyhseal-pituitary axis during anestrus period is not well defined especially during the absence of corpus luteum. Further, it must be reiterated that nutritional status and body condition score of buffalo at the time of hormonal treatments govern the efficacy of pharmacological methods to improve fertility.

Current trends and future prospects for optimum reproduction in suckled buffalo

The fundamental research regarding suckling-induced anestrous is likely to continue. These studies will enhance our knowledge with respect to neuroendocrine control mechanisms, therapeutic interventions and genetic up-regulation of hypothalamic-pituitary endocrine production. Further research is needed to study the interaction of body condition, lactation yield, dam health, metabolic status and suckling with hypothalamic and ovarian functioning. This is because the effects of suckling, independently, yielded varying degrees of anestrous that contribute the most to variability in economic efficiency of the post partum buffalo. Research conducted over the years has tended to focus on the extremes of populations. Several examples from published and unpublished data suggest that most buffalo ovulate within 60 days and rebreed within 120 days after calving in spite of intensive suckling. Now the question arises, what are the basic mechanisms that terminate normal signalling of hypothalamic-hypophyseal portal system during chronic suckling in buffalo? A simple way to study these systems is through remote sensing of multiunit brain electrical activity from distinct regions within the hypothalamus of buffalo.

Development of technology and transfer: The production of milk and sale of buffalo and/or calves are the main source of economic returns for rural farmers in developing Asian countries (Roy 2002). However, technology development has not affected buffalo production to the degree that it has influenced other agricultural products (Birthal and Jha 2005). Most dairy farms surveyed do not adopt the basic principles recommended by scientists to maximize profitability and optimize reproductive efficiency in the buffalo herd. Failure to transfer, and adoption of technology by agricultural producers resulted in different economic losses, equivalent to about 26% of the attainable output in buffalo (Birthal and Jha 2005). Based on current trends, adoption of more sophisticated techniques is needed to control problems of suckling-induced acyclicity. Many, if not most, reproductive management practices prescribed by researchers are viewed by a majority as not needed, not feasible and/or uneconomical. Hence, poor reproductive performance in buffalo is governed by geographical, environmental, biological and socio-economic traditions of the people who raise them (Nanda and Nakao 2003).

Suckling is a natural adaptation but considered a problem particularly when viewed from the perspective of production agriculture. The main intent of this review was to discuss the role of suckling on post partum reproduction in dairy buffalo. Recent development on post partum rebreeding in buffalo has provided valuable and interesting information into the control of suckling-induced anestrus. Good management practices, viz. early weaning, bull-cow interaction, calf removal along with endocrine interventions help in reducing the impact of suckling on reproductive performance in buffalo.

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