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REVIEW [REVISIÓN]

BIOSTIMULATION IN CATTLE: STIMULATION PATHWAYS AND MECHANISMS OF RESPONSE

[BIOESTIMULACIÓN EN BOVINOS: VÍAS DE ESTÍMULO Y MECANISMO DE RESPUESTA]

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SUMMARY

The stimulatory effects of males on female cyclic activity through genital stimulation, pheromones or other less defined external cues, is known as biostimulation. In cattle, biostimulation may be provoked with vasectomized bulls, testosterone-treated cows, or testosterone-treated steers. Several studies reported that exposure of cows to bulls decreases postpartum anestrous interval in cows, and advances puberty in heifers. Moreover, male exposure before the breeding period or estrous synchronization treatment, can improve breeding performance. However, stimulation pathways and mechanisms of response to male effect in cattle are not fully understood. The objective of this review is to summarize and discuss the principal advances in our understanding of biostimulation in cattle.

Key words:Anestrus; male effect; puberty; postpartum.

RESUMEN

El efecto estimulatorio de los machos sobre la actividad cíclica de las hembras mediante el estímulo genital, feromonas, u otras señales externas, es conocido como bioestimulación o efecto macho. En vacas, la bioestimulación puede llevarse a cabo con la utilización de toros vasectomizados, vacas ó novillos androgenizados. Muchos estudios han demostrado que la exposición a machos disminuye el intervalo de anestro posparto de las vacas, y adelanta el inicio de la pubertad en vaquillonas peripuberales. A su vez, la exposición a machos en forma previa a un entore ó a la aplicación de un tratamiento de sincronización, mejora la eficiencia reproductiva. Sin embargo, las vías de estímulo y los mecanismos de respuesta a la bioestimulación en vacas, han sido poco evaluados. El objetivo de ésta revisión es sintetizar y discutir los principales avances en la comprensión de la bioestimulación en vacas.

Palabras claves: anestro; efecto macho; pubertad; posparto.

INTRODUCTION

Anestrus is defined as the absence of estrous cycles. In livestock industry, one of the main objectives is to decrease the duration of anestrus periods in order to obtain a more sustainable production. In beef and dairy cattle, this imply: 1) reducing the age at first service (Patterson *et al.*, 1992) and 2) decreasing the interval to resumption of cyclic activity during postpartum (Yavas and Walton, 2000; Peter *et al.*, 2009). The first one determines a reduction in the age at first calving, and so it is necessary to achieve optimal lifetime productivity (Lesmeister *et al.*, 1973; Day and Grum, 2005). The second allows early postpartum re-breeding (80-85 d postpartum) in order to maintain a 365 d calving interval (review: Crowe, 2008). Many alternatives are available to achieve those goals (e.g. nutritional managements; review: Hess *et al.*, 2005). Although hormonal treatments appear to be highly effectives (Diskin *et al.*, 2002; Patterson *et al.*, 2003), growing concern in the development of *"clean, green and ethical"* techniques, in particular those linked to *"reduced usage, if not elimination, of practices that depend on drugs, chemicals and exogenous hormones"* (Martin *et al.*, 2004; Martin, 2009), have determined that the evaluation of other management tools, like socio-sexual stimuli, became more important during recent years.

Biostimulation (male or bull effect) can be defined as the stimulus provoked by the presence of males, which induce estrous and ovulation through genital stimulation, pheromones, or other external cues

(Chenoweth, 1983). In 1901, Heape proposed that the presence of males stimulates the onset of puberty in several mammals (cited by Izard, 1983). In cattle, Neresjan in 1959 reported that postpartum anestrus interval is reduced if cows are exposed to vasectomized bulls. Since then, many studies reported that male exposure stimulates cyclic activity in postpartum cows (Zalesky *et al*., 1984; Alberio *et al*., 1987; Rekwot *et al.,* 2000a; Landaeta-Hernández *et al*., 2004, 2006; Berardinelli and Joshi, 2005a; Tauck, 2008). However, there is scarce information on the stimulant effect of males on the advancement of puberty in heifers (Izard and Vandenbergh, 1982a; Roberson *et al.*, 1991; Rekwot *et al.*, 2000b; Lima *et al.*, 2008; Oliveira *et al.*, 2009). The objective of this review is to summarize and discuss the principal advances on the understanding of biostimulation in cattle.

STIMULATION PATHWAYS

The stimulus provoked by the introduction of the males can act through different pathways, including olfactory, visual and auditory signals (Ungerfeld, 2007). In small ruminants, olfactory cues are undoubtedly major components in the response of females to male effect, but recent work have determined that maximum ovulatory response is obtain even when females are in full contact with males, which indicates that non-olfactory signals are complementary or synergistic with chemical cues (Delgadillo *et al.,* 2009). A complementary explanation may be that chemical signals act –at least partially– as an individual signature (Wyatt, 2010). When it comes to olfactory cues, pheromones were the first ones considered as male effect mediators in ewes and pigs (Rekwot *et al.*, 2001), and, in several species, it has been documented the influence of male signals on puberty onset in prepubertal females (mouse: “Vandenbergh effect”: Vandenbergh, 1983; ewes: O’Riordan and Hanrahan, 1989; gilts: Thompson and Savage, 1978). Pheromones refer to airborne chemical substances released into the urine, feces or cutaneous glands, which cause a behavioural and/or specific endocrine reaction when they are perceived by a recipient of the same specie (Izard, 1983; Rekwot *et al.*, 2000a). In most mammals, pheromones are behavioral modulating substances (signals), and affect both maternal and reproductive behaviors, as the alarm and aggression responses (Swaney and Keverne, 2009). However, as discussed below, at least in small ruminants the type of signal exerted by the male does not strictly adjust to the pheromone definition (Delgadillo *et al.*, 2009), which determined that the term “olfactory cue” (Chanvallon and Fabre-Nys, 2009) or “chemical signal” (Ungerfeld *et al.*, 2008) instead of “pheromone” is sometimes prefered.

The detection and integration of olfactory signals in mammals occurs through the main olfactory system (MOS) and accessory olfactory system (AOS) pathways. Grus and Zhang (2008) developed the hypothesis that environmental cues are perceived by MOS, while specie-specific signals (e.g. pheromones) may be perceived by AOS. However, inactivation of the projections from the accessory olfactory bulb in ewes did not affect the response to ram odor (Cohen-Tannoudji *et al.*, 1989). In contrast, destruction of the main olfactory epithelium and inactivation of the cortical amygdale blocked the endocrine response to male odor, but did not affect the response to male presence (Gelez and Fabre-Nys, 2004). In turn, AOS neural pathways are activated during the response to ram odor in ewes (Gelez and Fabre-Nys, 2004). Thus, chemical signals associated to male effect may mainly act through MOS and not AOS, and, as mentioned before, sensory signals other than olfaction appear to be involved in the response to males (review: Gelez and Fabre-Nys, 2006).

Learning and effects of previous experience in the response to the male effect in small ruminants are other characteristics that differentiate these signals from the classic definition of pheromone (Delgadillo *et al.,* 2009). Unlike in adults and experienced ewes, the exposure to a ram or to ram odor in sexually naive ewes did not determined activation of AOS (Chanvallon and Fabre-Nys, 2009). Young and sexually naive females generally have poor responses to male effect, and those responses are not improved by prior sexual experience (Chanvallon *et al.*, 2010a). However, in adult and sexually inexperienced ewes, pre-exposure to rams influenced positively the response to the ram effect (Chanvallon *et al.*, 2010b). Endocrine response to ram odor in young and adult sexually naive ewes was reduced in contrast to the experienced ewes, but the response to the further exposure to males did not differ between naive and experienced females (Gelez *et al.*, 2004). Similarly, prior exposure to rams is not a pre-requisite for the endocrine response to ram exposure (Hawken *et al.*, 2008).

In cattle, males’ excretory products and cervical mucus from estrous females enhance ovarian function, both in postpartum cows (Berardinelli and Joshi, 2005a; Wright *et al.*, 1994) and prepubertal heifers (Izard and Vandenbergh, 1982a). Moreover, vaginal products can advance the luteolysis induced by the administration of PGF2α (Izard and Vandenbergh, 1982b). This demonstrates the existence of some sort of “pheromone” on females’ body fluids, which may exert a female-female effect, even though it remains unknown if stimulus provoked by females act similarly as products secreted by males (Wright *et al*., 1994).

Berardinelli and Joshi (2005a) evaluated resumption of cyclic activity in postpartum, anovular, primiparous cows exposed to bulls or to excretory products of bulls. They introduced cows for 12 h daily during 70 d in pens in where males were kept during the other 12 h of the day. Anestrus postpartum length did not differ between females exposed to males or to excretory products of males, and was shorter than in non-exposed females. On the other hand, continuous exposure (24 h/d) of primiparous cows to male urine using a urine delivery system during 64 d did not affect postpartum anestrus interval compared to cows not exposed to urine (Tauck and Berardinelli, 2005; Tauck *et al*., 2006). Therefore, authors concluded that in cattle urine may not be the biological agent by which pheromones are delivered, or that continuous urine exposure may "overstimulate" females. However, in contrast with these results, in prepuberal beef heifers, oronasal treatment with bull urine during 7 wk determined an increase of 35% in females that began cyclic activity in contrast to heifers treated with water (Izard and Vandenbergh, 1982a). Moreover, a 7 d length oronasal treatment with bull urine induced an increase in LH mean concentrations in postpartum dairy cows (Baruah and Kanchev, 1993), but these authors did not include information on resumption of cyclic activity. Therefore, although Tauck *et al*. (2006) explanation cannot be discarded, according to our knowledge there is no previous information on possible "overstimulation" of females by chemical signals action. Thus, even though positive effect of biostimulation in postpartum cows and prepubertal heifers may be at least partially mediated by olfactory cues, intensity of that stimulus and other communication pathways (visual and auditory) should affect cattle response.

MECHANISMS OF RESPONSE

In small ruminants, the first response to male exposure is an increase in LH pulse frequency that can be observed even a few minutes after males are introduced (reviews: Martin *et al.*, 1986; Walkden-Brown *et al*., 1999; Ungerfeld, 2007). The increase in LH pulse frequency is also observed in ovariectomized ewes, which means that the change on steroid negative to positive feedback is not the only mechanism involved in the response (Martin *et al.,* 1983). Although the first ovulation occurs approximately 48 h after the initial exposure to males, at least in ewes this ovulation is not associated with estrous behavior (Signoret, 1991), and in approximately half of the females the resulting corpus luteum is abnormal and regresses 6-7 d later (Gelez and Fabre-Nys, 2006; Ungerfeld, 2003). Estrus is normally displayed 17 to 25 d after the introduction of males.

In cattle, unlike in small ruminants, physiological mechanisms involved in the response to biostimulation are not well understood, and most studies have been performed with postpartum cows. In this section we aim to summarize the scarce information available on the responding mechanism of cows to biostimulation.

LH and ovarian response

Custer *et al.* (1990) did not observe any change in LH secretion pattern in primiparous beef cows exposed to bulls during postpartum period, although biostimulation reduced the interval to first estrus. In contrast, Fernandez *et al.* (1996) observed an increase in LH mean concentration and pulse frequency in postpartum cows during continuously or intermittently exposure to epididectomized bulls since 30 d postpartum. In dairy cows, Roelofs *et al.* (2007) found increased mean and basal LH concentration, and LH pulse frequency during 8 h fenceline contact with males. Similarly, as mentioned before, oronasal treatment with bull urine during 7 d enhanced LH mean concentrations in postpartum dairy cows (Baruah and Kanchev, 1993). In more recent studies, acute (5 h daily for 9 d; Tauck *et al.,* 2010a) exposure to males of primiparous, suckled cows since 67 d postpartum determined an increase in LH pulse frequency compared to females exposed to steers, but no differences were found on mean, baseline, amplitude and duration of LH pulses between treatments. Moreover, none of the females resumed cyclic activity during the experiment (Tauck *et al.,* 2010a). It should be noticed that sampling scheme was different between the above mentioned experiments: while Custer *et al.* (1990) began blood samples 10 d after males were introduced, and sampled at weekly intervals, on the other studies the first blood sample was taken at the moment (Baruah and Kanchev, 1993; Fernandez *et al.,* 1996), 1 d (Roelofs *et al.,* 2007) or 1 h (Tauck, 2008; Tauck *et al.,* 2010a) before male introduction, and were repeated daily (Tauck *et al.,* 2010a). On the other hand, Fernandez *et al.* (1996) took blood samples every three days. Those differences in sampling scheme may explain why Fernandez *et al.* (1996) observed an LH response that was undetected by other researchers. In that sense, unlike in small ruminants, the ovulating response of cows is widespread on time. Therefore, endocrine changes induced by males may also differ between animals, making difficult to detect changes due to the different times in which those may be observed. In summary, most of the information indicates that positive effects of biostimulation in cattle would be mediated by an activation of the hypothalamic-pituitary-ovarian axis, but the moment in which the response appears may differ from that observed in small ruminants.

The ovarian response of ewes to the introduction of rams is well documented (Atkinson and Williamson, 1985; Martin *et al.,* 1986; Ungerfeld *et al.,* 2002). In cattle, Bastidas *et al.* (1997) performed weekly ovarian activity ultrasound observations in prepubertal heifers exposed or isolated from males. Although there were no differences on the onset of cyclic activity, the number of small and large follicles increased after biostimulation. In turn, Berardinelli *et al*. (2009) reported that the interval between follicular waves is shorter, and the size of the dominant follicle is greater in females exposed continuously or every 6 or 12 h to males during the first 45 d postpartum. We evaluated daily follicular size development in anestrus beef heifers exposed to androgenized steers (AS) during 30 d, and − in accordance with previous results− observed that the follicular diameter was greater after exposing females during 15 d (Fiol *et al.,* 2010a). In summary, in cattle male effect appears to induce an increase of LH secretion which is associated with a greater follicular development rate.

Cortisol and stress

Stress and linked hormones, in particular cortisol, had been generally associated with negative effects on reproduction. High cortisol concentrations affect LH secretion through an inhibition of GnRH pulsatility (Tilbrook *et al.,* 2000; Breen and Karsch, 2004), or through the increase in the sensibility to estradiol negative feedback (Oakley *et al.,* 2009). In ewes exposed to different stressors on day -1, 0 and +1 of male exposure, greater cortisol concentrations were associated with a lower response to male effect in contrast to no stressed ewes (Chanvallon *et al.,* 2010a). However, in sexually naive ewes, females selected for "nervous" temperament, which were expected to be inhibited by some kind of stress, responded better to male effect than "calm" ewes (Chanvallon *et al.,* 2010b).

In rodents there is evidence that adrenal activation is linked to female response to the pheromonal stimulus of the males (Mora and Sanchez-Criado, 2004). However, in ewes there were no changes observed in cortisol concentrations after the introduction of rams (Ungerfeld, 2003), as happens in rams stimulated by the presence of estrual ewes (Gonzalez *et al.,* 1988). Tauck *et al.* (2007) evaluated the effects of close physical contact of primiparous, postpartum, anestrous cows to males during 30 d, or to bull, or steer urine during 64 d, on cyclic activity and plasma cortisol concentrations. Interval to resumption of ovarian activity was shortened in exposed cows compared to isolated ones, with no differences between females exposed to bulls or steer urine. Cortisol concentrations raised and remained high during exposure to the males, but decreased in cows exposed to urine. No differences were found between cows exposed to bulls or steers: in both groups cortisol gradually decreased during the experimental period (Tauck *et al.,* 2007). More recent studies reported no differences in mean cortisol concentrations between postpartum cows exposed acutely (5 h/d during 9 d; Tauck *et al.,* 2010a) or continuously and chronically (24 h/d during 44 d; Tauck, 2008) to males, with those isolated from males. However, cows exposed acutely to bulls had less cortisol pulse frequency and tended to have greater pulse duration than non-exposed females (Tauck *et al.,* 2010a). It should be considered that as mentioned before, in this experiment none of the females resumed ovarian cyclic activity (Tauck *et al.,* 2010a). Similarly, continuous exposure to males decreased cortisol pulse frequency, but differences were only seen before cows resumed cyclic activity (Tauck, 2008). In turn, cortisol and LH concentrations were negatively correlated in exposed groups: while cortisol pulse frequency decreased, LH pulse frequency increased (Tauck *et al.,* 2010a), which also agrees with results found in other species (Breen and Karsch, 2004). Considering all those findings, Tauck (2008) suggested that one component of male stimulus may be an alteration of cortisol secretion pattern before resumption of cyclic activity, which might determine an activation of hypothalamus-pituitary-ovarian axis.

Leptin

Leptin is a metabolic hormone (Clarke and Henry, 1999) that has also been evaluated in relation to biostimulation. Although the proportion of primiparous estrous cows increased with biostimulation during 40 d postpartum, leptin mean concentrations were not affected (Olsen *et al.,* 2009). Leptin concentrations increased in cows that resumed cyclic activity 15, 18 and 27 d after biostimulation began, but while in exposed females levels remained high during that period, in the cows that remained isolated leptin concentrations decreased earlier, by day 21. These authors considered that biostimulation may only have an indirect effect on leptin levels, as it advances postpartum rebreeding (Olsen *et al.,* 2009).

FACTORS THAT AFFECT THE RESPONSE TO BIOSTIMULATION

The main factors that affect the response to biostimulation in cattle may be classified as those linked to stimulus characteristics and management (type, intensity, males' characteristics, stimulus length), and those linked to females receptivity (breed, age and parity, time of the year, reproductive status, body development and nutritional status). Most of the information of factors affecting the response has been generated in postpartum cows.

Stimulus characteristics and management

Animals used for biostimulation

Positive effects of biostimulation in cyclic activity in cows have been demonstrated with bulls (Fernandez *et al.*, 1993; Berardinelli and Tauck, 2007), AS (Ungerfeld, 2009; Fiol *et al.*, 2010b) and androgenized cows (Burns and Spitzer, 1992). Burns and Spitzer (1992) observed a similar reduction in postpartum interval to first estrus in cows exposed to bulls or to androgenized females. Similarly, Ungerfeld (2009) reported an increase of pregnancy rates in heifers exposed to AS before the breeding period. Eventhough, others observed that the use of bulls was more effective than exposure to androgenized females (De Souza, 2002). According to our knowledge, there are no published articles comparing the effectiveness of AS and bulls. Despite the effectiveness, considering the positive results of the use of testosterone-treated animals, it may be affirmed that at least part of the biostimulatory signals on females' cyclic activity are androgen-dependent.

Stimulus intensity or proximity

The percentage of females' that respond to biostimulation is related to the intensity of the stimulus. Fenceline exposure to males (visual, chemical and auditory stimulus) stimulated resumption of postpartum cyclic activity in primiparous cows (Fike *et al.*, 1996). Similarly, Berardinelli and Tauck (2007) reported that fenceline contact of primiparous cows with bulls increased the proportion of cyclic females after 14 d of contact. However, a greater proportion of cyclic females was obtained with direct physical contact compared to fenceline exposure to males (Berardinelli and Tauck, 2007). In agreement, Sato *et al.* (1994) reported better results when cows were physically in contact with bulls than when they could only watch and smell them. Physical proximity also influences the response, as the distance between AS and females was positively associated with the probability of ovulating in prepubertal heifers (Fiol *et al.*, 2010b). Therefore, signals associated with courtship (tactile, physical contact) are also important, and stimulus is not only dependent upon chemical signals.

In dairy cows, response appears to be different. In high producing dairy cows, Shipka and Ellis (1999) did not find positive effects of direct physical contact with bulls during 120 d, nor of twice daily fenceline male exposure on resumption of postpartum cyclic activity. Eventhough, surprisingly postpartum anestrus was reduced in non exposed females. In turn, fenceline exposure of postpartum dairy cows to bulls did not affect estrus behavioral response (Shipka and Ellis, 1998; Roelofs *et al.*, 2008). Roelofs *et al.* (2007) found positive effects of fenceline male exposure on LH mean concentration in postpartum dairy cows, but cyclic activity was not determined in that study. It may be possible to speculate that the great negative energy balance that occurs during early postpartum in dairy cows may explain the different results reported in dairy and beef cows (Shipka and Ellis, 1998; Roelofs *et al.*, 2007).

Therefore, considering the relationship between intensity of male-female link and the response to biostimulation, the final response appears to be linked to a summatory of pathways by which females received the stimulus, and it is not possible to simplify the mechanism to the effects of olfactory signals only.

Males' characteristics and management

Males' sexual behavior and "novelty" effect influence the response to male exposure in sheep (Perkins and Fitzgerald, 1994) and goats (Delgadillo *et al.*, 2006). The alternate exposure to different males determined a greater response in females as a consequence of intensifying the stimulus with new males (Cushwa *et al.*, 1992; Hawken and Beard, 2009). In the same sense, Miller and Ungerfeld (2008) reported that weekly bull exchange during the breeding period of postpartum cows decreased the anestrus interval and increased early pregnancy rates. In contrast, Berardinelli *et al.* (2005) did not find any differences on resumption of cyclic activity in postpartum cows exposed to the same bulls during 95 d postpartum or after exchanging bulls once 35 d after parturition. Therefore, the effectiveness of bull exchange may be related to the frequency with which it is performed: positive results were obtained with weekly exchange (Miller and Ungerfeld, 2008), but not with a single exchange (Berardinelli *et al.*, 2005).

In sheep (Ungerfeld *et al.*, 2008) and swine (Kirkwood and Hughes, 1981) the response is greater when adult males rather than young males are used. However, no differences were found in either testosterone concentrations reached by adult or young rams used to stimulate anestrous ewes (Ungerfeld, 2003), or in sexual behavior between them (Ungerfeld *et al.*, 2008). However, more ewes ovulated and came into estrus after being in contact with wool from adult rams than with wool from young males. Thus, these authors proposed that chemical signals contained in wool may be responsible for that difference (Ungerfeld *et al.*, 2008). In cattle there is only one trial that compared the use of adult and young bulls. Cupp *et al.* (1993) observed a reduction in anestrus length in females exposed to males during 63 d postpartum, but of similar magnitude in cows exposed to young (1 yr old) or adult (> 3 yr old) bulls. Therefore, according to the scarce information available, bulls' age- at least in the evaluated ranges- appears not to affect females' response.

Duration of stimulation periods

The duration of the males' stimulation influences the response in sheep (Hawken and Beard, 2009) and goats (Rivas-Muñoz *et al.,* 2007). Intermittent exposure of postpartum primiparous suckled beef cows to males (2 h every 3 d, during 18 d) since 30 d postpartum had no effects on resumption of cyclic activity compared to isolated females (Fernandez *et al.,* 1996). Moreover, in those groups, postpartum anestrus was longer than in females continuously exposed to males since early postpartum or since 30 d postpartum. Berardinelli and Joshi (2005a) reported shorter anestrus intervals in females exposed to excretory products of bulls 12 h daily than in non exposed females. Recently, Tauck *et al.* (2010b) evaluated resumption of cyclic activity in postpartum cows exposed to males during 6 or 12 h daily, or not exposed for 45 d. Exposure during 6 or 12 h reduced anestrus postpartum compared to isolated females, but the cumulative proportion of cyclic females at 10 d intervals was greater for females exposed during 12 than during 6 h. Therefore, daily and continuous stimulus from the males appears to be necessary to obtain a positive response on cyclic activity, and it seems that there is a negative correlation between exposure periods length and time needed for resumption of cyclic activity. Eventhough, as daily exposure during 24 h to bull urine had no effects on cyclic activity (Tauck and Berardinelli, 2005; Tauck *et al.,* 2006), Tauck *et al.* (2010b) proposed that the alternation of "stimulation" and "relaxation" periods may be necessary to obtain a positive response to biostimulation.

In prepubertal heifers, most of the studies reported longer periods of exposure to males than those reported in postpartum cows to obtain a positive response (175 d, Roberson *et al*., 1991; 450 d, Rekwot *et al.,* 2000b; 180 d, Lima *et al.,* 2008; 210 d, Oliveira *et al.*, 2009). However, it seems that the length may be related to the time close to spontaneous puberty achievement that heifers are. In that sense, others found positive effects with shorter periods of exposure (75 d, Assis *et al.,* 2000; 50 d, Quadros and Lobato, 2004; 15 d, Ungerfeld, 2009; 30 d, Fiol *et al*., 2010b) (Table 1). In addition, there are some studies in which no effects were observed on the onset of puberty between heifers exposed during short (21 d, Macmillan *et al.,* 1979; 30 d, Berardinelli *et al.*, 1978) or long (152 d, Roberson *et al.*, 1987) periods. The inconsistency of the results obtained in prepubertal heifers may be due to the great influence of body development and nutritional status at the beginning of the exposure and during biostimulation on the response to male exposure.

Females receptivity

Breed, age and parity

Although effects of male exposure on cyclic activity have been evaluated mainly in *Bos taurus taurus*, others reported positive effects of biostimulation in zebu (*Bos taurus indicus)*, both in postpartum cows (Rekwot *et al.,* 2000a; Soto Belloso *et al.,* 1997; Bolaños *et al.,* 1998) and prepubertal heifers (Rekwot *et al*., 2000b). In turn, biostimulation was also effective to reduce anestrus periods in buffaloes females (*Bubalus bubalis*; Ingawale and Dhoble, 2004; Gokuldas *et al.,* 2010).

In sheep, age and female parity at the beginning of the exposure affect the response to biostimulation. As it was mentioned before, young and sexually naive females generally have poor responses as a consequence of sexual inexperience and the need of some "learning" related to the male effect (Gelez *et al.,* 2004; Chanvallon *et al.,* 2010a). In postpartum cows, biostimulation has been studied especially in primiparous females as this category presents long anestrus intervals compared to multiparous cows (Short *et al.,* 1990). In some studies, exposure to males was effective in reducing anestrus periods in primiparous but not in multiparous cows (Gifford *et al.,* 1989; Fike *et al.,* 1996), while others found positive effects in both categories (Soto-Belloso *et al.,* 1997). The greater duration of postpartum anestrus in primiparous cows could determine that multiparous females are less dependent on external stimuli. Thus, in those cows the effect of male exposure may be less effective in reducing anestrus length (Gifford *et al.,* 1989; Fike *et al.,* 1996).

Macmillan *et al.* (1979) reported positive effects of male exposure during 20 d on cyclic activity in postpartum cows but not in prepubertal heifers. In turn, Small *et al.* (2000) found positive effects of biostimulation in puberty onset in winter-born heifers (puberal females), but negative effects in spring-born heifers (prepuberal females). Those authors concluded that response to male effect may be related to the time close to spontaneous puberty achievement that heifers are at the beginning of the exposure. Sensitivity to stress in young female sheep exposed to males for first time, affected negatively the response to male exposure (Chanvallon, 2009). In cattle, regrouping with strange animals determines a stress response (Veissier *et al.,* 2001), similar to what may be happening when heifers were exposed to males for first time. Therefore, nutritional status and stress may be main factors that determined differences in the response to biostimulation between prepubertal heifers and postpartum cows.

Table 1. Summary of studies that reported positive effects on the onset of cyclic activity in heifers exposed to males, in relation to the length of the exposure period, age and body weight of the heifers, and the interval from the beginning of the exposure to the response (IETR).

Exposure length (d)	Age (mo-old)	Body weight (kg)	IETR (d)	Reference
30	22	282	15	Fiol and Ungerfeld, 2011b
35	12	226	21	Fiol *et al.*, 2010b
50	24.5	278	35	Quadros and Lobato, 2004
75	24	269	< 75	Assis *et al.*, 2000
154	9	300	14	Small *et al.*, 2000
210	12	180	210	Oliveira *et al.*, 2009
460	14.8	148	189	Rekwot *et al.*, 2000b

Reproductive status at the beginning of the exposure period

Physiological status of females exposed to males has a strong influence on their response. Moreover, it has been proposed that the wide variation between animals' physiological status in postpartum cattle at the time of male exposure may partially explain the high variability in the response to biostimulation (Ungerfeld, 2007). The exposure of multiparous cows from the first week postpartum during 50 (Gokuldas *et al.*, 2010) or 90 (Landaeta-Hernández *et al.*, 2008) d, decreased anestrus length compared to isolated females, but no effects on cyclic activity were found when exposure began 33 d postpartum (Bonavera *et al.*, 1990). The exposure of multiparous cows to bulls during early postpartum (day 3 to 85) decreased anestrus length compared to those females exposed only from day 53 to 85 postpartum (Zalesky *et al.*, 1984). In contrast, Gifford *et al.* (1989) using the same category did not find any difference between early (day 3 to 85 postpartum) or late (from day 55 to 85 postpartum) male exposure on duration of postpartum anestrus. The differences could be explained by postpartum anestrus length in cows exposed to males during late postpartum between experiments (62 and 31 d, Zalesky *et al.*, 1984 and Gifford *et al.*, 1989, respectively). According to those findings, it is interesting to speculate that positive response to male exposure during early postpartum in multiparous cows may be only observed when females present long anestrus intervals- e.g. 50 or more days.

It appears that the response of postpartum primiparous cows is more homogeneous than that of multiparous cows. Early postpartum exposure to males decreased anestrus interval more dramatically than late exposure (Gifford *et al.*, 1989), but Fernandez *et al.* (1993) reported no differences in anestrus length between primiparous cows exposed continuously to males since calving, exposed during the first 30 d postpartum, or only after the first 30 d postpartum. Moreover, in the three groups of females, anestrus was shorter than in cows isolated from males during all the postpartum period. Similarly, there were no differences on anestrus length between primiparous cows exposed to males since 15, 35 or 55 d postpartum (Berardinelli and Joshi, 2005b). However, cows exposed to males since 55 d postpartum had shorter intervals from the beginning of the exposure to resumption of cyclic activity than females exposed since 15 d, but the final interval between partum and resumption of cyclic activity was similar. Therefore, in primiparous cows the positive response to biostimulation appears to be faster in late postpartum. This might be related with a greater sensitivity to male stimulus in late postpartum cows.

The high variability of results could be due to one or more physiological events linked to ovarian cyclicity resumption during postpartum (Rekwot *et al.*, 2001; Berardinelli and Joshi, 2005b). During early postpartum, females' metabolism undergoes a period of negative energy balance (NEB), caused by high nutritional requirements and a decrease in food intake (Short *et al.*, 1990; Montiel and Ahuja, 2005). As reproduction is one of the more affected functions, there is a direct relation between resumption of postpartum cyclic activity and duration and severity of NEB (Short *et al.*, 1990). In turn, duration and severity of the NEB is determined by the energy stores present at partum, lactation and animal parity (Short and Adams, 1988; Montiel and Ahuja, 2005). In general, when age at first partum occurs at 2 years-old or earlier, growth requirements are added to lactation requirements, so severity and duration of postpartum anestrus is greater than in multiparous cows (Short *et al.*, 1990).

Summarizing all the above information, while primiparous cows appear to respond to male exposure during the entire postpartum period, in multiparous cows positive effects may be obtained during a shorter and more variable period of time. In multiparous cows with long postpartum anestrus intervals (more than 50 d), early exposure to males has positive effects (Zalesky *et al.*, 1984; Landaeta-Hernandez *et al.*, 2008). In turn, when multiparous cows presented short anestrus periods, or when exposure to males begins late in the postpartum, biostimulation may have no effect (Gifford *et al.,* 1989; Bonavera *et al.,* 1990). In contrast, in primiparous cows with extended postpartum anestrus, response to male exposure appears to be more homogeneous along the postpartum period, but it may be faster as postpartum time increases (Gifford *et al.,* 1989).

Time of the year

MacMillan *et al.* (1979) found positive effects of male exposure in postpartum cows during spring but not during winter. Similarly, anestrus postpartum decreased when multiparous cows were exposed to bulls during spring-summer, but not in winter (Alberio *et al.,* 1987; Agabriel *et al.,* 2004). Differences were attributed to the differences in food availability (Agabriel *et al.,* 2004), which determined that exposed females increased body weight during spring but lost body weight during winter (Alberio *et al.,* 1987). However, exposure to males during spring began 60 d postpartum, while winter exposure began 10 d postpartum (Alberio *et al.,* 1987). According to the authors, early exposure during winter could be the main factor contributing to the absence of effects of biostimulation. Moreover, regardless males' presence, winter females had short anestrus intervals (53.2 vs 36.6 d in exposed and isolated females, respectively; Alberio *et al.,* 1987). Overall, considering that reproduction in domestic cattle are not strongly influenced by photoperiodic changes, it seems that differences in responses in relation to the period of the year are more related to changes in food consumption, and thus in metabolic status, than to direct effects of season.

Heifers body development and nutritional status

Nutritional status and body weight gain are related to age at puberty in beef heifers (Wiltbank *et al.,* 1969; Short and Bellows, 1971; Quintans *et al.,* 2004), and both appear to affect the response to biostimulation. Period of time necessary to obtain a positive response might be related to heifers' body development at the beginning of male exposure (Table 1). More 25.5 mo-old heifers began cyclic activity after 50 d of bull exposure than 23.5 mo-old old heifers (Quadros and Lobato, 2004). Moreover, in heifers that were younger at the beginning of biostimulation, longer periods of exposure were necessary to obtain a positive response in cyclic activity (Roberson *et al.,* 1991; Oliveira *et al.,* 2009). Rekwot *et al.* (2000b) reported that heifers reared in mixed groups attained puberty at lower ages and body weights compared to those isolated from males.

In turn, Roberson *et al.* (1991) found that heifers with high body weight gains during male exposure began cyclic activity earlier than those with medium body weight gains. Oliveira *et al*. (2009) obtained positive effects of long exposure (210 d) on the onset of cyclic activity in 12 mo-old prepuberal heifers, but they did not obtained positive results of supplementing those heifers. However, exposed females had greater final body weight, which was positively correlated to age at puberty. Body weight at the beginning of the exposure period affected the response to male exposure: positive effects were found in heavier heifers (Quadros and Lobato, 2004; Fiol *et al.,* 2010b), which agree with previous studies performed in goats (Véliz *et al.,* 2006). Moreover, heavier heifers had closer proximity with the AS than lighter ones (Fiol *et al.,* 2010b). In order to isolate the attractiveness related to body weight from the competitive effects of having heifers from different body weights stimulated together, we evaluated sexual behavior of AS toward heavier or lighter heifers in competitive and non-competitive sexual tests (Fiol and Ungerfeld, 2011a). We found that males prefer heavier heifers only when they were in competitive situations with lighter heifers, but courtship was similar in individual tests despite heifers' body weight. We concluded that factors associated with females' competition and not the body weight of the heifers itself, may be determinant of the greater stimulus received by the heavier heifers. Body weight is one of the main factors implicated in the determination of social rank in cattle (Bouissou, 1972). In turn, social rank in goats affected the response to male exposure: dominant females maintained a closer contact with the male, and had a higher endocrine and ovulatory response to male exposure (Alvarez *et al.,* 2003, 2007, 2009). Therefore, it is possible to speculate that dominance-submission relationships when cattle of different body weights are mixed are major determinants in the different response to male exposure due to competition in access to males.

Nutritional status in postpartum cows

In postpartum cows, nutritional status influence resumption of cyclic activity (Montiel and Ahuja, 2005) and response to biostimulation, as reported in small ruminants (Wright *et al.,* 1990). Monje *et al.* (1992) evaluated the effects of two energy levels since 12 d postpartum (30% more and 30% less of energy requirements) and male exposure during 80 d (from 30 d postpartum). Those authors reported a positive relationship between nutritional status and response to biostimulation: cows with high energy level and exposed to males had more synchronized ovulations and less variability on resumption of cyclic activity than exposed cows that were submitted to low energy levels, and to non-exposed females. Moreover, between low energy groups, non-exposed females began cyclic activity earlier than exposed ones. The authors attributed that difference to the fact that cows in the low energy level, and those not exposed to males improved their nutritional status since the moment in which all the groups were joined together (110 d postpartum), and responded positively to male exposure later. In contrast, low energy cows exposed to males from 30 d postpartum might have been used to male presence, losing the novel effect when both groups were joined (Monje *et al.,* 1992).

Energy supplementation and male exposure during 180 d on multiparous zebu cows had a positive synergistic effect on resumption of postpartum cyclic activity (Rekwot *et al.,* 2004). Stumpf *et al.* (1992) evaluated the effects of body condition score (BCS) at partum on the response to biostimulation in postpartum multiparous cows, and found that cows with moderate BCS (4.9 units in a 1 to 10 scale) responded better to male exposure than cows with high BCS (5.9 units). Similarly, Madrigal *et al.* (2001) reported an interaction between BCS and biostimulation on resumption of cyclic activity and pregnancy rates, which was more pronounced in low BCS cows. In turn, Landaeta-Hernández *et al.* (2008) found that high BCS multiparous cows (4.8 units) exposed to bulls since the first week postpartum began cyclic activity earlier than non exposed females (38 vs 51 d, respectively).

Considering all the above information, nutritional status and body development may be main factors affecting the response to male exposure in beef cattle. In prepubertal heifers, body development at the beginning of the exposure period and body weight gain during biostimulation, influence the response to male exposure (Roberson *et al.,* 1991; Rekwot *et al.,* 2000b; Quadros and Lobato, 2004; Fiol *et al.,* 2010b). In postpartum cows, high nutritional status at the beginning of the exposure period determined a low response to biostimulation because females in those situations have short anestrus postpartum regardless males' presence (Stumpf *et al.,* 1992; Madrigal *et al.,* 2001). On the other hand, cows with very low BCS are unable to respond to male exposure due to the low nutritional status (Monje *et al.,* 1992). Therefore, moderate nutritional status appears to be necessary to obtain positive response to male exposure. This should be specifically considered under grazing conditions in which impact of nutritional status is more difficult to be controlled.

PRE-BIOSTIMULATION AND BREEDING PERFORMANCE

In Tables 2 and 3 we summarize the results of different studies that evaluated the effects of biostimulation before a bull or AI breeding period, both in prepubertal heifers (Table 2) and postpartum cows (Table 3). Exposure of beef heifers to AS (Ungerfeld, 2009) or to vasectomized bulls (Oliveira *et al.*, 2009) before the breeding period increased natural-service pregnancy rates. Moreover, male exposure improved AI pregnancy rates in beef heifers (Roberson *et al.,* 1991; Quadros and Lobato, 2004) and in primiparous (Fernandez *et al.,* 1993) and multiparous (Zicarelli *et al.,* 1997; Gokuldas *et al.,* 2010) cows. However, some of those studies did not find differences in overall pregnancy rates between exposed and isolated females (Roberson *et al.,* 1991; Fernandez *et al.,* 1993). As pregnancy rates are improved when beef heifers begin cyclic activity before the onset of the breeding season (Byerley *et al.,* 1987), the greater pregnancy rates reported in some of the aforementioned studies may be a consequence of a greater proportion of exposed females cycling at the beginning of the natural service or AI breeding periods. In turn, age and body weight of the heifers at the beginning of the exposure period influenced the response to males: positive and significant differences on pregnancy rates were limited to older (Quadros and Lobato, 2004) and heavier (Ungerfeld, 2009) females.

Table 2. Summary of studies that evaluated breeding performance in terms of onset of cyclic activity and pregnancy rates in heifers exposed to males (EXP) or isolated from males (ISO)

Exposure type and length (d)	Cyclic activity (%)		Pregnancy (%)		Reference
	EXP	ISO	EXP	ISO	
ASE/DPC (30 d)	55a	32b	83	86.5	Fiol and Ungerfeld, 2011b
TBU (56 d)	67a	32b	79	85	Izard and Vandenbergh, 1982a
BE/DPC (175 d)	**	---	50.5a	16.5b	Roberson *et al.,* 1991
BE/DPC (75 d)	86.9c	71.1d	89.1	88.9	Assis *et al.*, 2000
BE/DPC (200 d)	**	---	58.9a	32.5b	Small *et al.*, 2000
BE/DPC (50 d)	76c	56d	90c	73d	Quadros and Lobato, 2004
ASE/DPC (15 d)	---	---	61a	32.3b	Ungerfeld, 2009
BE/DPC (210 d)	**	---	63a	21.5b	Oliveira *et al.*, 2009

ASE: androgenized steers exposure; BE: bull exposure
DPC: direct physical contact; TBU: treatment with bull urine
**Decrease age at puberty in EXP heifers
Different letters in the same row and for each experiment: a vs b: $P < 0.05$; c vs d: $P=0.06$

Table 3. Summary of studies that evaluated breeding performance in terms of resumption of cyclic activity and pregnancy rates in postpartum cows exposed to males (EXP) or isolated from males (ISO).

Exposure type and length (d)	Cyclic activity (%)		Pregnancy (%)		Reference
	EXP	ISO	EXP	ISO	
ASE/DPC (20 d)	---	---	58.5	50.0	Ungerfeld, 2010
BE/DPC (60 d)	81a	41b	67	63	Berardinelli *et al.,* 2001
BE/DPC-EPB (63 d)	87a	19b	87a	56b	Anderson *et al.,*2002
BE/DPC-EPB (60 d)	85.1a	31.3b	66.3a	51.5b	Berardinelli *et al.,* 2007
BE/DPC (35 d)	100a	70.4b	85a	60b	Tauck and Berardinelli, 2007
BE/DPC (50 d)	82a	38.5b	54.5a	15.4b	Gokuldas *et al.,* 2010
BE/FCB (42 d)	86a	73b	58	77	Tauck and Berardinelli, 2007
TBU (64 d)	15	33	89.5a	55b	Tauck and Berardinelli, 2007

ASE: androgenized steers exposure; BE: bull exposure

DPC: direct physical contact; EPB: excretory products of bulls; FCB: fence-line contact with bulls; TBU: treatment with bull urine

Different letters in the same row and for each experiment: a vs b: $P < 0.05$

Different results have been obtained when cows were exposed to males before or during an estrous synchronization treatment (EST). Exposure of postpartum beef cows to bulls or excretory products of bulls before or during an EST increased fixed-timed AI pregnancy (Anderson *et al.,* 2002) and conception (Berardinelli *et al.,* 2007) rates, but no differences were found on cows bred by AI 12 h after estrus (Anderson *et al.,* 2002; Berardinelli *et al.,* 2007). Similarly, Small *et al.* (2000), using an EST that included two doses of PGF2α, reported a 30% increase in timed AI pregnancy rates in winter-born, but not in spring-born heifers, exposed to bulls before the beginning of the EST compared to isolated heifers. In contrast, others did not find any positive effect on pregnancy or conception rates with direct (Ungerfeld, 2010; Berardinelli *et al.,* 2001) or fence-line (Fike *et al.,* 1996; Tauck and Berardinelli, 2007) exposure to males before the beginning of an EST in postpartum cows and heifers. Recently, we evaluated the onset of cyclic activity and breeding performance of heifers exposed to AS for 30 d before the beginning of an EST with double injection of PGF2α (Fiol and Ungerfeld, 2011b). We found a positive but transitory effect of biostimulation on ovarian cyclic activity, which determined that similar proportion of exposed and isolated females was cycling at the beginning of the EST. However, no effects of biostimulation were found on estrous response and AI pregnancy rates (Fiol and Ungerfeld, 2011b). According to those results, the induction of differences in cyclic activity at the beginning of the EST appears as necessary to obtain positive effects of male exposure on breeding performance.

Results were different when exposure to male urine through a delivery device was evaluated. Conception rate increased in postpartum cows exposed to bull urine before an EST, but not in females exposed to steer urine (Tauck and Berardinelli, 2007). At the same time, no effects of exposure to bull or steer urine on resumption of ovarian cyclic activity were observed in those experiments, which agree with previous studies (Tauck *et al.,* 2006). Thus, proportion of cyclic females at the beginning of the EST was similar between females exposed to bull or steer urine. Based on those results, Tauck and Berardinelli (2007) hypothesized the existence of two components of the biostimulatory effect of bulls: one that accelerates the resumption of cyclic activity and another that improves breeding performance. According to the authors, the last may only be effective with very close proximity to bull urine.

Summarizing all the above information, in order to have positive effects of biostimulation on breeding performance in cattle, exposure length and type (physical presence vs male urine or excretory products of males), and natural vs artificial breeding and subsequent use of an EST, should be considered.

FINAL CONSIDERATIONS AND FUTURE PERSPECTIVES

Livestock production is challenged worldwide, especially because of the high competition for natural resources, particularly land and water (review: Thornton, 2010). Improving reproductive efficiency in beef and dairy cattle should be one of the main objectives to obtain a more sustainable production. In this context, socio-sexual stimulus, like biostimulation, represents low cost and hormone-free alternatives than can be used alone or in conjunction with other techniques to increase reproductive results. The information collected in this review regarding the effects of biostimulation in cattle, demonstrates the need of further studies to understand the mechanisms involved in this phenomenon. Differences in reproductive physiology in cattle determined that many of the characteristics of the male effect in small ruminants cannot be fully extrapolated to the first ones. In particular, some important questions remain to be answered, as: Why results in cattle are more unpredictable than those obtained in small ruminants? Which factors disperse the response in time? What is the role of non-olfactory cues in the response? What is the importance of sexual experience and learning in the response? The possibility to answer these questions and more will determine the most efficient use of biostimulation in cattle.

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