

Socio-sexual signalling and gonadal function: Opportunities for reproductive management in domestic ruminants

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The aims of this review are to summarize the common biological basis of the responses to social stimulus in domestic ruminants and to consider the research still required in order to put this knowledge to practical use on the farm. The mechanisms involved in the stimulation of sheep and goat females, including both the expected ovarian and behavioural responses, are described. In most breeds, the male effect may be used effectively to induce ovulation during seasonal anoestrus. Although good responses have been obtained in most sheep trials, in some experiments using more seasonal breeds of sheep, poor responses were observed. In goats, it seems that this can be partially overcome if teaser bucks are adequately stimulated (by light treatment and melatonin administration). The strategic use of these stimuli to induce fertile ovulations during the postpartum period is also discussed. In cattle, less is known about the physiological mechanisms by which cows respond to stimulation from the bull. Most trials have focused in trying to advance postpartum rebreeding, with very diverse outcomes. The wide variety of interacting factors and the paucity of data make it difficult to draw conclusions regarding the use of social stimuli in postpartum management. The challenge for researchers is to develop social management techniques that will induce oestrus and ovulation whenever farmers require them. Although more research is necessary to improve efficacy in some sheep breeds and in postpartum animals, social stimulation emerges as an inexpensive and hormone-free strategy that may be useful for farmers.

Introduction

Reproduction is a consequence of endogenous neuroendocrine regulating mechanisms and external factors that interact with them. Environmental conditions interact with the endogenous system by either stimulating or inhibiting physiological mechanisms and many of these mechanisms are related to the reproductive axis. In ruminants, social cues may act to either stimulate or inhibit reproductive activity. Social hierarchies or suckling are examples of inhibitory cues, which may be considered in management practice. On the other hand, there is considerable evidence that males may stimulate oestrus and ovulation in anovulatory females: the so called "male effect". Research on the use of the male effect has been increasing recently (Ungerfeld

2005), probably as a consequence of being described as a "clean, green, and ethical" practice (Martin *et al.* 2004).

The effects of social stimuli on reproductive physiology have been widely demonstrated in rodents and several farm species. In ruminants, several reproductive responses may be obtained in females following male stimulation (as in the male effect: Table 1). Although there is only preliminary information, male stimuli on female reproductive physiology may also exist in caribou, musk deer and camels (Green 1987; Claus *et al.* 1999; Adams *et al.* 2001).

Table 1. Ruminant species in which the male effect has been demonstrated and the main effects on the females.

Species	Effect	Reference
Sheep	Induction of oestrus in seasonal anoestrus	Underwood <i>et al.</i> 1944
	Shortening of postpartum in ewes	Geytenbeek <i>et al.</i> 1984
Goat	Advancement of puberty in lambs	O'Riordan & Hanrahan 1989
	Induction of oestrus in seasonal anoestrus	Chemineau 1985
	Advancement of puberty in goats	Mellado <i>et al.</i> 2000
Cattle	Synchronization of puberty onset	Amoah & Bryant 1984
	Advancement of postpartum rebreeding	Zalesky <i>et al.</i> 1984
Red deer	Advancement of puberty	Rekwot <i>et al.</i> 2000
	Advancement of the breeding season	Moore & Cowie 1986
Eld's deer	Advancement of puberty	Fisher <i>et al.</i> 1995
Fallow deer	Advancement of oestrus and the LH peak	Hosack <i>et al.</i> 1999
Reindeer	Advancement of the breeding season	Komers <i>et al.</i> 1999
Moose	Advancement of onset of breeding season	Shipka <i>et al.</i> 2002
	Synchronization of the breeding season	Whittle <i>et al.</i> 2000
Antelope	Induction of ovulation	Miquelle 1991
Oryx	Modification of oestrous cycle duration	Skinner <i>et al.</i> 2002
Impala	Advancement of puberty	Blanvillain <i>et al.</i> 1997
Blesbok	Advancement of the breeding season	Skinner <i>et al.</i> 1992
	Increase in length of breeding season	Skinner <i>et al.</i> 1992

The female reproductive responses to the male effect have been reviewed before (Walkden-Brown *et al.* 1999; Delgadillo *et al.* 2004; Ungerfeld *et al.* 2004a; Delgadillo *et al.* 2006). In the present review, information regarding the female reproductive responses to male stimulation of sheep and goats during seasonal anoestrus, and sheep, goats and cattle during the postpartum period are compared and summarized and areas in which further research is needed are proposed. In addition new previously unpublished information on sheep and cattle is included.

Male effect: evolutionary advantages

What is the evolutionary origin of the male effect? Seasonal patterns of reproduction should be a consequence of selective processes related to best environmental conditions for parturition and nursing. To measure the appropriate time for conception, animals would then be forced to use different environmental cues such as photoperiod, temperature, rainfall and nutrition. However, social cues may also trigger the onset of the breeding season in wild and feral ruminants. Domestic animals display some differences in their reproductive physiology compared with their wild ancestors. Wild or feral cattle and swine have short breeding seasons compared to their domesticated counterparts, which have been selected to breed throughout the year (Mauget 1981; Rowlands & Weir 1984; Reinhardt *et al.* 1986). The reproductive pattern of sheep is a bit different: wild sheep have a short breeding season and even the most developed breeds retain a seasonal reproductive pattern.

The high degree of breeding synchrony observed in wild and feral female ruminants may be at least partially a consequence of male introduction and other social interactions. The social structure throughout the year is similar in wild and feral sheep breeds (such as, Soay, Rocky Mountain Bighorn [*Ovis canadensis canadensis*], Punjab Urial [*Ovis orientalis ssp. punjabiensis*] and Mouflon), goats and in farmed breeds (Geist 1965; 1971; Grubb & Jewell 1973; Schaller & Mirza 1974; Knight *et al.* 1998; McClelland 1991). Outside the rutting period, social groups are comprised of several females with their offspring while males live in small same-sex groups (Stricklin & Mench 1987). When male offspring become mature they disperse from the female group (Shackleton & Schank 1984). Wethers (castrated male sheep) remain together or with females (Jewell 1997), suggesting that the testis (probably through androgens) is involved in segregation. As the time of breeding approaches, males join female groups. Nudging, blocking, rubbing and aggressive behaviours (Jewell 1976; Lincoln & Davidson 1977) by males begins before females come into oestrus, probably as a consequence of the earlier activation of the male reproductive system (including, increased pulsatile LH secretion and increased circulating concentrations of both FSH and testosterone: Lincoln & Short 1980). In sheep, natural joining may trigger, through the ram effect, an earlier onset of the breeding season.

The rut period causes an increase in the energy expenditure of males (Jewell 1997). So what is the significance of beginning the reproductive season before females are cyclic? Moreover, what is the sense of having a mechanism where males trigger the female reproductive system? The mechanism may be especially important in breeds that display a very short breeding season (for example, Soay have 1 to 3 oestrous cycles: Grubb & Jewell 1973). Moreover, late conception in Rocky Mountain Bighorn sheep during the breeding season increases lamb and ewe mortality (Hogg *et al.* 1992). The male stimuli may also promote an advancement of puberty in females, which may increase their reproductive success throughout their lifetime (Bérubé *et al.* 1999). The period from joining of males and females until the peak of oestrus may also be useful for males to sort out hierarchical ranks. Oestrous synchronization allows different males to mate different females thereby decreasing the risks of inbreeding and the reduction of genotype variation that would result. Komers *et al.* (1999) working with fallow deer postulated that the onset of females' cyclic activity in response to males is related to the "quality" of males. If so, females may be able to detect the better quality stimulus emitted by individual males and, if advantages may be obtained, advance their cyclic activity. Overall, the available information suggests that there is an evolutionary mechanism underlying the reproductive response of domestic ewes to the introduction of rams. Understanding this mechanism may allow us to manipulate the breeding activity of farmed breeds.

Considering all this information together, we speculate that most ruminant females would respond to the introduction of males at least 45 to 60 days before the onset of the breeding season. However, the challenge for researchers is to develop social managements to induce ovulation and oestrus whenever it is desired, and not only close to the breeding season onset, as happens in wild ruminants.

Sheep and goats: the basis of anoestrus and endocrine changes induced by males

Seasonal anoestrus is associated with reduced LH pulsatility compared to the breeding season and with an absence of preovulatory surges of FSH and LH. Low LH pulsatility is due to two inhibitory mechanisms: (1) an increased negative feedback effect of oestradiol in the hypothalamus; and (2) a direct effect of photoperiod on the hypothalamo-hypophyseal system controlling LH secretion.

The introduction of males induces an increase in the pulsatile secretion of LH in ewes and does (reviewed by Walkden-Brown *et al.* 1999), which may end with a LH surge followed by ovulation. In ewes, it has been demonstrated that after the introduction of the rams the negative oestradiol-LH feedback switches to a positive, stimulatory feedback but there is also a stimulus independent from oestradiol, acting directly at the hypothalamus-pituitary level (Martin *et al.* 1983). This response ends with a LH surge, similar to that observed during a follicular phase in cyclic ewes. A silent ovulation occurs, without signs of oestrus. When the corpus luteum (or corpora lutea) regresses after the first ovulation, another ovulation accompanied by oestrus occurs 17 to 19 days after the introduction of the rams. However, in some ewes, the corpus luteum regresses after 4 to 5 days and another silent ovulation takes place. After this ovulation, a corpus luteum of normal life span is formed, followed by oestrus 21 to 25 days after joining ewes and rams. Recently, we observed ultrasonographically other ovarian responses, like delayed ovulations occurring 5 to 7 days after the introduction of rams followed by normal or short luteal phases, or luteinized follicles (Ungerfeld *et al.* 2002; 2004b).

In goats, the ovarian and behavioural responses differ. An initial ovulation associated with oestrus is observed 2 to 3 days after the introduction of bucks, which is followed in most goats by a short ovarian cycle of 5 to 7 days. Afterwards a second ovulation which is also associated with oestrus occurs and is followed by a normal luteal phase (Delgadillo *et al.* 2004; 2006). Fig. 1A and 1B illustrates the more common patterns of response in sheep and goats, respectively. In Fig. 1C, a synthesis of the expected periods in which oestrus may be expected to occur in sheep flocks and goat herds is shown.

If ewes or does are primed with progestogens and then stimulated by teasers, all the first corpora lutea will have normal function. Although some attempts have been made to determine the physiological mechanisms producing each response pattern (normal *versus* short luteal phase) little has been elucidated. Studies determining the relationship between the ovarian response pattern with the follicle status present before the introduction of rams (Ungerfeld *et al.* 2004b), the follicular development after the introduction of rams (Pearce *et al.* 1987), the uterine effect on early luteolysis (Lassoued *et al.* 1997) and the possible existence of spontaneous short luteal phases produced by luteinised follicles or short-lived corpora lutea during the anoestrous season (Ferreria *et al.* 2005) have all failed to provide a definitive answer. A recently published review provides a working hypothesis of the physiological mechanisms involved (Chemineau *et al.* 2006).

Apparently in Merino sheep, in response to the introduction of the male a normal oestrous cycle will be induced in approximately 50% of the females while the other 50% will have first cycles with short luteal phases (Martin *et al.* 1986). However, in several experiments with Corriedale ewes we observed very few ewes in oestrus during the first expected period (days 17-19: Ungerfeld *et al.* 2003; Ungerfeld & Rubianes 2004). Some factors related to the percentage of ewes that initially respond with normal or short luteal phases are summarized in Table 2. Oldham *et al.* (1985: see Table 2) in sheep and Luna-Orozco *et al.* (2005) in goats, observed a higher incidence of short luteal phases in adult compared to young females. However, in sheep this has not been confirmed by other researchers (Thimonier *et al.* 2000). In agreement with Khaldi (1984) and Thimonier *et al.* (2000), we observed that Corriedale ewes in poor body condition as a consequence of postpartum status, showed delayed oestrous behaviour compared to control animals (25.8 ± 0.3 *versus* 24.6 ± 0.4 days after the introduction of the rams, $P=0.03$; R Ungerfeld, unpublished data), suggesting that first ovulations were delayed or that a higher percentage of ewes responded initially with short luteal phases.

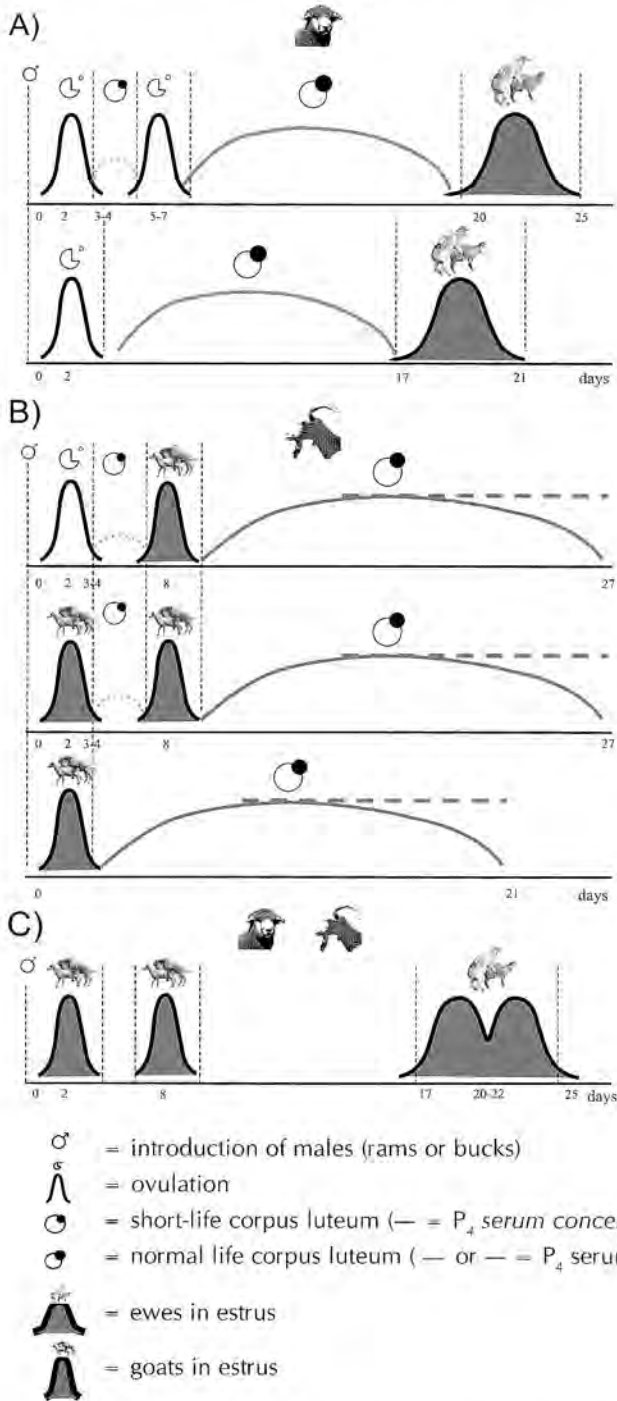


Fig. 1. Ovarian and behavioural response of A) ewes and B) does to the introduction of males. C) Synthetic scheme of the distribution of oestrus after the introduction of males in doe herds and ewe flocks.

Table 2. Factors that influence the length of the first luteal phase after the introduction of rams. NLP = normal luteal phase; SLP = short luteal phase.

Factor	Effect	Reference
Related to the stimuli		
High ram's sexual behaviour	Decreases the incidence of SLP	Perkins & Fitzgerald, 1994
Related to female status		
Percentage of cyclic ewes	Decreases the incidence of SLP	Lassoued, 1998
Underfed ewes	Increases the incidence of SLP	Khaldi & Lassoued, 1991
Increase of nutritional level	Decreases the incidence of SLP	Khaldi 1984; Thimonier <i>et al.</i> 2000
Postpartum interval	Longer postpartum interval decreases the incidence of SLP	Thimonier <i>et al.</i> 2000
Parity	Maiden have a higher percentage of NLP than adult	Oldham <i>et al.</i> 1985
Breed	More Dorset than Hampshire ewes seem to have SLP	Nugent III <i>et al.</i> 1988

Response to the male effect during the postpartum period in sheep and goats

The physiology of postpartum anoestrus is influenced by different factors; such as suckling, season, nutritional status and age. Although this period has not been studied as much as seasonal anoestrus, the male effect has been used to induce breeding during the postpartum period in both sheep and goats.

The postpartum interval may be reduced if rams are introduced to ewes that have lambed in autumn or spring (Wright *et al.* 1989; Silva and Ungerfeld 2006). In autumn-lambing Merino ewes, it was observed that the percentage of ewes ovulating during the first 4 days after the introduction of the rams increases progressively from 21 to 45 days postpartum (Geytenbeek *et al.* 1984). In contrast to what happens in cattle, in autumn-lambing ewes, parity does not seem to influence the response to the ram effect. We have recently compared the response to the introduction of rams of multiparous and primiparous non-cyclic ewes during the breeding season (30 to 60 days postpartum) primed with medroxy-progesterone acetate for 12 days. Although the percentage of multiparous ewes that ovulated, which was determined by ultrasound scanning, tended to be higher than that of primiparous ewes (92.5 *versus* 79.3 %, $P=0.08$), the percentage that came into oestrus (88.8 *versus* 75.8 %) was not significantly different (SP González-Pensado, MA Ramos, T de Castro & R Ungerfeld, unpublished results).

In one study performed during the non-breeding season, a similar percentage of postpartum ewes and ewes that had lambed several months before exhibited oestrus after the introduction of rams (Ungerfeld *et al.* 2004a). However, in agreement with Wright *et al.* (1990), probably as a consequence of suckling and low body condition, the conception rate was lower in the postpartum ewes. In ewes that had lambed during the non-breeding season Khaldi (1984) observed that the percentage of ewes that ovulated after the introduction of rams was higher at 75 days than at 15, 30, 45 or 60 days after parturition. It is interesting that in several experiments we observed a widespread distribution of oestrus, with ewes coming into oestrus on almost any day until 30 days after the introduction of rams. It remains to be elucidated as to how the range of physiological status between individuals present in a sheep flock affects the pattern of endocrine and ovarian responses to the introduction of rams.

Determinants of the response of sheep and goats to the male effect

In feral or wild populations, when males stimulate anoestrous females early before the onset of the breeding season, males have begun their reproductive recovery at least 40 to 60 days

before. Therefore, females are stimulated by active males, which display their own maximum reproductive capacity. However, at the time of the year that may be of productive interest for farmers to induce ovulation and obtain pregnancies in their female flocks/herds, the males may not have recovered their maximum reproductive capacity from the preceding low capacity period. Thus, both the male and the female, and the stimuli derived from interactions between them, may determine the final response in a sheep flock or a goat herd.

Male condition and stimulating capacity

Stimulating signals

The stimulation of anoestrous females by males involves different cues; such as, odour, sound, visual or behavioural signals (reviewed by Walden-Brown *et al.* 1999; Delgadillo *et al.* 2006). The relative importance of each signal has varied in different experiments but this may be a consequence of using females in different states of responsiveness. In both sheep and goats, it has been reported that castrated males treated with androgens may be effective teasers suggesting that the involved cues are at least partially androgen-dependent (Fulkerson *et al.* 1981; Mellado & Hernández 1996).

The scent of wool and wax from intact rams can be enough to trigger a response, in terms of ovulation, in ewes (Knight & Lynch 1980). Similarly, odours from bucks' hair have been proven to stimulate LH secretion in does and ewes, and ovulation in anoestrous does (Over *et al.* 1990; Walkden-Brown *et al.* 1993). Interestingly, odours produced by the goat buck can also stimulate LH pulse frequency and ovulation in anoestrous ewes (Knight *et al.* 1983; Over *et al.* 1990). While Morgan *et al.* (1972) observed that ewes with impaired smell did not respond to rams, a normal LH response was observed in ewes reported without vomeronasal activity (Cohen-Tannoudji *et al.* 1989). In agreement, Gelez *et al.* (2004a) demonstrated that inactivation of the neural projections of the main olfactory bulb (which includes projections from the olfactory epithelium) blocks the endocrine response to male odour, whereas inactivation of the projections from the accessory olfactory bulb (which come from the vomeronasal organ) has no effect. The destruction of the neuroreceptors of the olfactory epithelium blocked the endocrine response to the ram odour (Gelez & Fabre-Nys 2004). A general overview of the neural pathways involved in the ewe's response to male odours has been recently provided by Gelez & Fabre-Nys (2006). They observed that although male odours activate pathways involving the accessory olfactory bulb, its role seems to be limited compared to that of the main olfactory bulb.

The maximum response of anoestrous ewes to the male was obtained after full ram contact compared with either contact through an open or an opaque fence, or the application of masks containing ram's wool (odour) (Pearce & Oldham 1988). Similarly, a higher percentage of does ovulated after full contact with bucks than after odour stimulation alone (Walkden-Brown *et al.* 1993). Moreover, in sheep other authors observed that other sensory signals may completely replace the pheromone stimulus (Cohen-Tannoudji *et al.* 1986; 1989). Perkins & Fitzgerald (1994) demonstrated the importance of the sexual behaviour of rams: a higher number of ewes ovulated after mixing them with high- than with low-serving capacity rams.

Overall, although the main stimulating cues are known, it seems that we are still far from determining the relative importance of each cue and how to manage them, as happens in swine, in which synthetic pheromones are utilized in production management.

Male characteristics and management

Little is known regarding those characteristics of the ram that may improve the percentage of

anoestrous ewes that respond to teasing. Some authors observed that Dorset rams are better teasers than Suffolk, Romney, Romney X Finn or Coopworth rams (see Table 1 in review: Ungerfeld *et al.* 2004a).

At least under subtropical conditions, the reproductive activity of bucks is strongly depressed during the non-breeding season: plasma testosterone concentrations, sexual behaviour assessed by ano-genital sniffing, nudging and mounts, sexual odour and vocalizations are all at a low level (reviewed by Delgadillo *et al.* 2006). However, treatments with artificial long days and melatonin implants improve the biostimulatory effect of males. Therefore, these authors consider the reproductive condition of the buck as the limiting factor determining the response of anoestrous does to the male effect.

Another strategy to improve the stimulus of the male effect is to include a group of oestrous females when teasers are joined with anoestrous females (Rodríguez-Iglesias *et al.* 1991). Ewes in oestrus also influence the reproductive activity of rams, mainly by inducing an increase in LH pulse frequency and testosterone concentrations (Yarney & Sanford 1983). The increases may continue for at least 4 days if ewes in oestrus are still present (Ungerfeld & Silva 2004). While the increase in testosterone concentrations is similar in adult or yearling teaser rams, as happens during the developmental period (Sanford *et al.* 1982), LH concentrations reach higher values in yearling rams (Ungerfeld 2003). A possible explanation is that although concentrations are similar, testosterone may be less effective in yearling than in adult rams, as is reflected by a weak effect on the inhibition of pituitary activity. This may be attributed to an increase of feedback inhibition by androgens on the hypothalamo-pituitary axis during the developmental period (Foster *et al.* 1978) and/or to the maturation of the negative feedback mechanism (Courot *et al.* 1975). Therefore, as stimulating signals are related to androgen concentration, we compared the response of ewes to adult or yearling teasers. Significantly more ewes came into oestrus and ovulated after teasing with adult rather than with yearling teasers (MA Ramos & R Ungerfeld, unpublished data: Fig. 2). Moreover, significantly more ewes ovulated after being stimulated with masks containing adult than yearling ram's wool (53.3 versus 29.8%: V Miller, M Cuadro & R Ungerfeld, unpublished data). Therefore, the explanation of the greater effectiveness of adult than of yearling teasers is at least partially explained by quantitative and/or qualitative differences in odour secretion.

The effect of the presence of oestrous ewes is similar if teaser rams had been in contact with oestrous ewes for a short period before being joined with anoestrous ewes (Knight 1985). Rams that have been isolated from ewes and then placed with ewes in oestrus are more effective in stimulating ovulation in anoestrous ewes than are rams that have been in contact with ewes long before the procedure takes place (Knight *et al.* 1998).

Depth of anoestrus

Several parameters have been used to describe the "depth of anoestrus": such as, length of time until the ewe would spontaneously begin to cycle; arbitrary percentages of how many animals are cyclic; responsiveness to the introduction of rams; ovulation rate; LH pulse frequency; and basal circulating LH concentrations (Ungerfeld 2003). Thomas *et al.* (1988) proposed that differences between breeds in the depth of anoestrus could be related to differences in the sensitivity of the hypothalamus to both negative feedback by oestradiol and the direct effects of photoperiod. Overall, LH pulsatility has been consistently proposed as one parameter to assess the depth of anoestrus. We also observed that FSH concentrations before the introduction of rams were significantly higher in ewes that subsequently had a luteal phase than in those that do not (Ungerfeld *et al.* 2004a).

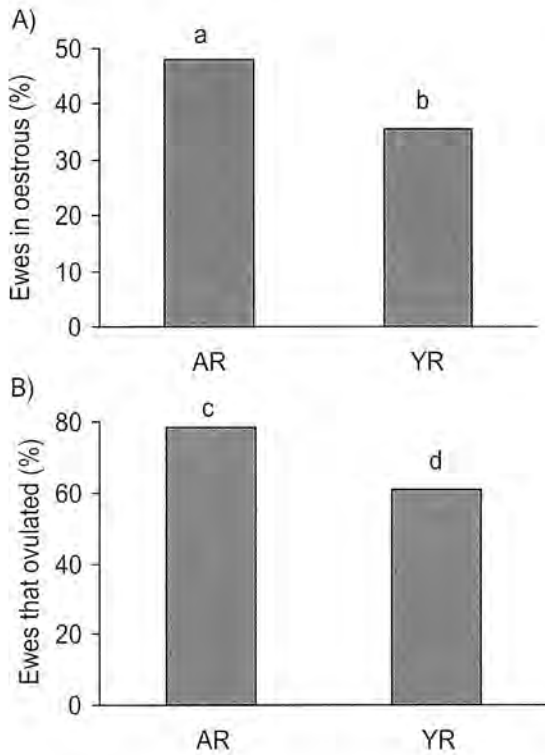


Fig. 2. Percentage of ewes that A) came into oestrus and B) ovulated after a 6-days medroxyprogesterone priming and the introduction of adult rams (AR) or yearling rams (YR) (MA Ramos & R Ungerfeld, unpublished data). The experiment was performed during October (Southern Hemisphere, mid non-breeding season) with Merlin sheep.

The percentage of females that respond to the introduction of males is related to factors such as period of the anoestrous season, parity, previous experience of contact with males and breed (Oldham *et al.* 1985; Nugent III *et al.* 1988; Rodríguez-Iglesias *et al.* 1991; Restall 1992; Gelez *et al.* 2004b; Gelez & Fabre-Nys, 2006). More ewes from a less seasonal breed (for example, Dorset) than from a more seasonal breed (for example, Hampshire) ovulate and conceive after stimulation with rams (Nugent III *et al.* 1988). Ewes from more seasonal breeds may not necessarily respond to the ram effect by ovulating even if they display an increase in LH pulsatility (Minton *et al.* 1991).

Management practices that may improve the effectiveness of stimulation in other breeds may be ineffective in strong seasonal breeds. Three hundred Lincoln ewes, strong seasonal breeders, were stimulated in two consecutive years during January (Southern Hemisphere) joining them with 10 rams from the same breed and twenty ewes in estrus. Forty-eight and 46 ewes were examined laparoscopically 5 days after joining in each year: 2/48 and 0/46 had ovulated (H Irazoqui & RM Rodríguez-Iglesias, personal communication). In another recent experiment using another strong seasonal breed, 46 and 47 Texel ewes were joined during November (Southern Hemisphere) with 6 Texel rams that had been either isolated ($n=3$) or kept near oestrous ewes for 3 days before ($n=3$), respectively. Fifteen and nine ewes respectively were marked by the rams over the 25 days they were together although none of them

became pregnant (MA Ramos, SP González-Pensado & R Ungerfeld, unpublished data). As we could not discriminate the effects of photoperiod on males and females, it remains to be tested in these breeds whether strategies that are effective with bucks may overcome seasonal inhibition (reviewed by Delgadillo *et al.* 2006).

Response to the male effect during the postpartum period in cattle

In cattle, less is known about the physiological mechanisms by which cows respond to stimulation by the bull. Most trials have focused in trying to advance postpartum rebreeding, with very diverse outcomes. The diversity of outcomes and paucity of data makes it difficult to draw conclusions about the possibilities of using social stimuli in postpartum management.

As primiparous beef cattle have an especially long postpartum anoestrous period, it is interesting to determine the potential use of social-signals as stimulators of early rebreeding. The postpartum anoestrous interval in beef cows is shortened after bull introduction (Zalesky *et al.* 1984; Custer *et al.* 1990; Fernández *et al.* 1993; 1996; Rekwot *et al.* 2000; Landaeta-Hernández *et al.* 2004). Similar results have been also obtained with androgen-treated cows, suggesting (as in rams and bucks) that the bull stimulatory effect is also mediated by androgen stimulation (Burns & Spitzer 1992). A female-female effect, has also been described which may result in ovulation (Wright *et al.* 1994). In both the bull and cow effect, it has been demonstrated that odours (probably pheromones) are the main stimulating cues (Izard & Vandenberg 1982; Anderson *et al.* 2002; Berardinelli & Joshi 2005a). Moreover, it has been recently reported that social interactions between bulls and cows seem not to be necessary to obtain the maximum response (Berardinelli & Joshi 2005a). Bull stimulation has been used to stimulate postpartum rebreeding in zebu and buffalo cattle as well as to advance puberty in beef cattle (Izard & Vandenberg 1982; Roberson *et al.* 1987; Bolaños *et al.* 1998; Roberson *et al.* 1991; Ingawale & Dhoble 2004).

However, in some experiments cows failed to respond to bull stimulation (Naasz & Miller 1987; Gifford *et al.* 1989). In the few experiments performed with dairy cattle, no positive response has been observed (Shipka & Ellis 1998; 1999). However, in dual purpose cattle, bull teasing advanced rebreeding (Pérez-Hernández *et al.* 2002). There is also some contradictory information on the physiological mechanisms by which cows respond to bull stimulation: while Fernández *et al.* (1996) observed higher LH serum concentrations and pulsatility, this was not consistent with the results of Custer *et al.* (1990). If the increase of LH pulsatility is slower than that observed in small ruminants, the increase in LH may have not been detected due to the fact that individual animals may show an increase at different times after bull exposure.

The influence of many factors, such as body condition, nutritional status, season and postpartum interval, on the response to bull stimulation has been reported (Alberio *et al.* 1987; Monje *et al.* 1992; Stumpf *et al.* 1992; Larson *et al.* 1994; Berardinelli & Joshi 2005b). Other factors, like bull familiarity to cows and the bulls' age (in contrast to what we observed with rams), seem not to affect the response (Cupp *et al.* 1993; Berardinelli *et al.* 2005). Considering the previous information, it is possible that when bulls are introduced, the diversity of physiological status present in a herd of postpartum cows, at least under extensive conditions, determines that many of them do not respond to the stimulation. If this happens with a significant percentage of cows, no response may be observed in the herd. Therefore, when cows gradually enter a responsive condition, the acute stimuli of bull introduction may have disappeared. Thus, the greater variation between individuals, compared with ewes or goats during seasonal anoestrus, may explain the lack of consistent and predictable results.

Therefore, one strategy for synchronizing parturition in cattle may be to obtain more homogeneous conditions within the herd. Another strategy may be to prolong the stimuli, allowing cows to respond individually as they develop better physiological conditions. We recently tested this strategy by comparing the time of postpartum rebreeding in two groups of multiparous cows which were extensively managed. At 30-60 days postpartum bulls were introduced to suckling Hereford and Angus cows. In one group, two bulls were changed every week to prolong the stimuli time, while the other group remained continuously with the same two bulls. After 7 weeks 91.1% and 47.8% of the cows from the groups with or without bull rotation, respectively, were cycling ($P < 0.001$: V Miller, M Rodríguez-Irazoqui & R Ungerfeld, unpublished results).

Overall view

Overall, insights into the mechanisms involved in the natural socio-sexual stimulation of wild or feral ruminants will promote the inclusion of these management techniques in domestic ruminant production. Better comprehension of the involved mechanisms, strategies to strengthen the stimuli according to female condition and the use of different stimulating techniques may open interesting perspectives. The challenge for researchers is to develop standardized treatments with predictable results in strong seasonal breeds of sheep and goats and during the postpartum period in the three species. We are still far from developments such as those used in swine, in which the application of synthetic stimulating odours to induce ovulation in females is commonly used in reproductive management.

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References

- Adams CA, Bowyer RT, Rowell JE, Hauer WE & Jenks JA 2001 Scent marking by male caribou: an experimental test of rubbing behavior. *Rangifer* **21** 21-27.
- Alberio H, Schiersmann G, Carou N & Mestre J 1987 Effect of a teaser bull on ovarian and behavioural activity of suckling beef cows. *Animal Reproduction Science* **14** 263-272.
- Amoah EA & Bryant M 1984 A note on the effect of contact with male goats on occurrence of puberty in female goat kids. *Animal Production* **38** 141-144.
- Anderson KA, Berardinelli JG, Joshi PS & Robinson B 2002 Effects of exposure to bull or bull excretory products of bulls on the breeding performance of first-calf restricted suckled beef cows using a modified CO-Synch protocol. In *Realistic solutions for maintaining the sustainability of Montana's livestock industry*. Proceedings of the Montana Nutrition Conference, May 7-8, GranTree Inn, Bozeman, Montana, USA.
- Berardinelli JG & Joshi SA 2005a Initiation of postpartum luteal function in primiparous restricted-suckled beef cows exposed to a bull or excretory products of bulls or cows. *Journal of Animal Science* **83** 2495-2500.

- Berardinelli JG & Joshi SA 2005b Introduction of bulls at different days postpartum on resumption of ovarian cycling activity in primiparous beef cows. *Journal of Animal Science* **83** 2106-2110.
- Berardinelli JG, Joshi SA & Tauck SA 2005 Postpartum resumption of ovarian cycling activity in first-calf suckled beef cows exposed to familiar or unfamiliar bulls. *Animal Reproduction Science* **90** 201-209.
- Bérubé CH, Festa-Bianchet M & Jorgenson JT 1999 Individual differences, longevity, and reproductive senescence in Bighorn ewes. *Ecology* **80** 2555-2565.
- Blanvillain C, Ancrenaz M, Delhomme A, Greth A & Sempère A 1997 The presence of the male stimulates puberty in captive female Arabian oryx (*Oryx leucoryx* Pallas, 1777). *Journal of Arid Environments* **36** 359-366.
- Bolaños JM, Forsberg M, Kindahl H & Rodríguez-Martínez H 1998 Biostimulatory effects of estrous cows and bulls on resumption of ovarian activity in postpartum anestrus zebu (*Bos indicus*) cows in the humid tropics. *Theriogenology* **49** 629-636.
- Burns PD & Spitzer JC 1992 Influence of biostimulation on reproduction in postpartum beef cows. *Journal of Animal Science* **70** 358-362.
- Chemineau P 1985 Effects of a progestagen on buck-induced short ovarian cycles in the Creole meat goat. *Animal Reproduction Science* **9** 87-94.
- Chemineau P, Pellicer-Rubio M-T, Lassoued N, Khaldi G & Monniaux D 2006 Male-induced short oestrous and ovarian cycles in sheep and goats: a working hypothesis. *Reproduction Nutrition Development* **46** 417-429.
- Claus R, Kaufmann B, Dehnhard M & Spitzer V 1999 Demonstration of 16-unsaturated C-19 steroids ("boar pheromones") in tissues of the male camel (*Camelus dromedarius*). *Reproduction in Domestic Animals* **34** 455-458.
- Cohen-Tannoudji J, Lavenet C, Locatelli A, Tillet Y & Signoret JP 1989 Non-involvement of the accessory olfactory system in the LH response of anoestrous ewes to male odour. *Journal of Reproduction and Fertility* **86** 135-144.
- Cohen-Tannoudji J, Locatelli A & Signoret JP 1986 Non-pheromonal stimulation by the male of LH release in the anoestrous ewe. *Physiology & Behavior* **36** 921-924.
- Courot M, De Reviers M-M & Pelletier J 1975 Variations in pituitary and blood LH during puberty in the male lamb. Relation to time of birth. *Annales de Biologie Animale Biochimie Biophysique* **15** 509-516.
- Cupp AS, Roberson MS, Stumpf TT, Wolfe MW, Werth LA, Kojima N, Kittok RJ & Kinder JE 1993 Yearling bulls shorten the duration of postpartum anestrus in beef cows to the same extent as do mature bulls. *Journal of Animal Science* **71** 306-309.
- Custer EE, Berardinelli JB, Short RE, Wehrman M & Adair R 1990 Postpartum interval to estrus and patterns of LH and progesterone in first-calf suckled beef cows exposed to mature bulls. *Journal of Animal Science* **68** 1370-1377.
- Delgadillo JA, Fitz-Rodríguez G, Duarte G, Veliz FG, Carrillo E, Flores JA, Vielma J, Hernández H & Malpaux B 2004 Management of photoperiod to control caprine reproduction in the subtropics. *Reproduction Fertility and Development* **16** 471-478.
- Delgadillo JA, Flores JA, Veliz FG, Duarte G, Vielma J, Hernández H & Fernández IG. 2006. Importance of the signals provided by the buck for the success of the male effect in goats. *Reproduction Nutrition Development* **46** 391-400.
- Fernández DL, Berardinelli JG, Short RE & Adair R 1993 The time required for the presence of bulls to alter the interval from parturition to resumption of ovarian activity and reproductive performance in first-calf suckled beef cows. *Theriogenology* **39** 411-419.
- Fernández DL, Berardinelli JB, Short RE & Adair R 1996 Acute and chronic changes in luteinizing hormone secretion and postpartum interval to estrus in first-calf suckled beef cows exposed continuously or intermittently to mature bulls. *Journal of Animal Science* **74** 1098-1103.
- Ferreria J, Rodríguez-Iglesias RM, Ciccioli NH, Pevsner DA & Rosas CA 2005 Características del cuerpo lúteo de ovejas Corriedale en anestro tratadas con acetato de medroxiprogesterona (MAP) en diferentes momentos previo a una bioestimulación. In 28 Congreso Argentino de Producción Animal. Bahía Blanca, Buenos Aires, Argentina. *Revista Argentina de Producción Animal* **25**, Supplement 1 117.
- Fisher MW, Meikle LM & Johnstone PD 1995 The influence of the stag on pubertal development in the red deer hind. *Animal Science* **60** 503-508.
- Foster DL, Mickelson IH, Ryan KD, Coon GA, Drongowski RA & Holt JA 1978 Ontogeny of pulsatile luteinizing hormone and testosterone secretion in male lambs. *Endocrinology* **102** 1137-1146.
- Fulkerson WJ, Adams NR & Gherardi PB 1981 Ability of castrated male sheep treated with oestrogen or testosterone to induce and detect oestrus in ewes. *Applied Animal Ethology* **7** 57-66.
- Geist V 1965 On the rutting behavior of the mountain goat. *Journal of Mammalogy* **45** 551-568.
- Geist V 1971 *Mountain sheep. A study in behaviour and evolution*. University of Chicago Press, Chicago, IL, USA.
- Gelez H & Fabre-Nys C 2004 The "male effect" in sheep and goats: a review of the respective roles of the two olfactory systems. *Hormones and Behavior* **46** 257-271.
- Gelez H & Fabre-Nys C 2006 Role of the olfactory systems and importance of learning in the ewes' response to rams or their odours. *Reproduction Nutrition Development* **46** 1-10.
- Gelez H, Archer E, Chesneau D, Magallon T & Fabre-Nys C 2004a Inactivation of the olfactory amygdala prevents the endocrine response to male odour in anoestrous ewes. *European Journal of Neuroscience* **19** 1581-1590.
- Gelez H, Archer E, Chesneau D, Campan R & Fabre-Nys C 2004b Importance of learning in the response of

- ewes to male odor. *Chemical Senses* **29** 555-563.
- Geytenbeek PE, Oldham CM & Gray SJ** 1984. The induction of ovulation in the postpartum ewe. *Proceedings of the Australian Society of Animal Production* **15** 353-356.
- Gifford DR, D'Occhio MJ, Sharpe PH, Weatherly T & Pittar RY** 1989 Return to cyclic ovarian activity following parturition in mature cows and first-calf heifers exposed to bulls. *Animal Reproduction Science* **19** 209-212.
- Green MJB** 1987 Scent-marking in the Himalayan musk deer (*Moschus chrysogaster*). *Journal of Zoology, London (B)* **1** 721-737.
- Grubb P & Jewell PA** 1973 The rut and the occurrence of oestrus in the Soay sheep on St Kilda. *Journal of Reproduction and Fertility (Supplement)* **19** 491-502.
- Hogg JT, Hass CC & Jenni DA** 1992 Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. *Behavioral Ecology and Sociobiology* **31** 242-251.
- Hosack DA, Miller KV, Ware LH, Mashburn KL, Morrow CJ, Williamson LR, Marchinton RL & Monfort SL** 1999 Stag exposure advances the LH surge and behavioral estrus in Eld's deer hinds after CIDR device synchronization of estrus. *Theriogenology* **51** 1333-1342.
- Ingawale MV & Dhoble RL** 2004 Buffalo reproduction in India: an overview. *Buffalo Bulletin* **23** 4-9.
- Izard MK & Vandenberg JG** 1982 The effects of bull urine on puberty and calving date in crossbred beef heifers. *Journal of Animal Science* **55** 1160-1168.
- Jewell PA** 1976 Selection for reproductive success. In *The evolution of reproduction*, pp 71-109. Eds CR Austin and RV Short. Cambridge: Cambridge University Press.
- Jewell PA** 1997 Survival and behaviour of castrated Soay sheep (*Ovis aries*) in a feral island population on Hirta, St. Kilda, Scotland. *Journal of Zoology* **243** 623-636.
- Khalidi G** 1984 Variations saisonnières de l'activité ovarienne, du comportement d'oestrus et de la durée de l'anoestrus post-partum des femelles ovines de race Barbarine: influence du niveau alimentaire et de la présence du mâle. PhD Thesis, UST Languedoc, France.
- Khalidi G & Lassoued N** 1991 Interactions nutrition-reproduction chez les petits ruminants en milieu méditerranéen. In *Proceedings of the International Symposium on Nuclear and Related Techniques in Animal Production and Health*. AIEA/FAO, 15-19 April, Vienna pp 379-390.
- Knight TW** 1985 Are rams necessary for the stimulation of anoestrous ewes with oestrous ewes? *Proceedings of the New Zealand Society of Animal Production* **45** 49-50.
- Knight TW & Lynch PR** 1980 Source of ram pheromones that stimulate ovulation in the ewe. *Animal Reproduction Science* **3** 133-136.
- Knight TW, Tervit HR & Lynch PR** 1983 Effects of boar pheromones, ram's wool and presence of bucks on ovarian activity in anovular ewes early in the breeding season. *Animal Reproduction Science* **6** 129-134.
- Knight TW, Ridland M & Litherland AJ** 1998 Effect of prior ram-ewe contact on the ability of rams to stimulate early oestrus. *Proceedings of the New Zealand Society of Animal Production* **58** 178-180.
- Komers PE, Birgersson B & Ekvall K** 1999 Timing of estrus in fallow deer is adjusted to the age of available mates. *The American Naturalist* **153** 431-436.
- Landaeta-Hernández AJ, Giangreco M, Meléndez P, Bartolomé J, Bennet F, Rae DO, Hernández J & Archbald LF** 2004 Effect of biostimulation on uterine involution, early ovarian activity and first postpartum estrous cycle in beef cows. *Theriogenology* **61** 1521-1532.
- Larson CL, Miller HL & Goehring TB** 1994 Effect of postpartum bull exposure on calving interval of first-calf heifers bred by natural service. *Canadian Journal of Animal Science* **74** 153-154.
- Lassoued N** 1998 Induction de l'ovulation par "effet bélier" chez les brebis de race Barbarine en anoestrus saisonnier. Mécanismes impliqués dans l'existence du cycle ovulatoire de courte durée. PhD Thesis, Univ Tunis II.
- Lassoued N, Khalidi N, Chemineau P, Cognie Y & Thimonier J** 1997 Role of the uterus in early regression of corpora lutea induced by the ram effect in seasonally anoestrous Barbarine ewes. *Reproduction Nutrition Development* **37** 559-571.
- Lincoln GA & Davidson W** 1977 The relationship between sexual and aggressive behaviour, and pituitary and testicular activity during the seasonal sexual cycles of rams, and the influence of the photoperiod. *Journal of Reproduction and Fertility* **49** 267-276.
- Lincoln GA & Short RV** 1980 Seasonal breeding: nature's contraceptive. *Recent Progress in Hormone Research* **36** 1-43.
- Luna-Orozco JR, Flores JA, Hernández H, Delgadillo JA & Fernández IG** 2005 La respuesta de la actividad estral de las cabras nulíparas no diñere de las múltiparas al someterlas al efecto macho. In *Proceedings of the Memorias de la XX Reunión Nacional sobre Caprinocultura*, October 5-7, Universidad Autónoma de Sinaloa, Asociación Mexicana de Producción Caprina, Culiacán Sinaloa, México, pp 397-401.
- Martin GB, Scaramuzzi RJ & Lindsay DR** 1983 Effect of the introduction of rams during the anoestrous season on the pulsatile secretion of LH in ovariectomized ewes. *Journal of Reproduction and Fertility* **67** 47-55.
- Martin GB, Oldham CM, Cognie Y & Pearce DT** 1986 The physiological responses of anovulatory ewes to the introduction of rams - a review. *Livestock Production Science* **15** 219-247.
- Martin GB, Milton JTB, Davidson RH, Banchemo Hunzicker GE, Lindsay DR & Blache** 2004 Natural methods for increasing reproductive efficiency in small ruminants. *Animal Reproduction Science* **82/83** 231-246.
- Mauget R** 1981 Behavioural and reproductive strategies in wild forms of *Sus scrofa* (European wild and

- feral pigs). In *The welfare of pigs*. Ed W Sybesma. *Current Topics in Veterinary Medicine and Animal Science* **11** 3-13.
- McClelland BE 1991 Courtship and agonistic behavior in mouflon sheep. *Applied Animal Behaviour Science* **29** 67-85.
- Mellado M & Hernández JR 1996 Ability of androgenized goat wethers and does to induce estrus in goats under extensive conditions during anoestrus and breeding seasons. *Small Ruminant Research* **23** 37-42.
- Mellado M, Olivas R & Ruiz F 2000 Effect of buck stimulus on mature and pre-pubertal norgestomet-treated goats. *Small Ruminant Research* **36** 269-274.
- Minton JE, Coppinger TR, Spaeth CW & Martin LC 1991 Poor reproductive response of anoestrus Suffolk ewes to ram exposure is not due to failure to secrete luteinizing hormone acutely. *Journal of Animal Science* **69** 3314-3320.
- Miquelle DG 1991 Are moose mice? The function of scent urination in moose. *American Naturalist* **138** 460-477.
- Monje AR, Alberio R, Schiersmann G, Chedrese J, Carou N & Callejas S 1992 Male effect on the post-partum sexual activity of cows maintained on two nutritional levels. *Animal Reproduction Science* **29** 145-156.
- Moore GH & Cowie GM 1986 Advancement of breeding in non-lactating adult red deer hinds. *Proceedings of the New Zealand Society of Animal Production* **46** 175-178.
- Morgan PD, Arnold EW & Lindsay DR 1972 A note on the mating behaviour of ewes with various senses impaired. *Journal of Reproduction and Fertility* **30** 151-152.
- Naasz CD & Miller HL 1987 Effects of bull exposure on postpartum interval and preproductive performance in beef cows. *Journal of Animal Science* **65** (Supplement) 426.
- Nugent III RA, Notter DR & Beal WE 1988 Effects of ewe breed and ram exposure on estrous behavior in May and June. *Journal of Animal Science* **66** 1363-1370.
- O'Riordan EG & Hanrahan JP 1989 Advancing first estrus in ewe lambs. *Farm and Food Research* **20** 25-27.
- Oldham CM, Pearce DT & Gray SJ 1985 Progesterone priming and age of ewe affect the life-span of corpora lutea induced in the seasonally anovulatory Merino ewe by the "ram effect". *Journal of Reproduction and Fertility* **75** 29-33.
- Over R, Cohen-Tannoudji J, Dehnhard M, Claus R & Signoret JP 1990 Effect of pheromones from male goats on LH-secretion in anoestrous ewes. *Physiology & Behavior* **48** 665-8.
- Pearce GP & Oldham CM 1988 Importance of non-olfactory ram stimuli in mediating ram-induced ovulation in the ewe. *Journal of Reproduction and Fertility* **84** 333-339.
- Pearce DT, Oldham CM, Haresign W & Gray SJ 1987 Effects of duration and timing of progesterone priming on the incidence of corpora lutea with a normal life-span in Merino ewes induced to ovulate by the introduction of rams. *Animal Reproduction Science* **13** 81-89.
- Pérez-Hernández P, García-Winder M & Gallegos-Sánchez J 2002 Bull exposure and an increased within-day milking to suckling interval reduced post-partum anoestrus in dual purpose cows. *Animal Reproduction Science* **74** 111-119.
- Perkins A & Fitzgerald JA 1994 The behavioral component of the ram effect: the influence of ram sexual behavior on the induction of estrus in anovulatory ewes. *Journal of Animal Science* **72** 51-55.
- Reinhardt C, Reinhardt A & Reinhardt V 1986 Social behaviour and reproductive performance in semi-wild Scottish highland cattle. *Applied Animal Behaviour Science* **15** 125-136.
- Rekwot PI, Ogwu D, Oyedipe EO & Sekoni VO 2000 Effects of bull exposure and body growth on onset of puberty in Bunaji and Friesian X Bunaji heifers. *Reproduction Nutrition Development* **40** 359-367.
- Restall BJ 1992 Seasonal variation in reproductive activity in Australian goats. *Animal Reproduction Science* **27** 305-318.
- Roberson MS, Ansotegui RP, Berardinelli JG, Whitman RW & McInerney MJ 1987 Influence of biostimulation by mature bulls on occurrence of puberty in beef heifers. *Journal of Animal Science* **64** 1601-1605.
- Roberson MS, Wolfe MW, Stumpf TT, Werth LA, Cupp AS, Kojima ND, Wolfe PL, Kittok RJ & Kinder JE 1991 Influence of growth rate and exposure to bulls on age at puberty in beef heifers. *Journal of Animal Science* **69** 2092-2098.
- Rodriguez-Iglesias RM, Ciccioli N, Irazoqui H & Rodriguez BT 1991 Importance of behavioural stimuli in ram-induced ovulation in seasonally anovular Corriedale ewes. *Applied Animal Behavior Science* **30** 323-332.
- Rowlands IW & Weir BJ 1984 Mammals: non-primate eutherians. In *Marshall's Physiology of Reproduction. Vol. 1. Reproductive cycles of vertebrates*, edn 4, pp 455-658. Ed GE Lamming. Churchill Livingstone, Edinburgh, London, Melbourne, and New York.
- Sanford LM, Palmer WM & Howland BE 1982 Influence of age and breed on circulating LH, FSH and testosterone levels in the ram. *Canadian Journal of Animal Science* **62** 767-776.
- Schaller G & Mirza ZB 1974 On the behaviour of Punjab Urial *Ovis orientalis punjabensis*. In *The behaviour of ungulates and its relation to management. Vol. 1*. Eds V Geist & FR Walther. IUCN Publications, Morges, Switzerland.
- Shackleton DM & Shank CC 1984 A review of the social behavior of feral and wild sheep and goats. *Journal of Animal Science* **58** 500-509.
- Shipka MP & Ellis LC 1998 No effects of bull exposure on expression of estrous behavior in high-producing dairy cows. *Applied Animal Behaviour Science* **57** 1-7.
- Shipka MP & Ellis LC 1999 Effects of bull exposure on

- postpartum ovarian activity of dairy cows. *Animal Reproduction Science* **54** 237-244.
- Shipka MP, Rowell JE & Ford SP 2002 Reindeer bull introduction affects the onset of the breeding season. *Animal Reproduction Science* **72** 27-35.
- Silva L & Ungerfeld R 2006 Reproductive response in suckling Corriedale ewes to the ram effect during the non-breeding season: effect of postpartum condition and of the use of medroxyprogesterone primings. *Tropical Animal Health and Production* **38** 365-369.
- Skinner DC, Cilliers SD & Skinner JD 2002 Effect of ram introduction on the oestrous cycle of springbok ewes (*Antidorcas marsupialis*). *Reproduction* **124** 509-513.
- Skinner JD, Jackson TP & Marais AL 1992 The "ram effect" in three species of African Ungulates. *Ungulates* **91** 565-568.
- Stricklin WR & Mench JA 1987 Social Organization. In *Farm Animal Behavior*. Ed EO Price, WB Saunders Company. *The Veterinary Clinics of North America, Food Animal Practice* **3** 307-322.
- Stumpf TT, Wolfe MW, Wolfe PL, Day ML, Kittok RJ & Kinder JE 1992 Weight changes prepartum and presence of bulls postpartum interact to affect duration of postpartum anestrus in cows. *Journal of Animal Science* **70** 3133-3137.
- Thimonier J, Cognie Y, Lassoued N & Khaldi G 2000 L'effet mâle chez les ovins: une technique actuelle de maîtrise de la reproduction. *INRA Productions Animales* **13** 223-231.
- Thomas GB, Pearce DT, Oldham CM, Martin GB & Lindsay DR 1988 Effects of breed, ovarian steroids and season on the pulsatile secretion of LH in ovariectomized ewes. *Journal of Reproduction and Fertility* **84** 313-324.
- Underwood EJ, Shier FL & Davenport N 1944 Studies in sheep husbandry in W.A.V. The breeding season of Merino, crossbreed and British Breeds ewes in the agricultural districts. *Journal of Agriculture W. A.* **11**, Series 2 135-143.
- Ungerfeld R 2003. The reproductive response of anoestrous ewes to the introduction of rams. Ph.D. Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden. *Acta Universitatis Agriculturae Sueciae, Veterinaria* **163**, pp. 66.
- Ungerfeld R 2005 Sixty years of the ram effect (1944-2004): how we have learned what we know about it? *Journal of Animal and Veterinary Advances* **4** 698-701.
- Ungerfeld R & Rubianes E 2004 Estrous distribution in anoestrous ewes primed with estradiol-17beta 3 or 5 days before the introduction of the rams (the ram effect). In *Proceedings of the International Congress of Animal Reproduction*, August 8-12, Porto Seguro, Brasil.
- Ungerfeld R & Silva L 2004 Ewe effect: endocrine and testicular changes in adult and young Corriedale rams used for the ram effect. *Animal Reproduction Science* **80** 251-259.
- Ungerfeld R, Pinczak A, Forsberg M & Rubianes E 2002 Ovarian and endocrine responses of Corriedale ewes to "ram effect" in the non-breeding season. *Canadian Journal of Animal Science* **82** 599-602.
- Ungerfeld R, Suárez G, Carbajal B, Silva L, Laca M, Forsberg M & Rubianes E 2003 Medroxyprogesterone priming and response to the ram effect in Corriedale ewes during the nonbreeding season. *Theriogenology* **60** 35-45.
- Ungerfeld R, Forsberg M & Rubianes E 2004a Overview of the response of anoestrous ewes to the ram effect. *Reproduction Fertility and Development* **16** 479-490.
- Ungerfeld R, Dago AI, Rubianes E & Forsberg M 2004b Response of anoestrous ewes to the ram effect after follicular wave synchronization with a single dose of estradiol-17beta. *Reproduction Nutrition Development* **44** 1-10.
- Walkden-Brown SW, Restall BJ & Henniawati. 1993 The male effect in Australian cashmere goats 2. Role of olfactory cues from the male. *Animal Reproduction Science* **32** 55-67.
- Walkden-Brown SW, Martin GB & Restall BJ. 1999. Role of male-female interaction in regulating reproduction in sheep and goats. *Journal of Reproduction and Fertility (Suppl.)* **52** 243-257.
- Whittle CL, Bowyer RT, Clausen TP & Duffy LK 2000 Putative pheromones in urine of rutting male moose (*Alces alces*): evolution of honest advertisement? *Journal of Chemical Ecology* **26** 2747-2762.
- Wright PJ, Geytenbeek PE, Clarke IJ & Hoskinson RM 1989 The efficacy of ram introduction, GnRH administration, and immunisation against androstenedione and oestrone for the induction of oestrus and ovulation in anoestrous post-partum ewes. *Animal Reproduction Science* **21** 237-247.
- Wright PJ, Geytenbeek PE & Clarke IJ 1990 The influence of nutrient status of post-partum ewes on ovarian cyclicity and on the oestrous and ovulatory responses to ram introduction. *Animal Reproduction Science* **23** 293-303.
- Wright IA, Rhind SM, Smith AJ & Whyte TK 1994 Female-female influences on the duration of the post-partum anoestrous period in beef cows. *Animal Production* **59** 49-53.
- Yarney TA & Sanford LM 1983 The reproductive-endocrine response of adult rams to sexual encounters with estrual ewes is season dependent. *Hormones and Behavior* **17** 169-182.
- Zalesky DD, Day ML, Garcia-Winder M, Imakawa K, Kittok RJ, D'Occhio MJ & Kinder JE 1984 Influence of exposure to bulls on resumption of estrous cycles following parturition in beef cows. *Journal of Animal Science* **59** 1135-1139.