

Review

The ‘ram effect’ as a way of modifying the reproductive activity in the ewe

H.J.D. Rosa^{a,*}, M.J. Bryant^b

^a Universidade dos Açores, 9701-851 Angra do Heroísmo, Portugal

^b Department of Agriculture, University of Reading, Whiteknights, P.O. Box 236, Reading RG6 6AT, UK

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Abstract

The seasonality of breeding activity in sheep represents an important constraint in the breeding program of commercial flocks. The ‘ram effect’ is one among various techniques available to manipulate reproduction during the anoestrous season but with the advantages of being inexpensive, of easy application and free from causing problems to the consumer of animal foods (i.e. hormone residues). The aim of this paper is to summarize the most important aspects of the ram effect, including the nature of the ram stimuli involved, the behavioural and physiological events elicited in the ewe as a result of the presence of the ram, the neuroendocrine basis of the phenomenon and the various factors associated with variation in response. The effects of a wide range of social relationships on reproductive activity in sheep and other species are also discussed. © 2002 Elsevier Science B.V. All rights reserved.

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1. The importance of social interactions in reproductive activity and a definition of the ‘ram effect’

The social relationships that an animal has with others of the same species can affect many aspects of the reproductive process. This is true for many species and for both sexes. In sheep this effect has been found in all sexual group associations, i.e. male–male, female–female and male–female.

1.1. Male-to-male interaction

The male social environment under which ram lambs are reared can affect the way the future mature

rams perform sexually. It has been suggested that the rearing of rams in all male groups may facilitate the formation of social relationships among males and prevent or delay the development of sexual interest in females (Hulet et al., 1964; Price et al., 1988). In support of this view, Orgeur and Signoret (1984) found that the sexual segregation of ram lambs between 3 and 6 months of age clearly delayed the occurrence of the first copulation. Male stimuli can also have an immediate effect on the reproductive performance of rams. While viewing the courtship and mating behaviours of other rams does not improve the observing rams’ sexual performance (Price et al., 1991), which is in contrast to male cattle (Mader and Price, 1984), goats (Price et al., 1984), pigs (Hemsworth and Galloway, 1979) and horses (Pickett et al., 1977), exposure to a ram that has recently copulated may enhance their reproductive behaviour (Maina and Katz,

* Corresponding author. Tel.: +351-295-402200;
fax: +351-295-402205.
E-mail address: hrosa@angra.uac.pt (H.J.D. Rosa).

1997). These latter workers speculated that an olfactory cue associated with the ewes or the mating act may be emitted by rams following mating with oestrous ewes.

1.2. Female-to-female interaction

The continuous presence of cyclic ewes (Nugent and Notter, 1990; Sunderland et al., 1990; O'Callaghan et al., 1994) or the sudden introduction of oestrous ewes (usually by hormone induction) (Muir et al., 1989; Zarco et al., 1995) to seasonally anoestrous ewes is capable of inducing and synchronizing ovulation in these ewes and thus advancing the onset of the breeding season. This phenomenon is known as social facilitation and because the stimulation is provided by social cues emanating from females it has more recently been designated as the 'female–female effect'. As most observations of this effect have been made in experiments in which rams were also included, it has been suggested that the effect is acting via the rams and therefore the role of the oestrous ewes would be to stimulate the rams which in turn would become more effective at stimulating the anoestrous ewes (Knight, 1985; Nugent and Notter, 1990). However, in addition to this male-mediated effect, a direct female–female effect has recently also been identified (O'Callaghan et al., 1994; Zarco et al., 1995). It appears that a high ratio of oestrous to anoestrous ewes is required for the direct effect to be clearly detected (ratios of 100 and 50%, respectively were used in the two studies reported). On the other hand, the exposure to non-cyclic female flockmates has no effect on the reproductive state of anoestrous ewes (Donovan et al., 1991). Reproductive responses to female-to-female contact have also been observed in goats (Walkden-Brown et al., 1993a,b,c; Restall et al., 1995), cows (Wright et al., 1994), wild boar (Delcroix et al., 1990), humans (McClintock, 1971; Stern and McClintock, 1998) and in many other mammals.

1.3. Male-to-female interaction

Some studies have demonstrated that the sudden introduction of oestrous ewes in a group of rams induces certain changes in the behavioural and endocrinological state of these rams, a phenomenon which can be referred to as the 'female effect'. The presence

of females generally improves the level of sexual activity (Rosa et al., 2000a) and leads to increases in luteinizing hormone (LH) and testosterone concentrations (Sanford et al., 1974; Gonzalez et al., 1991a,b; Perkins et al., 1992). Curiously, these effects seem to be more pronounced during the anoestrous season (Yarney and Sanford, 1983; Schanbacher et al., 1987; Gonzalez et al., 1988), and when the ewes are introduced at sunrise as compared to noon (Gonzalez et al., 1988). The effect is not expressed in homosexual rams (Perkins and Fitzgerald, 1992). Non-oestrous ewes also seem to elicit a response (Gonzalez et al., 1991a; Rosa et al., 2000a). The 'female effect' can even originate at a very young age. Katz et al. (1988) reported that the exposure of ram lambs to ewes during the post-weaning prepubertal period enhanced their sexual performance even though it did not ensure that all males developed sexual preferences for females. It seems, however, that the absence of contact with the opposite sex during rearing is not the reason why some rams fail to mate oestrous ewes, rather it seems to be a consequence of their sexual orientation (Zenchak et al., 1981; Price et al., 1988). On the other hand, yearling rams kept close to ewes in oestrus for 6 months have been found to have larger testes, higher plasma testosterone levels and greater sexual activity than control rams isolated from ewes (Illius et al., 1976). The 'female effect' has also been identified in goats (Walkden-Brown et al., 1994), cattle (Lunstra et al., 1989) and pigs (Ellendorff et al., 1975).

However, of all reproductive effects caused by social interactions, the regulation of the ovarian activity in females brought about by male proximity is the most evident and the best known phenomenon. Because of considerable economic benefits, it is still the most widely investigated socially mediated reproductive effect in sheep reproduction. The exposure of ewes to rams can induce in the reproductive physiology of the ewes either a chronic or an acute effect. In the first case, the continuous presence of a ram can change the timing of the onset and the end of the reproductive season and the duration of oestrus in adult ewes and advance puberty in ewe lambs. Donovan et al. (1991) reported that when ewes were kept in the presence of vasectomized rams during the breeding season, the breeding season ended about 3 weeks later and the onset of the subsequent breeding season was advanced 1 month, compared to ewes without

rams. The period of anoestrous was therefore shortened about 2 months in ewes kept with rams. Also, the results of [Sunderland et al. \(1990\)](#) showed that the continuous presence of rams throughout the year delayed the date of the end of the reproductive season by about 6 weeks. In practice, however, the apparent advantage of keeping rams continuously in ewe flocks disappears because these ewes take more time to begin mating than isolated ewes stimulated to breed by the sudden introduction of rams in late anoestrus as was shown by [Notter \(1989\)](#). Ewes are receptive to rams during oestrus for a shorter period of time when they are permanently associated with males than when they are only allowed occasional contact ([Parsons and Hunter, 1967](#); [Fletcher and Lindsay, 1971](#)). The continuous presence of rams throughout pro-oestrus and oestrus advances ovulation relative to the onset of oestrus (by 8–16 h) by advancing the preovulatory surge of LH ([Lindsay et al., 1975](#)). A chronic effect of ram presence was also identified in ewe lambs by [Al-Mauly et al. \(1991\)](#); first ovulation occurred significantly earlier in those animals kept close to rams for 1.5 or 2 months before ovulation compared to isolated controls.

The acute effect caused by the contact of ewes with rams has long been known as the ram effect. It is characterized by rapid response of the ewes to the unaccustomed presence of the rams. Exposure to rams initiates the endocrine events that lead to ovulation which occurs in most responsive ewes within 50 h ([Martin et al., 1986](#)) of first contact with the rams. This response has been identified in prepubertal, lactational and seasonal anoestrous ewes. The effect of the presence of the ram on the onset of puberty in the young ewe has been reported by several authors and for several breeds. [Oldham and Gray \(1984\)](#) reported that 60% (beginning of breeding season) and 28% (middle of breeding season) of 9–19 months old Merino ewes had ovulated within 4 days of ram introduction compared to 0% of isolated controls. [Kassem et al. \(1989\)](#) found that exposure of Awassi ewe lambs to rams reduced the mean age at first oestrus by 16 days and the mean age to conception by 19 days. The same period of 16 days was reported by [Al-Mauly et al. \(1991\)](#) as the advancement of ovulation in the Suffolk × Mule type. The fact that ewes in lactational anoestrus during their normal breeding season can begin cyclic oestrous activity earlier as a response to the introduction of rams

was probably first suggested by [Mauléon and Dauzier \(1965\)](#). In the work of [Poindron et al. \(1980\)](#) where rams were introduced during the breeding season to lactationally anoestrous ewes on day 21 post-partum, only 1 out of 21 ewes did not show a clear-cut response to rams in terms of LH secretion and 14 out of 18 of these ewes ovulated 3 days after ram introduction. The occurrence of oestrus in post-partum anoestrous ewes, following a sudden introduction of rams was studied by [Wright et al. \(1989\)](#), who found that within 7 days of ram introduction (when ewes were 20–37 days post-partum) 16 out of 19 progestagen pre-treated ewes showed oestrus, against 4 out of 20 progestagen pre-treated ewes which had been in continuous association with rams for the last 3 months.

The term ram effect is, however, most used in the literature to designate the acute effect that ram presence has in adult seasonally anovular ewes, inducing ovulation and oestrus when ewes are exposed to rams in late anoestrous/early oestrous season in the most highly seasonal breeds. The effect may be induced at almost any time in less seasonal breeds such as the Merino ([Lindsay, 1996](#)) and Mediterranean breeds ([Folch, 1990](#)). For this reason, and also because the present paper deals with seasonally anoestrous ewes, the expression ram effect will more often be used, from this point onwards, in its restricted sense.

In addition to sheep, the ‘male effect’, understood as the general effects caused by the presence of the male on the reproductive physiology of the female, has been found to be exhibited in a wide range of other species including goats (earlier occurrence of puberty, [Amoah and Bryant, 1984](#); earlier resumption of ovulation in seasonal anoestrous, [Walkden-Brown et al., 1993a,b,c](#)), cattle (earlier occurrence of puberty, [Izard and Vandenberg, 1982](#); earlier resumption of ovulation in post-partum anoestrus, [Zalesky et al., 1984](#)), pigs ([Hemsworth and Barnett, 1990](#); [Hughes et al., 1990](#); [Soede, 1993](#)) and red deer (advancement of breeding season, [McComb, 1987](#); [Fisher and Fennessy, 1990](#); advancement of puberty, [Fisher et al., 1995](#)).

From both the practical and economic points of view, the ram effect not only has the advantage of substantially increasing the efficiency of breeding, allowing the reproductive season to be advanced by 4–6

weeks or more (in highly or lowly seasonal breeds, respectively) it can also provide a good degree of female synchrony at the time of mating and therefore later at the time of lambing. Thus, the use of this phenomenon as a technique in the sheep industry, has clear advantages in most production systems, but especially in extensive systems where technologies based on prostaglandins or progestagens are relatively expensive and difficult to apply. In wool flocks in Australia, for instance, where over 10 million Merino ewes are mated annually during the anoestrous season (Martin et al., 1986), the ram effect has and probably always will have, according to Martin (1995), far more impact than those technologies based on exogenous hormones.

2. Source and nature of ram stimuli

In spite of some contradictions and many unanswered questions found in the literature, it has become quite clear that the stimuli involved in the ram effect originate primarily from pheromones (according to the definition of Karlson and Luscher, 1959) produced spontaneously by the rams (Signoret, 1991), in association with behavioural cues generated mainly during the courtship activity. It is also clear that the ewe uses the senses of smell, sight, hearing and touch to perceive these stimuli. There is also mounting evidence to support the concept that, despite the fact that different sensory cues can act alone with positive results, the maximum effect can in many cases only be achieved when they act together in a synergistic way. The existence of a stress component, associated with the physical contact of the ewes with the rams has also been suggested (Edgar and Bilkey, 1963; Pearce and Oldham, 1988).

2.1. Pheromonal stimuli

The ram effect was first documented by Underwood et al. (1944), and in subsequent years many research groups have studied the effect of ram introduction on oestrous activity in ewes (Schinckel, 1954; Riches and Watson, 1954; Radford and Watson, 1957; Smith et al., 1958; Edgar and Bilkey, 1963). None of these studies provided information regarding the nature of the stimulation involved. The first work designed to

investigate this subject was carried out by Watson and Radford (1960). After testing the effects of various degrees of associations of ewes with rams, these authors concluded that olfactory and auditory cues originating from the ram were sufficient to stimulate the ewes, and full contact between the sexes (including visual and tactile cues) was not necessary to obtain the response. Some years later, Morgan et al. (1972) working with ewes with various senses impaired (smell, hearing and touch around the mouth) found that only the deprivation of smell significantly affected the number of ewes showing oestrus. This observation led them to suggest that the ram stimulates oestrous activity in anoestrous ewes through olfactory receptors existing in the ewe. The results of these last two studies provided perhaps the first indication that the effect of ram presence on the ewe's reproductive physiology is mediated via pheromones. This hypothesis was investigated in detail by Knight and Lynch (1980a) who sprayed rams' urine over a group of ewes, smeared wax collected from around the eyes and the bare skin of the rams' flanks on the nostrils of ewes in a second group and applied wool recently shorn from rams over the muzzle of ewes in a third group. These authors found that the wool and wax stimulated ovulation in a proportion of ewes similar to those exposed to rams, while urine did not stimulate a significant number of ewes. These results not only demonstrated the involvement of pheromones in the ram effect but also indicated that pheromones are present in the wool and wax of the rams and, unlike the situation in other animals such as rodents, ram's urine is not a major source of pheromones contributing to the ram effect. These observations were subsequently confirmed by Knight and Lynch (1980b) and Knight et al. (1983). It is now known that fleece from any part of the ram's body as well as ethanol or methylene chloride extracts of this fleece and secretion from orbital glands (but not the urine or inguinal wax) are equally effective at stimulating the ewes (Cohen-Tannoudji, 1988 cited by Signoret, 1991; Cohen-Tannoudji et al., 1994). This gives a good indication of the body distribution of the pheromones. The site of synthesis of the pheromones, though not yet demonstrated, appears to be the sudoriferous glands from where they are secreted with the suint (Knight and Lynch, 1980b).

Considering the similarities between sheep and goats in the ability of the females to ovulate as a response to the presence of a male of the same species and that in both cases the phenomenon is mediated by pheromones (Chemineau, 1987), the possibility that ewes could be stimulated by the presence of a male goat (buck), or its pheromones, has been investigated. Knight et al. (1983) compared entire bucks with rams and found that bucks stimulated ewes to ovulate but not as effectively as rams did (57% vs 75%, respectively ovulated). The difference was not, however, statistically significant. This ability of male goats to induce ovulation in ewes was later confirmed by McMillan (1987), although the difference between the proportions of ewes which ovulated when teased by bucks or rams was larger and statistically significant (42% vs 95%, respectively). Interestingly, in this experiment, ewes that did not respond to bucks ovulated after being introduced to rams and the pattern of response was similar to that achieved when isolated ewes were teased by rams. This finding challenges the traditional notion of a period of male–female separation before ram introduction as a requisite for achieving the ram effect. The direct effect of pheromones produced by bucks was investigated by Over et al. (1990). Using masks containing either hairs collected from the head of different breeds of bucks or cotton pads with chemical fractions extracted from the buck hair, these workers detected immediate increases in LH secretion in 9 out of 11 ewes wearing buck hair masks and in 16 out of 21 ewes wearing masks containing the extracts. Curiously, only 1 out of 6 goats responded to rams' wool and none of them reacted to rams' wool extracts. These results seem to suggest that buck and ram pheromones might be a complex of substances, some with similar and some with distinct chemical structures. Attempts to isolate and identify these compounds have been unsuccessful. Knight and Birch (1983) found that neither 4-ethyl-octanoic acid (OA) nor 4-methyl-OA, two of the most important fatty acids responsible for typical 'goaty' odours (4-methyl-OA is also present in mutton fat), are not involved in the ram effect. The study of Birch et al. (1989) confirmed this finding and showed that crude extracts of fatty acids made from bucks' hair obtained from the head and neck region were effective at stimulating ewes to ovulate. However, the complexity of the free fatty acid fraction demonstrated by the gas chromatography technique used did not allow

the identification of the pheromones. More recently Cohen-Tannoudji et al. (1994) found that the separation of an extract of rams' wool (contaminated with anti-orbital secretion) in acid and neutral fractions resulted in each case in a complete loss of capacity to stimulate LH secretion in anoestrous ewes whereas both together were efficient, suggesting again that the pheromonal action involves several components.

The pheromones produced by boars, which have long been identified as 3 α -hydroxy-5 α -androst-16-ene and 5 α -androst-16-ene-3-one, have also been tested in sheep. However, unlike goats' pheromones, these are not effective at stimulating ewes to ovulate (Knight et al., 1983).

An interesting point related to the action of pheromones on the reproductive physiology of the female sheep is the way in which the chemical information is received and processed in order to activate the centres of control of reproductive function. Most mammals have two distinct olfactory systems (Martin et al., 1986; Weller, 1998); the main olfactory system, which receives sensory inputs from receptors localized in the olfactory epithelium in the nose and transmits information to the central nervous system via the main olfactory bulbs, and the accessory olfactory system which receives information through receptors found in a specialized structure known as the vomeronasal organ (VNO). The VNO is localized close to the nasal cavity and transfers the information to the accessory olfactory bulb and other regions of the brain, including the anterior part of the hypothalamus which controls the neuroendocrine systems involved in reproduction. A detailed description and the schematic representation of the two olfactory systems are presented by Martin et al. (1986). These two different systems are the only candidates to constitute the pathway whereby pheromone information is transferred to the hypothalamus. Mammals usually use the accessory system to receive and process the pheromonal information (Weller, 1998). In sheep, however, Cohen-Tannoudji et al. (1989) questioned the involvement of this pathway when the destruction of the VNO did not prevent ewes from responding to rams' odor (only wool was presented). As the surgery did not affect the main system, leaving the general sense of olfaction intact, the authors suggested that this might be the system involved in the process.

2.2. Behavioural stimuli

For many years, reports in the literature assumed that the ram effect was mediated only by pheromones, or at least, the suggestions that other cues could be involved were very rare. Knight (1983) in his review of the literature only reports the role of pheromones. Much emphasis on pheromones is also given in the review of Haynes and Haresign (1987). Martin et al. (1986) in their extensive review, pay more attention to a behavioural component mainly supported by the data of Signoret et al. (1982) which showed that androgen-treated wethers (castrated males) that displayed intense sexual activity induced ovulation in anoestrous ewes more effectively than males given the same dose of androgen but which were relatively inactive. The hypothesis that sensory cues other than smell could influence the response of ewes to rams was tested by Cohen-Tannoudji et al. (1986) using ewes with their olfactory bulbs surgically ablated (both main and accessory olfactory systems were destroyed). This study showed that these ewes displayed a similar LH response to rams as control intact ewes. The authors suggested that non-olfactory sensory cues were also involved and could not only act synergistically with the pheromones but also replace them in triggering the same physiological response. In a series of three experiments designed to test the relative importance of non-olfactory ram stimuli, Pearce and Oldham (1988) exposed intact ewes to various degrees of contact with rams (e.g. full physical contact, contact through a clear fence, contact through an opaque fence, contact with rams' wool in face masks, complete isolation from males). The results indicated that the contact through the opaque fence (mainly olfactory cues) was less effective than through the clear fence and the maximum effect was achieved in all cases when the ewes were allowed full physical contact with the rams. This study demonstrated the involvement of a combination of stimuli from rams. From the results obtained, the authors speculated that in ewes more sensitive to the rams (less 'deep' in anoestrus, i.e. more close to oestrous season) the contact with rams through a fence can be effective at stimulating them but in less sensitive ewes (animals in 'deep' anoestrus) full physical contact is needed. The physical contact between the sexes seems, therefore, to be a potent way of facilitating the release

of certain stimuli which could maximize the effectiveness of the ram effect. Assuming this, Perkins and Fitzgerald (1994) explored the idea that intensive sexual behaviour displayed by the rams towards the ewes would increase the intensity of those stimuli and consequently improve the response. These authors compared rams exhibiting high and low levels of sexual performance and found that the high performance rams had a significantly greater effect on anoestrous ewes than did the low performing rams, with 95% vs 78% of ewes showing oestrus, respectively. However, the analysis of behavioural data revealed that low libido rams spent more time close to the ewes than high libido rams. It was thus demonstrated that the 'physical contact' requires more than just the presence of the ram. This study illustrated the importance of sexual behaviour in the ram effect. Non-pheromonally mediated effects have also been reported in the response of female goats to the presence of bucks (Chemineau et al., 1986).

2.3. Stress stimuli

The fact that stress can affect some aspects of reproduction in various species is not a new concept and is well documented in the literature (Rivier and Rivest, 1991; Dobson and Smith, 1995). In a general way, the diversity of types of stressors (e.g. physical, psychological, physiological) have a deleterious effect on reproductive efficiency of farm animals. In the ewe, for instance, stress associated with confinement causes a decrease in LH pulse frequency (Rasmussen and Malven, 1983) while high temperature (Sawyer et al., 1979), repeated laparoscopy examinations (Martin et al., 1981) or electrical stimulation applied to the feet (Przekop et al., 1984), have been shown to inhibit or delay the preovulatory LH surge and ovulation. In contrast, some authors have observed induced ovulations in anoestrous ewes when they were subject to acute stress caused by long distance transport (Braden and Moule, 1964). Edgar (1958) noted the same effect in ewes receiving rectal electrical stimulations. Others (Adams et al., 1993), have reported that intensive blood samplings (e.g. at intervals of 4 h for 4 days including one period of 12 h at 20 min intervals and another period of 4 h at 10 min intervals) have significantly increased the plasma concentration of gonadotrophins and the ovulation rate in ewes bearing

progestagen-containing sponges. The Pearce and Oldham (1988) proposal that a stress reaction was involved, resulted from the observation that a significantly greater number of ewes wearing empty masks (used as controls for ewes wearing masks containing rams' wool) ovulated as compared to non-masked ewes. Nevertheless, such high levels of stress are unlikely to be generated merely by the joining of rams to ewes in normal situations. Therefore, the role that stress can have in the attainment of the ram effect is likely to be small, and of no practical significance.

The implication of androgens in the ram's ability to induce ovulation in anoestrous ewes has been demonstrated in various studies in which ewes and castrated rams, which are both ineffective in being able to induce ovulation, became able to induce ovulation following a treatment with high doses of testosterone (e.g. 105 mg testosterone propionate three times at weekly intervals) (Fulkerson et al., 1979, 1981; Croker et al., 1982; Signoret et al., 1982). Similar results have also been found in goats with goat wethers and does (Mellado and Hernández, 1996). This fact has strongly suggested the dependence of pheromones on androgen concentrations. On the other hand, testosterone also influences sexual activity (D'Occhio and Brooks, 1982) which is another component of stimuli involved in the ram effect. This, together with the observation that some rams with higher concentrations of testosterone are less effective at stimulating ewes than rams with lower concentrations (Tervit and Peterson, 1978) raises the question, still not answered, of what kind of correlation exists between the testosterone status of the rams and their ability to produce pheromones and to display sexual activity and in the end their ability to induce reproductive activity in anoestrous ewes.

3. Endocrine mediation of the ram effect

The first endocrine response of the ewe to the introduction of the ram is an increase in basal LH secretion, within 2–4 min, leading up to a peak which can occur within 10–20 min (Martin et al., 1980a, 1986; Poindron et al., 1980). This ram-induced pulse is then followed by a dramatic increase in pulse frequency which is known to be maintained for at least 12 h (Martin et al., 1986) and to have already declined by 24 h, remaining low thereafter (Atkinson and

Williamson, 1985). There is a diurnal variation in the LH response with ewes responding earlier when rams are introduced in the morning than in the evening (Martin et al., 1985). The increase in LH pulsatility is accompanied by a decrease in pulse amplitude which plays no role in the ram effect (Martin et al., 1986). In contrast to LH, the secretion of follicle-stimulating hormone (FSH) has been reported either to remain unchanged (Martin et al., 1980a,b) or to decrease and remain low (Atkinson and Williamson, 1985).

The best way to understand the endocrine mediation of the ram effect is by comparing the events that take place during the period from ram introduction to ovulation in the anovular ewe with the normal follicular phase of the cyclic ewe. On introduction of the ram, the initial response in LH, i.e. an increase in pulse frequency accompanied by a decrease in pulse amplitude, is similar to what happens during the follicular phase. It is well known that this increased pulse frequency of LH is the critical step in the ram effect, leading up to the preovulatory LH surge and consequent ovulation. The question which arises at this stage is whether the LH secretion increases because the presence of rams attenuates the negative feedback effect of the steroids, reversing the effect of photoperiod, or whether or not a direct mechanism independent of the negative feedback of the steroids exists. This issue has been discussed by Pearce and Oldham (1984) and Martin et al. (1986) for whom some observations strongly suggested the existence of a direct mechanism. Firstly, the immunization of anovular ewes against oestradiol-17 β does not increase the frequency of LH pulses until 12 h after treatment, indicating that the effect of negative feedback of the steroids cannot be reversed rapidly and the increase in LH pulsatility is observed within minutes of ram introduction. Secondly, in the absence of oestrogen, the introduction of rams can increase LH pulsatility in ovariectomized ewes. Thirdly, the ram stimuli must be maintained for the response to be continued. Fourthly, the presence of rams can also affect cyclic ewes which are not very sensitive to the negative feedback of oestradiol. The exact relationship between LH and oestradiol during this period is not yet well established. It seems, however, that in the majority of ewes, the sequence of events during pro-oestrus and oestrus that normally leads to ovulation also takes place, with the involvement of the normal system of positive feedback of oestradiol

on LH (Martin, 1984). In a minority of ewes the LH surge seems to be the result of LH secretion increases induced by the ram. In fact, in some ewes, LH surges have been observed within 6–12 h of ram introduction (Oldham et al., 1978; Pearce et al., 1985). Although an LH surge can be induced in anoestrous ewes after 6–8 h of oestradiol injections, Martin et al. (1986) consider it unlikely that those LH surges are the result of the positive feedback system because time is required for oestradiol levels to increase. Whatever the mechanism regulating it, the preovulatory LH surge occurs usually within less than 48 h of first contact with the rams (Pearce and Oldham, 1984) but this period varies widely (e.g. 11–50 h; Rosa, 1998).

4. Commencement of ovarian activity and oestrus

Follicular development and maturation begins immediately after ram introduction, presumably in response to the initial rise in LH basal levels and pulse frequency (Atkinson and Williamson, 1985). According to Martin et al. (1986), laparoscopic examination of the ovaries at different times after ram introduction has revealed morphological changes similar to those observed in cyclic ewes. The interval from ram introduction to ovulation is shorter than the follicular phase of cyclic ewes. Most ewes ovulate within 50–65 h (Knight, 1983; Martin et al., 1986) but the response can range from 30 to 72 h (Oldham, 1980). The interval from the onset of the LH surge to ovulation is more constant ranging from 22 to 26 h (Martin et al., 1986). The relatively high degree of synchronization observed in the induced ovulation is not seen at the first observed oestrus. There is usually a spread of 10 days, with peaks in oestrous activity around day 18 and 24 after ram introduction. The literature is abundant in reports describing this phenomenon and the two reasons which explain it (Corke, 1980; Cognie et al., 1982; Knight, 1983; Pearce and Oldham, 1984; Martin et al., 1986). Firstly, the first ram-induced ovulation is never accompanied by oestrous behaviour and secondly, the corpus luteum (CL) which follows this ovulation is normal in some ewes but has a short life-span in other ewes. In a flock, from the ewes that respond, about 50% develop a normal CL which is maintained during the normal period of the luteal phase and end up with a new ovulation, this time with

oestrus, around day 18–19. The remaining 50%, however, develop a subnormal CL with a short life-span which regresses around day 7, causing a short cycle and a second ‘silent’ ovulation, followed this time by a CL which persists normally, resulting in a second grouping of oestrus around day 24.

5. Cause and prevention of short cycles and ‘silent’ ovulations

Short oestrous cycles associated with abnormal corpora lutea are not an exclusive characteristic of ram-induced ovulations. It is often observed at the onset of puberty (Keisler et al., 1983), at the initiation of cyclic activity following post-partum anoestrus (Sharpe et al., 1986) or when ovulation is induced with gonadotropin-releasing hormone (GnRH) infusions in seasonal anoestrous ewes (Southee et al., 1988a). It is well known that if the ewes which ovulate in response to the ram effect (Cognie et al., 1982; Oldham et al., 1985; Pearce et al., 1985, 1987; Lassoued et al., 1997) or to treatment with GnRH (Hunter et al., 1988; Southee et al., 1988a) are pre-treated with progesterone, all CL formed have a normal function. Progesterone can be administered by intramuscular injections, subcutaneous implants or intravaginal sponges. If ewes are treated with a single injection, the response is dependent upon the dose, with 20 mg being the minimum amount to ensure a 100% response (Cognie et al., 1982; Oldham et al., 1985) but this response is independent of the timing of administration (at the time of ram introduction or up to 5 days before; Pearce et al., 1987). If the progesterone is administered by intravaginal devices, the duration of treatment can be important and the results of Pearce et al. (1987) showed a positive correlation between the duration of progesterone priming and the incidence of normal corpora lutea at least up to 24 h before ram introduction. However, a 24 h period was not enough to maximize the response. These results, together with the observation that a single injection of 20 mg progesterone will raise plasma concentrations for 30–38 h, led Pearce et al. (1987) to suggest that a minimum period of about 30 h exposure to elevated progesterone might be required to guarantee normal luteal development.

The mechanism by which progesterone pretreatment prevents the occurrence of abnormal corpora

lutea and consequent short cycles was investigated by [Pearce et al. \(1985\)](#). These authors found that when ewes received an injection of 20 mg of progesterone immediately before ram introduction, the preovulatory surge of LH was delayed (progesterone attenuates but does not completely block the ram-induced LH increase) and subsequent short cycles were prevented. However, when a premature preovulatory LH surge was induced (at 26 h as opposed to 72 h) in progesterone-primed ewes with GnRH injections, the priming effect of progesterone disappeared and most ewes displayed CL of short life-span. This observation led the authors to suggest that progesterone acted by delaying the LH surge and thereby exposing the developing follicles to a longer period of stimulation by gonadotrophins, ensuring that they were mature when ovulation occurred. This explanation was later proved to be wrong when [Pearce et al. \(1987\)](#) demonstrated that the beneficial effect of progesterone on the proportion of CL with normal life-span was maintained even when the injections were administered up to 5 days before ram introduction, while the timing of the LH surge was only delayed when progesterone was given at the time of ram introduction. Since the studies of [Southee et al. \(1988b\)](#) and [Keisler and Keisler \(1989\)](#) have demonstrated that hysterectomy prevents the premature regression of the abnormal CL in seasonal anoestrous ewes treated with GnRH, it has been accepted that the short life-span of the CL is the result of premature release of uterine prostaglandin (PGF_{2α}). Later, [Chemineau et al. \(1993\)](#) found that hysterectomy also prolongs the life-span of CL in seasonally anoestrous ewes induced to ovulate by the introduction of rams and more recently, [Lassoued et al. \(1997\)](#) made the observation that the occurrence of these ram-induced abnormal CL can be eliminated either by hysterectomy or by the administration of an inhibitor of PGF_{2α} (flunixin). Both these studies support the view that premature release of prostaglandin is the cause of early luteal regression and show that it is independent of the cause which induces the ovulation (GnRH injection or ram effect). However the mechanism by which progesterone pretreatment inverts this process is not known and the fact that progesterone could induce altered uterine activity during folliculogenesis has been suggested ([Hu et al., 1991](#)). [Lassoued et al. \(1997\)](#) suggested that the lack of progesterone and its inhibitory action on oestradiol secretion allows the establish-

ment of endometrial oxytocin receptors on day 5, following ram introduction, with consequent increase in prostaglandin release (PGF_{2α} secretion depends on oxytocin receptor concentration in the uterus which increases in response to the decrease of progesterone and increase of oestradiol concentrations in plasma). Thus, with the pretreatment with progesterone, both the establishment of oxytocin receptors and the response of prostaglandins to oxytocin are inhibited and the premature regression of the CL is prevented. The first ovulation will be accompanied by oestrous behaviour if progesterone (or progestagen) is administered for at least 10 days and rams are introduced at sponge removal or at the last injection ([Cognie et al., 1982](#); [Knight, 1983](#); [Martin et al., 1986](#)).

6. Requirement for pre-isolation of the rams

Since the early reports on the ram effect ([Underwood et al., 1944](#); [Schinckel, 1954](#)), it has been assumed that ewes must be anovular and have been preconditioned by a period of isolation from rams for them to ovulate in response to the re-introduction of rams. In spite of the many reports on the ram effect, very little work has been done in this area and the precise duration of isolation required is not known. It probably depends upon many factors such as breed of both sexes, period of the year, location etc. [Oldham \(1980\)](#) reported 34 days and probably 17 days isolation to be sufficient in Merino ewes and 21 as sufficient in Ile-de-France ewes, while [Martin et al. \(1986\)](#) reported that as little as 2 weeks could be adequate. In practice, this issue does not seem to be very important since most workers take no chance and isolate the sexes for a number of weeks. As the male goat can be effective at stimulating ewes ([Knight et al., 1983](#)) it has been recommended to keep bucks away from the ewes during the period of ram isolation. This notion of the importance of isolation of the two sexes has, however, been challenged by some findings. [McMillan \(1987\)](#) reported that ewes remaining anovular after 4 days of contact with bucks subsequently ovulated in response to contact with rams. [Pearce and Oldham \(1988\)](#) found that between 89 and 95% of ewes remaining in anoestrus after 65 days of contact with rams, ovulated 4 days after contact with novel rams. Furthermore, [Cushwa et al. \(1992\)](#) reported that a period of isolation

before mating did not increase the percentage of ewes ovulating compared with ewes maintained adjacent to or in contact with rams for up to 90 days before novel rams were introduced (86% vs 85% for isolated and adjacent ewes, respectively). All these results probably indicate that in some situations at least ewes habituate to the presence of particular rams when in continual contact with them but retain the ability to be stimulated by novel males.

An important question to ask is whether or not occasional contact with males is sufficient to induce in the ewes a refractory state to rams which prevent them from responding to the ram effect. [Cohen-Tannoudji and Signoret \(1987\)](#) showed that a short exposure to rams for 2 or 3 h does not compromise the response, in terms of elevated LH pulsatility, to a new stimulation taking place 2, 5 or 15 days later.

7. Period of presence of the rams

Although LH will increase within a few minutes of ram introduction, the secretion of this hormone is high only during the period when rams are present ([Pearce and Oldham, 1984](#)). As a sustained high LH secretion is needed for the preovulatory events to take place, it seems inevitable that the rams must be present for more than just the initial few minutes if the ewes are to ovulate. This subject is well documented in the literature ([Oldham and Cownie, 1980](#); [Signoret et al., 1982](#); [Murtagh et al., 1984a](#); [Folch, 1990](#)) where the results are clear that the presence of rams until ovulation is necessary to maximize the proportion of ewes ovulating. A reduced percentage of ewes ovulate if the rams are withdrawn after 8 or 24 h ([Signoret et al., 1982](#)). The continued presence of rams is also necessary for the maintenance of ovulatory cycles after the first ovulation. Despite the presence of rams, some ewes which have ovulated once or twice can return to the anovular condition.

Ewes of breeds less sensitive to seasonality can respond to rams some months before the beginning of the reproductive season, and if they are introduced to rams in the middle of the anoestrous season, they quickly return to anoestrus following the first ovulations. As an example, in Merino ewes introduced to rams on 18 October (Australia), 22% had become anovular 24 days post-teasing and 42% after 50 days

([Knight, 1983](#)). In contrast, ewes of more seasonal breeds which can only be stimulated by rams 2–4 weeks before the onset of the breeding season, keep cyclic activity until the next anoestrous season.

8. Factors affecting the response of anoestrous ewes to the rams

8.1. Factors associated with the ewe

The major factor responsible for the variability in the response of ewes to rams is the 'depth of anoestrus' of ewes. This concept, introduced long ago by [Marshall \(1903\)](#), although theoretical and difficult to define, has been used to describe a physiological state by which the ewe is more or less sensitive to be stimulated to ovulate. It cannot be objectively measured in individual ewes, and the best indicator of its level is the proportion of ewes that are ovulating spontaneously in the flock. [Oussaid et al. \(1993\)](#) were probably the first and the only group to distinguish, at the anatomical and physiological levels, two types of anoestrus: a 'slight anoestrus', detected at the beginning of the anoestrous season, characterized by high plasma FSH concentrations and the presence of normal follicles in the ovary, and 'deep anoestrus', detected at mid-anoestrous season, characterized by low plasma FSH concentrations and a severe reduction of the number of antral follicles. Both the breed of ewe and the stage of seasonal anoestrus are major determinants of the 'depth of anoestrus'. Therefore, in a flock, the breed and the time of the year interact to substantially influence the proportion of ewes that ovulate spontaneously at a particular time. The more ewes that are cycling, the better is the response of the anoestrous flockmates to the introduction of rams ([Lindsay and Signoret, 1980](#)). In breeds such as the Merino, which have a short anoestrus of 1–2 months and even then with over 5% continuing to cycle ([Martin et al., 1986](#)), most of the anovulatory ewes will respond to rams throughout anoestrus. In contrast, in breeds with long anoestrus (such as Romney and Suffolk) during which no ewes ovulate spontaneously, very few if any ewes respond to rams before the period of 2–4 weeks that precedes the normal breeding season. Comparative studies have shown that Dorset ewes responded better to ram teasing than Hampshire ewes ([Nugent](#)

et al., 1988a), Suffolk and Targhee pure bred ewes responded better than various crossbred ewes sired by Finn sheep, Dorset or Barbados rams (Thompson et al., 1990) and Dorset-cross and Booroola-cross ewes responded better than seven other crossbred ewes sired by different local and imported breeds from New Zealand (Meyer, 1979). The large within breed and between years variations in 'depth of anoestrus' (Scott and Johnstone, 1994) associated with individual ewes and environmental factors make the predictability of the response at a fixed time of the year very difficult.

Other factors linked with the ewe which can affect its response to the ram effect are the age, and the time of previous lambing and weaning. Murtagh et al. (1984b) reported results of two experiments in which significantly more adult (multiparous) Merino ewes ovulated in response to rams than 14–15 months old ewes (75% vs 25%, and 74% vs 38% in the two experiments, respectively). Oldham et al. (1985) did not find significant differences between the proportion of adult and nulliparous Merino ewes ovulating after the introduction of testosterone-treated wethers, but significantly fewer nulliparous ewes were detected in oestrus. Pearce and Oldham (1984) pointed out that the reproductive performance of young ewes after the introduction of rams in spring may be poor and is typically worse than that of adults. A period of 4-months difference in lambing date of Mule ewes (Bluefaced Leicester × Scottish Blackface) resulted in a difference of 20 days in the mean onset of the breeding season (Mitchell et al., 1997) which indicates differences in the 'depth of anoestrus' in late non-breeding season and suggests that if rams are introduced around this time, a greater proportion of early lambed ewes will respond compared to late lambed ewes. Late weaning increases the duration of the post-partum anoestrus (Shevah et al., 1974; Pope et al., 1989) and for a fixed time of ram introduction, those ewes in a flock which have been suckling for a longer period will be in 'deeper anoestrus' than early weaned ewes and consequently the response in those ewes is expected to be weaker.

Little information is available on the relationship between nutritional status of the ewe and her ability to respond to the ram effect. Although it has been shown that in cycling ewes low level of food intake and poor body condition can enhance the sensi-

tivity of the hypothalamus to the negative feedback of oestradiol (Rhind et al., 1991), neither of those factors seems to affect the proportion of ewes ovulating in late anoestrus (Montgomery et al., 1988; Forcada et al., 1992). This fact suggests little or no impact of the nutritional level of ewes on the 'depth of anoestrus' and consequently, on the efficacy of the ram effect. This idea is supported by the results of Wright et al. (1990) who demonstrated that, in spite of delaying the occurrence of first oestrus, restricted nutrition from mid-pregnancy onwards did not affect the incidence of ovulation in post-partum ewes nor the ability of the ewes to ovulate in response to ram introduction on 21–27 days post-partum (the occurrence of ram-induced oestrus was however inhibited). Specific studies on this matter involving seasonally anoestrous ewes have yet to be undertaken before definitive conclusions can be drawn.

8.2. *Factors associated with the ram*

The characteristics of the ram important for expression of the ram effect were reviewed by Haynes and Haresign (1987). Apart from the breed, the age and the sexual experience are recognized as major factors. The few reports of breed comparisons available have established some relationships. Dorset rams are more effective at stimulating anovular ewes to ovulate and commence oestrous activity than are Suffolk rams (Nugent et al., 1988b), and Romney or Romney × Finn rams (Meyer, 1979), while Merino rams seem to be intermediate between Dorset and Romney (Knight and Lynch, 1980b). Poll Dorset rams are better at inducing ovulation than are Coopworth rams (Scott and Johnstone, 1994). Assuming that pheromone production and libido are higher in older than in younger rams and that contact with females will enhance these parameters, Haynes and Haresign (1987) suggested that adult rams, which were reared near females and were mixed with supernumerary ewes before being introduced to the main flock of ewes to be stimulated, should be used in order to achieve the best results. Another factor which, although indirectly, also affects the rams' ability to stimulate the ewes to ovulate is the 'season'. Rams treated with melatonin (which mimics the 'reproductive season') in the 'out-of-season' are much more effective than untreated rams (Rosa et al., 2000b).

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