Small Ruminant Research 235 (2024) 107286

Contents lists available at ScienceDirect

Small Ruminant Research

journal homepage: www.elsevier.com/locate/smallrumres

Advances in photoperiodic and bio-stimulations of seasonal reproduction in small ruminants

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ARTICLE INFO

Keywords:
Sheep
Goats
Reproduction season
Photoperiod

ABSTRACT

In small ruminants, photoperiod synchronizes reproductive seasonality, and this environmental factor has been used to stimulate the sexual activity of males and females in months of seasonal sexual rest. However, socio-sexual interactions between males and females can also be used to stimulate the sexual activity of females in the seasonal anestrus. In this review, we describe how photoperiodic treatments can stimulate the sexual activity of bucks and rams in the months of sexual rest. In addition, we describe how sexually active males can be used to stimulate reproduction in goats and sheep in seasonal anestrus or to prevent seasonal anovulation through the classic "short-term male effect", and or through the newly discovered so-called "long-term male effect". We conclude with a description of the very recently documented "male-to-male effect". The "male-effect" is a socio-sexual stimuli caused by the sudden introduction of males and close contact with anestrous females in sheep and goats. After introduction of the male, the levels of pituitary luteinizing hormone (LH) in the blood of females increase quickly (< 10 min), and remain high for at least 4 h. That stimulus triggers the resumption of ovulatory activity in females, which occurs within 48 h. Prior separation of male and females, the intensity of anestrus, and the age, diet, and body condition of females can affect the response of the females to the male introduction. The long-term "male effect" phenomenon consists of a permanent contact of females with males that had been made sexually hyperactive in the usual period of sexual rest by light treatments applied in winter. This stimulation causes strong activity of the hypothalamic-pituitary axis, which releases the gonadotropic hormone LH at a frequency that allows a succession of ovulatory cycles during the anoestrous period as it does in the usual estrous period. The introduction of a male into a group of males in sexual rest stimulates the secretion of LH and testosterone, and their sexual behavior; this has been called the "male-to-male effect" ("buck-to-buck effect" or "ram-to-ram effect"). The intensity of sexual behavior displayed by the stimulatory males influences the responses of bucks and rams in sexual rest to the "male-to-male effect". Moreover, bucks that had been stimulated by the "buck-to-buck effect" are as effective in inducing high ovulatory and estrous activities in females as bucks that had been made sexually hyperactive by the photoperiodic treatment. In conclusion, these effects illustrate the power of socio-sexual relationships in controlling seasonal reproduction in sheep and goats, and shifts their importance in the final control of seasonal reproduction throughout the year compared with photoperiod.

1. Introduction

In both sexes of small ruminants at temperate and subtropical latitudes, the seasonal anovulation in females and the seasonal sexual rest in males are primarily controlled by variations in photoperiod; i.e., the duration of daylight that animals are exposed to daily. Indeed, photoperiod influences the negative feedback of estradiol and testosterone on LH secretion, which constitutes an important neuroendocrine mechanism responsible for reproductive seasonality (Pelletier and Ortavant, 1975; Legan and Karsch, 1980).

Since photoperiod synchronizes reproductive seasonality, this environmental factor has been used to stimulate the sexual activity of males and females in months of seasonal sexual rest (Chemineau et al., 2007); however, socio-sexual interactions between males and females can also be used to stimulate the sexual activity of females in the seasonal anestrus. The introduction of a male into a group of goats or sheep that

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https://doi.org/10.1016/j.smallrumres.2024.107286
Received 26 March 2024; Received in revised form 4 May 2024; Accepted 12 May 2024
Available online 15 May 2024

are in seasonal anestrus stimulates LH secretion, as well as estrous behavior (goats) and ovulations within the first five days after the first contact between males and females, which is known as the "male effect" (sheep: Underwood et al., 1944; Martin et al., 1986; Ungerfeld et al., 2004; goats: Shelton, 1960; Chemineau, 1983; Delgadillo et al., 2002). Furthermore, the endocrine and sexual responses of females to the male effect are influenced by the sexual behavior displayed by males; i.e., males that display intense sexual behavior, which we call “sexually hyperactive males”, are more effective in stimulating reproductive activity in females than those display weak sexual behavior (“sexually hypoactive males”) (Chasles et al., 2016; Abecia et al., 2018, Zarazaga et al., 2019). Recently, a "male-to-male-effect" ("buck-to-buck effect" or "ram-to-ram effect"; Delgadillo et al., 2022; Abecia et al., 2022) has been described in which the introduction of a sexually hyperactive male into a group of males in sexual rest can stimulate the secretion of LH and testosterone, and their sexual behavior.

In this review, we describe how photoperiodic treatments can stimulate the sexual activity of bucks and rams in the months of sexual rest. In addition, we describe how sexually active males can be used to stimulate reproduction in goats and sheep in seasonal anestrus or to prevent seasonal anovulation through the classic “short-term male effect” and/or through the newly discovered so-called “long-term male effect”. We conclude with a description of the very recently documented “male-to-male effect”.

2. Photoperiodic treatments to stimulate sexual activity in males

2.1. Principles used for light treatments on farms and artificial insemination (AI) centers

In both sheep and goats, short days (SD) are stimulatory if they follow long days (LD) and, conversely, LD are inhibitory if they follow SD. The relative duration of daily lighting is important in the design of treatments that can be used on farms or in AI centers. For example, two months of LD in winter followed by a return to natural photoperiod is perceived by the animal as the LD-SD sequence, which triggers sexual activity at the end of winter (Sweeney et al., 1997); however, as the season progresses, the more the return to natural photoperiod (increasing and long) weakens the phenomenon, and the animals are no longer stimulated. At that point, they must be exposed to natural SD (which is difficult to do on a farm) or given exogenous melatonin (Chemineau et al., 1986b). Similarly, the “artificial LD in winter” followed by “permanent lighting” (which is prohibited in Europe) is functionally equivalent to the LD-SD sequence (Delgadillo et al., 2016, Chesneau et al., 2017). The stimulatory (SD) and inhibitory (LD) photoperiods are not permanent and, therefore, there are refractory states to SD in which activity decreases (Lecorre and Chemineau, 1993, Delgadillo et al., 2011), and refractory states to LD in which sexual activity resumes. In other words, the two photoperiods, that are applicable on farms, are not permanently stimulatory or inhibitory, respectively.

2.2. How to “mislead” animals

Four methods to “mislead” animals about their photoperiodic state are as follows:

(1) In open buildings (i.e., where the animals continue to perceive the natural photoperiod), SD can be replaced by a return to the natural photoperiod (if it is early in the season), a melatonin treatment, or continuous lighting (outside the EU).
(2) A refractory state can be ‘broken’ by subjecting the animals to the photoperiod that is opposite to that to which they have been subjected (i.e., LD to break the refractory state at SD, and vice versa), which provides the basis for the main effects of the two opposite photoperiods. Continuous administration of melatonin is equivalent to long-term administration over 24 h, which has led to the development of subcutaneous implants (Melovine® or Regulin®).
(3) Artificial light only in the photosensitive phase, which occurs 16–17 h after a fixed dawn, leads to the same results as those produced by long days, saving electricity during the treatment.
(4) A rapid sequence of LD and SD (e.g., 1 month/1 month, or 2 months/2 months), known as "accelerated rhythm," in rams and bucks in more than one year prevents a too high increase in testosterone, which will reduce sexual activity through negative feedback. Thus, seasonality can be abolished in rams and bucks, which is of particular interest to AI centers for semen production (rams: Pelletier and Almeida, 1987, Almeida & Pelletier, 1988; bucks: Delgadillo, Chemineau 1992a and b). A recent study on goat bucks showed that accelerated rhythm works in open buildings if a sequence that alternates between a month of LD and a month of continuous lighting is used (Delgadillo et al., 2024). It is important to note that this lighting sequence does not have an effect on females.

2.3. Objectives of photoperiodic treatments, results, and uses on farms and in AI centers

On farms, treatments must be administered in open buildings and, therefore, the options are to provide additional lighting or a melatonin treatment. In AI centers, treatments can be done either in open buildings, or in closed buildings in which light is controlled because of the high monetary value of breeding males.

For females, the objective of farmers is to obtain the highest fertility in the off-season so as to maximize the number of autumn lambings from the group of females that had been joined by males. For that objective, the treatment is always the same: provide LD in winter, followed by SD, with either a return to natural photoperiod or the insertion of melatonin implants.

For males, the same objective and treatment can be applied on the farm to produce males that are capable of stimulating females through a successful “male effect” and fertilizing as many females as possible in a short period (see below). At intermediate latitudes (e.g., Mexico, Spain, Mediterranean Basin), typically, the treatment of males only is sufficient. In an AI center, if the AI period in spring is short, that type of treatment makes possible the preparation of males that produce an increased quantity of high quality semen and, in turn, greated fertility from liquid semen, especially in sheep (Chemineau et al., 1992, 2007).

In some AI centers, particularly, for goats, the semen is frozen before it is used several months later, and the implementation of "accelerated" treatments over several years makes it possible to have continuously sexually active males, which shortens the total semen collection period. Furthermore, under those conditions, the quantity and quality of semen is greatly increased, which leads to a stockpile of frozen doses that is much larger than that from males that had been left in the natural photoperiod (Delgadillo et al., 1992b, 1993). Those treatments were applied for at least three consecutive years without any negative effect on the animals, and they have been used for > 15 yr in the only AI center in France that produces goat semen.

On goat farms, photoperiodic treatments consisting of two months of long days followed by nothing or the insertion of a melatonin implant are common. In the 2010 s, about half of the 1800 farms in the Capgènes cooperative used photoperiod in an attempt to increase fertility in spring without resorting to traditional hormonal treatments. Nevertheless, the photoperiodic treatment can be associated with a progestagen treatment if the injection of eCG/PMSG is replaced by a buck effect in the implementation of AI (Pellicer-Rubio et al., 2008).

On sheep farms, melatonin implants are the primary choice to achieve mating in advance of the season. In addition, they increase double births and weaning rate. In sheep semen production centers, light treatments that combine long days and short days in a non-accelerated mode are used to advance puberty in young rams and, thereby, put them in AI from their first year and, in adults, to increase the number of sperm doses for AI and obtain higher fertility in spring by using fresh semen (Chemineau et al., 1992).

3. The short-term male effect

The "male-effect" is a socio-sexual stimuli caused by the sudden introduction of males and close contact with anestrous females in both sheep and goats. After introduction of the male, the levels of pituitary luteinizing hormone (LH) in the blood of females increase quickly (< 10 min), and remain high for at least 4 h. That stimulus triggers the resumption of ovulatory activity in females, which occurs within 48 h (Martin et al., 1986). Many research groups have been investigating that phenomenon in sheep and goats for the purposes of developing a simple, effective, non-invasive, and inexpensive technique for promoting out-of-season reproduction.

3.1. Mechanisms of male action

3.1.1. Sensory pathways used

Olfaction plays an essential role in the stimulation of the neuroendocrine activity of females by the male. If does (Claus et al., 1990) or ewes (Knight and Lynch, 1980) sniff buck hair and ram fleece, respectively, LH in their blood increases immediately and in the same way as it does in females that have been brought into physical contact with a male. Research to identify the olfactory molecules that are responsible for activating LH had been carried out in goat and sheep and, in a study of the Shiba goat in Japan, 4-Ethyloctanal was identified as the molecule that acts on the olfactory system and causes pulsatile release of LH (Murata et al., 2014). It has not been confirmed whether that molecule is capable, on its own, of restoring a full ovulatory response. Furthermore, the temporary or permanent neutralization of the olfactory system does not prevent an LH response to the introduction of sexually active males (Chemineau et al., 1986a), which suggests that other sensory pathways are involved in this response. In the same way, the introduction of sexually active, but sedated bucks (= under anesthesia), stimulates LH, but does not restore a complete ovulatory response like that observed in control females that have been kept in direct contact with active males (Martinez-Alfaro et al., 2014). Auditory stimulation of goats by the vocalizations of bucks leads to a release of LH, but only in goats that had been in contact with males earlier in their life (Delgadillo et al., 2012).

Apparently, under normal breeding conditions, the entire behavioral and sensory repertoire of males must be expressed to stimulate the activity of females to a degree that the response is maximum and high fertility can be achieved in the anoestrus period.

3.1.2. Neuroendocrine mechanisms involved

Stimulation by the male occurs in the anestrus period, when there is a strong negative feedback from the circulating E_2 on the hypothalamic-pituitary axis, especially, the pulsatility of LH. The "male effect" "bypasses" this inhibition very effectively and quickly. The most likely explanation is that the lifting of inhibition occurs via stimulation of hypothalamic neurons, connected to GnRH neurons, which control the release of pituitary LH into the blood (Bedos et al., 2016, 2018). Once the pulsatile release of LH increases, and strong stimulation by the male is maintained for at least 4 h, the processes leading to ovulation are identical to those of the estrous cycle and almost all females follow this physiological pattern.

3.2. Ovulatory and estrous activities induced by the introduction of males

According to the development of the corpus luteum (CL) after the first induced ovulation, the females either have a CL of normal duration (associated with a cycle of 16.5 d in sheep and 21 d in goats), or they have a short cycle of identical duration in both species (about 6 d). The production of plasma P_4 in the induced short cycle is abnormal, and P_4 rises slightly for a single day (day 3–4 after the introduction of the male), before decreasing rapidly. That induced short cycle is followed immediately by a second ovulation (day 8), followed by a CL of normal duration. In most breeds, goats have more short cycles (around 80%) than do sheep (50%).

In large proportion, those short cycles undoubtedly come from poor follicular growth in anoestrus, which leads to a CL that produces less P_4, which is insufficient to prevent LH stimulation of the following follicular wave, and leads to a new ovulation 8 d after the introduction of the male (Chemineau et al., 2006).

Thus, the temporal sequence of ovulatory cycles is identical in goats and sheep, unlike the length of the normal cycle. In sheep, a second ovulation occurs after normal cycle around Day 17 (1+16) and a third around day 23 (1+6+16), and, in goats, a second ovulation after normal cycle at around day 22 (1+21) and a third around day 28 (1+6+21) (Chemineau, 1989; Thimonier et al., 2000).

Goats and sheep differ in their estrous behavior because, in sheep, it is induced by the sequence $P_4 \Rightarrow E_2$, but E_2 is sufficient in goats. Thus, ewes do not come into estrus at the first or second ovulation after the short cycle (the secretion of P_4 is insufficient), but all ewes do after the normal luteal phases that precede the second or third ovulation (at days 17 and 23). Both of those ovulations lead to fertilization by rams. In goats about 60% of the females are in estrus from the first induced ovulation, but they are not fertilized because most of them have a short cycle that is always sterile. They are all in estrus at the second ovulation following the short cycle, and fertilization occurs in this last period.

Consequently, seen from the outside, by the rams or the bucks, or by the breeder who observes the induced heat, the responses of the two species are very different, even though the underlying mechanisms are identical. In any case, the fertilization of most goats whose sexual activity has been induced by the buck effect occurs around day 8 after introduction of the buck, while those of most sheep occur at the two peaks 17 d and 23 d after the introduction of the ram. When the male effect is successful, fertility is high (>75%), even though the flock is in out-of-season.

3.3. Factors of variation in the response to the male effect

3.3.1. Sexual activity of males

Seasonal sexual inactivity in males and anestrus in females coincide fairly closely (except for a few weeks before the end of the breeding season and a few weeks before its start). Therefore, in most cases, when a male effect is achieved in anestrus, males are not very active and risk not developing sufficient sexual activity to produce good induction of ovulations in females. Indeed, if the bucks or rams receive a simple additional light treatment (in open buildings) of 16 h of illumination per day for two months (e.g., Dec-Jan; long days-LD), they trigger a "short sexual season" (high testosterone and libido, same smell as in sexual season) which starts about 30 (rams) or 45 (bucks) days after the end of the long days and continues for about two months. Those bucks and rams are much more effective than are control males in inducing a maximal ovulatory and estrous response, which leads to a large difference in fertility (Delgadillo et al., 2002; Abecia et al., 2017). That simple technique has been used on many small farms in Northern Mexico and its effectiveness makes it possible to very significantly improve the income of breeders because of the reduction in the mortality of kids born at a more favorable period, the lengthening of lactation, and more attractive milk and kids price conditions in relation to the market.

3.3.2. Prior separation of male and females?

In the earliest tests of the male effect, particularly in Australia, it appeared beneficial to separate the sexes before creating the effect, which has been recommended to breeders, repeatedly. It took some time and several experiments to demonstrate that the separation was unnecessary; it was the novelty (a new male) that prompted a good response from females (goats, Delgadillo et al., 2006; ewes, De St Jorre et al., 2012). The use of sexually active bucks (LD treated) is even more effective. In most cases, however, it is useful to separate the sexes in the previous sexual season so that the females are not pregnant or post-parturient when we want to achieve the male effect. Out of precaution, that practice has persisted.

3.3.3. Intensity of anestrus

The intensity of anestrus, which remains poorly defined, can be estimated as the proportion of females in a group that are spontaneously cyclic before the male effect. It is one of the important factors that influence the response in the two species. In the Creole goat in Guadeloupe, the proportion of females that were spontaneously cyclic before stimulation was positively correlated with the proportion of females in estrus at the first ovulation, and of those that had induced cycles of normal duration (Chemineau, 1983). In Merino sheep, the proportion of ewes that ovulated after exposure to rams and the proportion of ewes that were cyclic before exposure were positively correlated (Martin et al., 1986). Both studies, however, used untreated males and we wonder whether the use of sexually active bucks (LD treated) would prevent the maximum responses in all cases.

3.3.4. Age, diet, and body condition of females

The age and prior sexual experiences of females influence the response to the male effect. In ewe lambs and other naïve ewes, the response is weaker than it is in adult or experienced females, which is also true in goat; however, the presence of (LD treated) sexually active males can eliminate the difference in responses, which nevertheless persists in fertility after the male effect.

In sheep and goats, diet and body condition of females have a significant effect on the response to the male effect. In the Barbarine ewe in Tunisia, undernutrition around autumn parturition reduced the proportion of ewes that were spontaneously cyclic in spring and increased the proportion of short cycles induced by the male effect (Lassoued and Khaldi, 1989). In goats in Northern Mexico that had been kept on a pasture that had low food resources, if the response to the buck effect was not modified, the fertility that followed was lower than it was in females that had received concentrated feed on their return to the farm each day (Delgadillo et al., 2021).

3.4. The male effect and artificial insemination

In sheep and goat, administration of P_4 or an analogue to females, prior to the introduction of males, completely eliminates short cycles (Lassoued et al., 1995). Furthermore, this prior treatment induces estrous behavior after the first ovulation in both species, increases fertility and, consequently, to strong synchronization of parturitions similar to that obtained from conventional hormonal treatments, which favors AI. In goats, in the same way as in the conventional treatment, AI is performed with frozen semen, "blind", without prior detection of heat, with a slightly modified AI timing after joining with bucks carrying marking harnesses with adapted aprons. In that scenario, fertility can be $>$ 60%, which is similar to that produced by the conventional hormonal treatment (Pellicer-Rubio et al., 2008). Those experiments have not been conducted in sheep.

4. The long-term male effect

4.1. Permanent presence of males among females affects seasonal anoestrus

In goats and sheep, the permanent presence of males among a group of females extends the length of the breeding season, because it begins earlier and ends later than it does if females have been isolated from males throughout the year (Restall, 1992; Delgadillo et al., 2015). Similarly, the regular re-introduction of males once a month shortens the anoestrus period. In those two scenarios, males responded to the natural changes in photoperiod, which caused them to exhibit an annual period of sexual rest characterized by reductions in spermatogenesis, testicular weight, plasma testosterone, odor, and libido. Periods of activity and inactivity in males and females almost coincide but, as mentioned above, males are about a month ahead of females in the initiation and cessation of the activity of the hypothalamus-pituitary-gonads axis, which creates the possibility that males might advance seasonal ovulatory activity in females if the sexes are in permanent contact.

4.2. Gradual start of activity in anoestrus

The gradual start of activity can occur in the anestrous season if males that have previously received light treatment, are used. The photoperiodic treatment in winter that causes sexual hyperactivity in spring described above, involves a sequence of two-month of long days, followed by a return to natural photoperiod, which can be coupled with a melatonin treatment (via subcutaneous implants). Under those conditions, the end of long days and the onset of hypersexual activity, reflected in increases in testicular weight, plasma testosterone concentrations, and libido, occur four (for rams) and six (for bucks) weeks apart. In that period of four or six weeks, males are still in seasonal sexual rest, exhibit very low activity and, if they are introduced into a group of females just before the beginning of anoestrus (e.g., in Feb), they do not have an effect in the short term. The gradual resumption of hypersexual activity induced by the long day (LD) treatment gradually leads to ovulatory activity in females, all of which are in cyclical activity by Apr, the middle of the anestrous period (Delgadillo et al., 2015).

4.3. Suppression of seasonal anoestrus

The above long-term "male effect" phenomenon has led to questions about the roles of photoperiod and socio-sexual relationships in the expression of seasonal reproduction in sheep and goats. Following the results described above, rather interesting questions have emerged: What would happen if female goats or sheep were brought into contact with sexually hyperactive males throughout anoestrus? Would those females maintain ovulatory activity year round? In that regard, important experiments were performed on goats in Mexico (Delgadillo et al., 2015) and on sheep in Spain (Abecia et al., 2015). From Jan of year 1, and for a period of 18 mo, a group of goats were kept in permanent contact with bucks that had been made sexually hyperactive in the usual period of sexual rest by light treatments applied in winter (several groups of bucks were used, successively). Another group of goats were kept without a buck for the above mentioned experimental period, and a third group was kept with control bucks that had been exposed to the natural photoperiod (Fig. 1). As hypothesized, anoestrus was "longest" (from Feb to Sep) in goats that had been kept in the absence of a buck, and "shortest" (from Mar to Jul) in goats that had been kept in the presence of control bucks. In a surprising and novel way, almost all of the goats that had been kept in permanent contact with bucks that had been made sexually hyperactive by prior photoperiodic treatments were in cyclical ovulatory activity throughout the experiment, including the two usual seasons of anoestrus. To confirm whether permanent sexual activity was caused by the presence of the buck, in May of the second year, the bucks were removed from half of the cyclic females, and the activity in those females immediately stopped. The same experiment was performed on Rasa Aragonesa sheep in Spain and the results were similar, even if the difference between groups was less marked because of the weaker seasonality of this Mediterranean breed. All Rasa Aragonesa ewes that had been kept with sexually hyperactive rams (previoulsy received a photoperiodic treatment in winter) were cyclic during the usually anoestrous season, and most of the control ewes had ceased ovulatory activity.

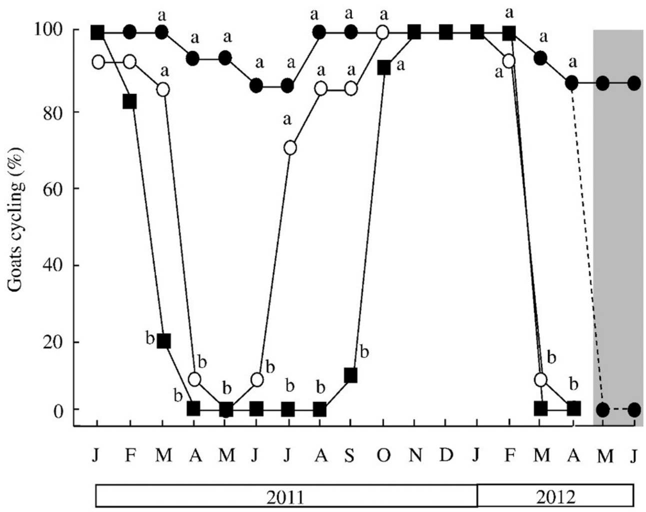

Fig. 1. Effects of the continuous presence of sexually active bucks on ovulatory cyclic activity of female goats in two consecutive anestrous seasons. The proportion (%) of female goats that were cycling each month in does that had been either separated from bucks (closed squares, n = 11), maintained with untreated control bucks (Open circles, n = 13), or kept with sexually active males (closed circles, n = 14) in two consecutive anestrous seasons in Mexico. For each month, proportions that have different superscripts differed significantly (Fisher exact P ≤ 0.001). Sexually active males were removed (gray area) from half of the females (closed circles, dashed line) in the two last months of the study. Ovulatory cyclicity was monitored by weekly measurements of blood plasma progesterone. Adapted from Delgadillo et al. (2015) with permission from Elsevier.

As in the case of the short-term male effect, the effect of the presence of sexually hyperactive males on the seasonal sexually active females occurs via stimulation of the central nervous system. Ovariectomized goats that carried an estradiol implant in the presence of sexually hyperactive bucks maintained high luteinizing hormone (LH) activity in the anoestrus period, but the LH levels of goats that had been kept in the presence of control bucks decreased (Muñoz et al., 2017) (Fig. 2). In the anestrous season, that stimulation causes strong activity of the hypothalamic-pituitary axis, which releases the gonadotropic hormone LH at a frequency that allows a succession of ovulatory cycles as it does in the usual estrous period.

4.4. *Onset of puberty*

The long-term male effect influences the timing of puberty in Rasa Aragonesa ewe-lambs born in autumn (Abecia et al.; 2016). The permanent presence of sexually hyperactive rams (which received a long-day treatment the previous winter) among ewe lambs from Mar onwards, significantly advanced puberty. Those ewe lambs reached puberty in Apr and May, whereas the control ewes, which had been kept in permanent contact with rams that had been exposed to natural light, did not reach puberty until Jun or Jul (Fig. 3). This effect is very useful for autumn-born lambs, because their age and timing of introduction of those lambs into the flock are the most appropriate.

5. The male-to-male effect

5.1. *"Male-to-male effect" stimulates sexually dormant males*

As mentioned above, in bucks and rams, socio-sexual interactions can eliminate the natural inhibition of sexual activity in the seasonal sexual rest. In fact, the introduction of a male into a group of males in sexual rest can stimulate the secretion of LH and testosterone, and their sexual behavior. We call this phenomenon the "male-to-male effect" ("buck-to-buck effect" or "ram-to-ram effect"; Delgadillo et al., 2022; Abecia et al., 2022). The intensity of sexual behavior displayed by the stimulatory males influences the responses of bucks and rams in sexual rest to the "male-to-male effect". Bucks exposed to artificially long days from Nov to mid-Jan, followed by the natural photoperiod stimulated testosterone secretion and increased sexual behavior around 45 d after the end of long days; i.e., during the sexual rest. Bucks that had been kept under natural photoperiod before joining sexually hyperactive males (that had received the photoperiod treatment) at the beginning of Apr, exhibited an immediate increase in plasma LH and testosterone concentrations. The increase in LH occurred in the minutes following contact and persisted the following day, although at a lower level because of the negative feedback of testosterone on LH. From 6 h after contact, testosterone increased significantly and remained higher than it did in bucks kept with control bucks (Fig. 4; Delgadillo et al., 2022). Similarly, in Rasa Aragonesa rams in Spain, immediate, dramatic increases in plasma LH and testosterone concentrations occurred in rams that had been kept under natural photoperiod until mid-Apr when they joining rams that had been exposed to two months of long days starting on 15 Dec. Control rams that had been placed in contact with rams that

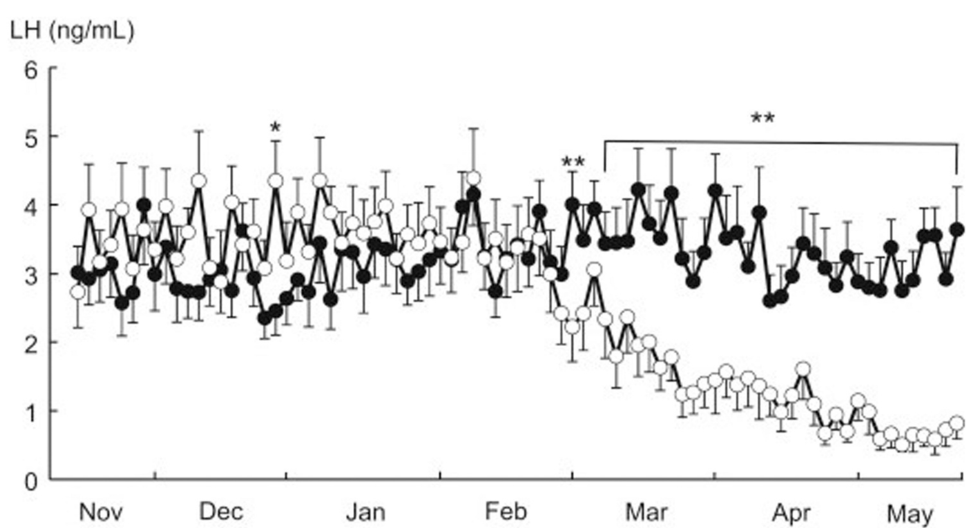

Fig. 2. Plasma LH concentrations throughout the season in Creole goats in Mexico that either had (black circles) or had not (white circles) been kept in permanent contact with sexually active bucks. Goats were ovariectomized and carried a subcutaneous estradiol implant (*P < 0.05; **P < 0.01).
Adapted from Muñoz et al. (2017) with permission from Elsevier.

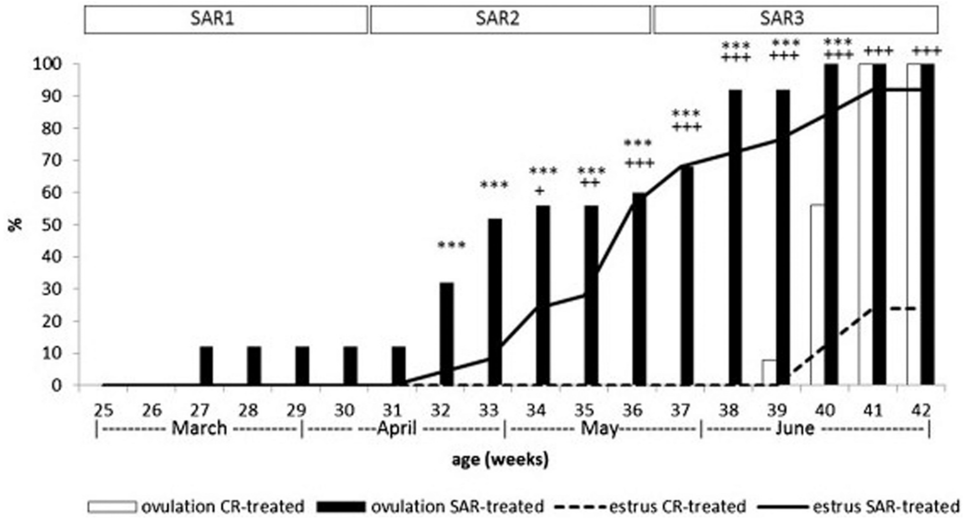

Fig. 3. Acceleration of puberty in Rasa Aragonesa lambs that had been kept in continuous contact with sexually active rams (SAR) or Controls (CR) (for ovulation: *** P < 0.001; for estrus: +P<0.05; ++P < 0.01 +++ P < 0.001). Adapted from Abecia et al. (2016) with permission from Elsevier.

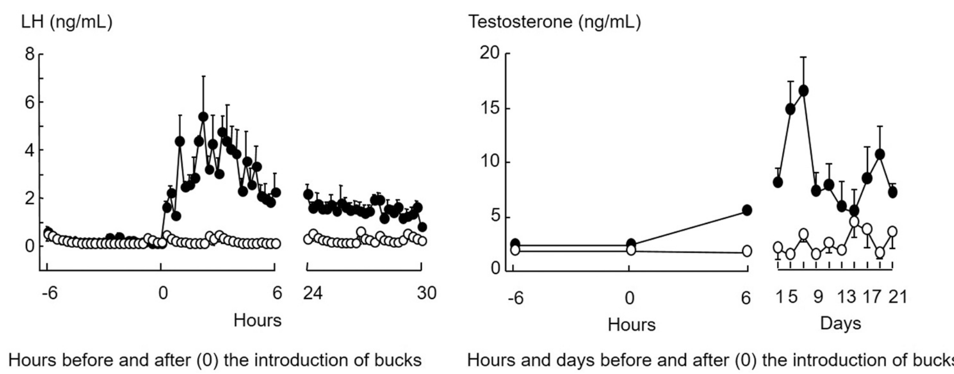

Fig. 4. Plasma LH (left) and testosterone (right) concentrations in Mexican Creole bucks that had been placed in contact at the beginning of Apr, either with bucks that had been rendered sexually active by a prior photoperiodic treatment (black circles) or with control bucks (white circles). From Delgadillo et al. (2022) with permission from Elsevier.

had been kept under natural photoperiod did not exhibit significant increases in those two hormones (Fig. 5).

Thus, the "male-to-male effect" strongly resembles the classic "short-term male effect" that occurs in ewes and female goats. The "male-to-male effect" immediately stimulates the hypothalamo-pituitary-gonadal axis and very quickly and effectively 'bypasses' the seasonal inhibition of photoperiod on the central nervous system. It is assumed that there is not a unidirectional specificity in the sexual activity of males towards females, and the intense hypersexual activity induced by autumn-winter light treatments could be exerted on males. Although it remains to be demonstrated, it is probable that the "male-to-male effect" and the classic "male effect" may involve the same sensory pathways. In both cases, stimulation causes a resumption in sexual activity in stimulated males in the usual period of sexual rest, which might be important on a

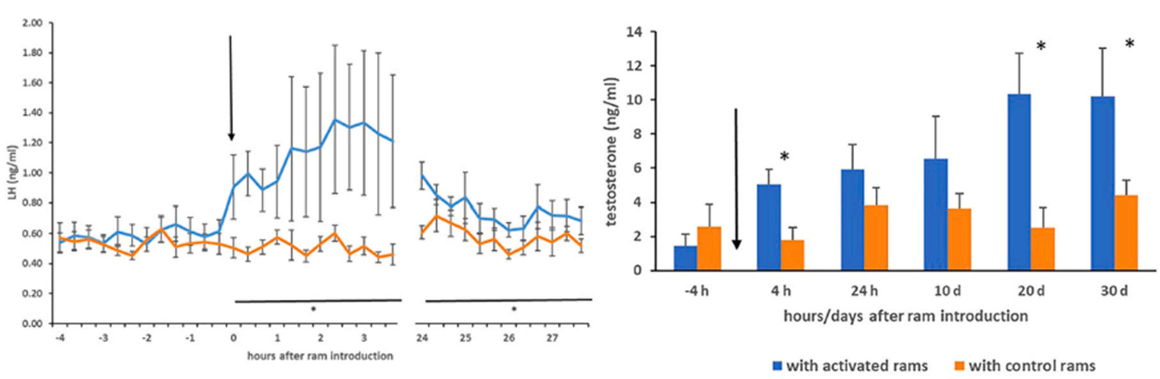

Fig. 5. Plasma LH (left) and Testosterone (right) concentrations in Rasa Aragonesa rams in Spain that had been placed in contact at the beginning of Apr with rams that had been made sexually active by a prior photoperiodic treatment (blue) or with control rams (orange). Adapted from Abecia et al. (2022).

practical level.

5.2. The “male-to-male effect” persists as long as the inducing males are sexually hyperactive

In bucks and rams, plasma testosterone levels remained significantly higher in males that had been exposed to sexually hyperactive inducer males for at least 30 consecutive days than they were in males that had not (Delgadillo et al., 2022; Abecia et al., 2022). Similarly, the short- and medium-term sexual behaviors of males that had been stimulated by sexually hyperactive males were significantly higher than in males that had been kept with control males and it was similar to that of males that had received the photoperiod treatment earlier. The stimulation of the secretion of testosterone and, probably, LH caused by exposing males in seasonal sexual rest to hyperactive males (by photoperiodic treatments) persists for at least 30 d, which is equivalent to the duration of the short period of sexual activity induced by the light treatments in inducing males (which received the photoperiod treatment earlier). Probably, the activity of previously sexually rest males gradually stops because that of hyperactive males also reduced; however, the sexual behavior of sexually rest males begins to being stimulated from the first day after contact with sexually hyperactive males, undoubtedly under the influence of testosterone, which increases after 6 h and, perhaps, other hypothalamic hormones.

5.3. Sexually hyperactive males can cause a classic “male effect” to sexually rest males

The last step of experimentation was to confirm whether males induced in sexual hyperactivity by other males can stimulate females in anestrus in the same way as do males that have directly received the photoperiod treatment themselves. Thus, it was reported that bucks in sexual rest that had been stimulated by the "buck-to-buck effect" were as effective as bucks that had been made sexually hyperactive by the photoperiodic treatment in inducing high ovulatory and estrous activities, producing fertility and prolificacy rates in the females that did not differ significantly between bucks (Delgadillo et al., 2022).

6. Conclusions

Even though the neuroendocrine mechanisms that mediate the effects of photoperiod on the reproductive season of small ruminants are not fully understood, light treatments in open or closed buildings can maximize fertility in the off-season or keep males in a continuous sexually active state. Those treatments are used on farm and in AI centers.

The short-term male effect, which induces synchronous ovulations in almost all females in anestrus within 48 h following contact with males, is a phenomenon that concentrates births within a short period in seasonally breeding species. Undoubtedly, a key factor in its success is the sexual activity of males, which has attracted the recent attention of the scientific community, and, certainly, should be an aspect of the specific recommendations to breeders.

Medium- and long-term male effects, and the effects of sexually hyperactive males on other males have been recently identified; this fact has provided reasons to reassess the role of socio-sexual relationships in the regulation of seasonal reproductive activity by photoperiod. Although a long-term male effect has been confirmed, it cannot be used in breeding programs, directly, because the objectives of breeders are to maximize the fertility and prolificacy of their females within a period, chosen in advance, rather than to have cyclic females year round. However, the long-term effect illustrates the power of socio-sexual relationships in controlling seasonal reproduction in sheep and goats and shifts the importance of these relationships in the control of seasonal reproduction throughout the year. The experimental evidence of the induction of continuous cyclical activity in seasonal breeds of goats and sheep over almost two years is a particularly novel finding that, to our knowledge, has never been reported in a photoperiodic mammal. Furthermore, by “bypassing” the very strong seasonal inhibition of the hypothalamus-pituitary-ovary axis caused by photoperiod, it might permit a better understanding of the underlying neuroendocrine mechanisms.

Until recently, an effect of sexually active males on other males has been considered only from the perspectives of aggression between conspecifics and dominance relationships within groups, and not from that of the induction of out-of-season sexual activity in males in seasonal sexual rest. Probably, that was because, typically, all the males in the same flock, generally of the same breed, are at rest or sexually active simultaneously, which reduces the likelihood that a sexually active male can influence the sexual state of another male at the beginning or the end of the breeding season. New, simple, effective photoperiodic treatments have made it possible to have sexually hyperactive males in the middle of the off-season, which has identified the important role that those males can play in very effectively countering the seasonal inhibition caused by photoperiod. Although the male-to-male effect has been confirmed indisputably, it has not been used in breeding operations, which have used hyperactive males, directly, to induce ovulation and fertilize females in a flock. However, the effect illustrates the power of socio-sexual relationships in controlling seasonal reproduction in sheep and goats, and, once again, it shifts the importance of these relationships in the context of photoperiod in the final control of seasonal reproduction throughout the year. If female cyclic activity can be maintained year round by permanent contact with sexually active males, one might wonder whether the same is true for males whose intense sexual activity might be maintained year round by keeping them in contact with other sexually active males.

Bio-stimulation, a natural technique employed in animal husbandry, serves to enhance reproductive performance. With a rising emphasis on creating environmentally friendly and ethically sound practices, alongside the reduction in drug and hormone usage, alternative management approaches like bio-stimulation are gaining traction. Understanding methods of bio-stimulation in domestic animals is crucial for devising new reproductive strategies that minimize or eliminate hormone use, meeting the needs of farmers. Utilizing the "male effect" in sheep and goats to induce cyclic behavior in females presents an opportunity to reduce or eliminate hormone use in animal production. Consequently, bio-stimulation emerges as a cost-effective, minimally invasive breeding management tool that aligns with social acceptability in the sheep and goat sector.

CRediT authorship contribution statement

Philippe Chemineau: Writing – review & editing, Writing – original draft, Conceptualization. **JOSE ALFONSO Alfonso ABECIA:** Writing – review & editing, Writing – original draft, Conceptualization. **José Alberto Delgadillo:** Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of Competing Interest

The authors declare no conflict of interest.

Acknowledgements

We thank Bruce MacWhirter for the English revision of the manuscript. This review did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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