

Importance of the signals provided by the buck for the success of the male effect in goats

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Abstract – Under temperate and subtropical latitudes, ewes and goats display a reproductive seasonal pattern and their sexual activity during the anestrus period can be stimulated and synchronized by the introduction of males in the group, which is called the “male effect”. The response of females to the male effect in the middle of the anestrus season is weak or absent. This failure may be due to the inability of the female to respond to males, as a result of a refractoriness of the female to the male stimulus. But, it may also be due to a low quality stimulus provided by the male which is, as the females, in seasonal rest. We tested this latter hypothesis in seasonally inactive goats kept under subtropical conditions by comparing the use of males with their sexual behavior stimulated or not by photoperiodic treatments. Treated males were able to induce estrous activity of females during the whole anestrus season. We have also determined that previous separation of the males and continuous contact during teasing are not absolute requisites when active bucks are used. While odor from the male and its sexual behavior play a primary role in inducing ovulation, vocalizations appear to facilitate the display of the does’ estrous. It remains to be determined to which extent these conclusions apply under temperate latitudes and with more seasonal breeds.

goat / male effect / buck vocalizations / male odor / sexual behavior / photoperiodic treatment

1. INTRODUCTION

The social interactions between partners of the same species may lead to important changes in their reproductive status [1]. Exposure of seasonally anovulatory goats and ewes to males can stimulate and synchronize their sexual activity [2, 3]. This phenomenon of sexual biostimulation is known as the “male effect” or “teasing” and has been extensively studied in goats and sheep [4, 5]. In these species, the response of females to the introduction of males involves a rapid increase of luteinizing hormone (LH) secretion that culmi-

nates in a preovulatory surge provoking ovulation [6, 7]. In sheep the first ovulation is not accompanied by behavioral estrus whereas in goats, a variable number of females show estrus behavior at the first induced ovulation 2–4 days after male introduction. Most goats have a short ovarian cycle of 5–7 days of duration, followed by a second ovulation, which is associated with estrous behavior and a normal luteal phase [2,8]. Ewes may, however, also show a short cycle, but it is only after the first cycle of normal length that they display estrus. The characteristics of the response of females to teasing are variable and may depend on several internal and external

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factors operating in both sexes, such as the variation of the females' responsiveness to the presence of males because of the photoperiod, genetic factors, or the quality of the stimulus provided by the males [9]. In this article, we focus only on the role of the male, with the aim of underlining the importance of the sexual behavior showed by the males during teasing. In the first part of the paper we summarize the factors from males that are classically considered important when using the male effect under natural conditions (i.e. with no or minimal preparation of the males). In the second part, we review the specific situation of the male effect in goats under subtropical conditions, which illustrates the importance of using adequate males for the success of teasing.

2. FACTORS FROM THE MALE INFLUENCING THE RESPONSE TO THE MALE EFFECT UNDER NATURAL CONDITIONS

In sheep and goats, the quality of the stimulation depends at least on the degree of contact between the two sexes, previous separation between sexes, duration of contact and the intensity of the sexual behavior of the males [9].

2.1. Degree of contact between the two sexes

The degree of contact between the two sexes may affect the response of the females to the male effect. Pearce and Oldham [10] exposed ewes to various degrees of contact with rams (e.g. full physical contact, contact through an openwork fence, contact through an opaque fence, contact with rams' wool in facial masks or complete isolation from males). Contact through an opaque fence was less effective than through an openwork fence, and the maximum effect was achieved in all cases when the ewes were allowed full physical

contact with the males. In Angora goats, 41% of 85 does separated from bucks by a wire fence (weak stimulation) ovulated, compared with 69% (out of 66) when put in direct contact with the males (strong stimulation) [4]. In both ewes and goats, a high response of females is obtained when both sexes are in full physical contact, showing that the degree of response of the female is influenced by the type of contact with males.

2.2. The duration of contact between sexes

The duration of contact between the two sexes is another factor that influences the ovulatory response of the females. Even in females that are likely to respond to teasing (e.g. at the end of the non breeding season), the continued presence of the male is required to obtain a maximum ovulatory response, or to prolong the induced ovulatory activity [6, 11, 12]. In ewes, three hours of contact with rams induce a rapid increase of LH secretion but it is not enough to provoke ovulation [12]. Then, LH secretion returns to pre-stimulation levels after the male is removed. Signoret et al. [11] determined that the duration of contact also affects the percentage of females ovulating during the male effect. While only 20% of ewes ovulated when exposed to teasers for 24 h, 51% ovulated after 4 days of contact with males. Moreover, the percentage increased to 61% in females exposed to rams for 13 days [11]. In goats, while the exposure to males for 16 h per day during 10 days induced only 19% of goats to ovulate, the continuous exposure induced ovulation in 95% of them [13]. These results suggest that the continuous presence of males is required during at least 4 days to obtain a good response of females to teasing.

2.3. Previous separation between sexes

From early studies carried out in ewes, it was assumed that females must be

preconditioned by a period of isolation of at least three weeks from males, to be able to ovulate in response to the re-introduction of other males [14, 15]. Later, some results suggested that this separation may not be necessary and that in some cases ewes are able to respond to males without previous separation. For example, previous exposure to rams for 2–3 h did not affect the LH response of females when the males were re-introduced 24 h later [12]. In a similar way, in ewes in contact with rams, the introduction of new males induced ovulation in a similar percentage of females (85%), than those that had previously been totally separated from the rams (86%) [16]. Finally, in ewes, Pearce and Oldham [10] found that between 89% and 95% of ewes remaining in anestrus after 65 days in contact with rams, ovulated 4 days after the introduction of novel rams. However, these results should be carefully considered before assuming that the introduction of new males may not be effective in other breeds or periods.

2.4. Intensity of libido of the males

Several studies have indicated that the sexual behavior of the male is an important determinant of the response of females to the male effect. Androgen-treated castrated rams, who display intense sexual activity, induce ovulation more effectively than males given the same dose of androgen but which are relatively inactive [11]. Likewise, Fulkerson et al. [17] reported that wethers treated with testosterone or estradiol, who displayed higher sexual behaviors than untreated castrates, were more effective to induce a sexual activity in anovulatory ewes. Recently, Rosa et al. [18] found that stimulating sexual activity of rams through melatonin administration improved the ovulatory response to teasing (56%), compared with that of ewes put in contact with non treated rams

displaying a low sexual behavior (24%). Perkins and Fitzgerald [19] compared the use of high or low serving capacity rams as teasers, obtaining a higher percentage of ewes ovulating with the first (78% vs. 59%). In goats, the bucks' libido also affects the response of females to the male effect. Well nourished bucks, who show a high sexual activity, stimulated estrous behavior in a higher percentage of anestrus does than undernourished bucks displaying a poor sexual activity (67% vs. 38%) [20].

2.5. Sensory cues from the male involved in the male effect

The male effect is a multi-sensory phenomenon involving olfactory, visual, tactile and auditory cues. High percentage of females respond to male stimulation when all cues are active [2, 4, 19, 21–23]. In ewes [21] and goats [24], olfactory cues from the male appear to be involved in mediating the male effect. In ewes, the male odor stimulates an increase of the frequency of LH pulses, and induces ovulation in a high proportion of them. However, in other trials a lower proportion of ovulating goats was obtained compared with those teasing with full male contact [13, 25]. However, in the dwarf Creole goat from the French West Indies Islands in the Caribbean, peripherally induced anosmia does not prevent the response to the male effect, although the proportion of females showing estrus or ovulation decreases (50% in anosmic females vs. 89% control females) [7]. Overall, these results indicate that olfactory cues are involved in the response of females to the male effect, but whole male-female behavioral interactions are likely to play some stimulatory role.

Although in lower percentage than with full buck contact, some does ovulate in response to male odor and vocalizations (19.5% vs. 41.2%) [4]. In the sow,

vocalizations may compensate for the absence of olfactory signals and allow immobilization behavior of the female [26]. Also, in birds, male courtship vocalizations have a stimulatory effect on ovarian activity [27, 28]. In the red deer (*Cervus elaphus*), the play-back of recorded vocalizations from males during courtship advanced the onset of the breeding season compared with that of isolated females [29].

2.6. Limitations of the male effect

A limitation for the practical use of the male is the wide variation of responses in relation to the moment of the anestrus period in which teasing is performed. That is more critical in strong seasonal breeds of sheep and goats. In such breeds, since the response of females is low or absent during mid-seasonal anestrus, the practical use of the male effect is limited to the period just preceding the onset of the normal breeding season [2, 6, 30]. However, in breeds exhibiting only a moderate seasonality such as the Merino sheep or Creole dwarf goats from the tropical Guadeloupe Island, the introduction of males induces an ovulatory response at most times of the non-breeding season [31, 32].

3. THE USE OF THE MALE EFFECT IN THE GOAT UNDER SUBTROPICAL CONDITIONS

There are at least two non exclusive hypotheses to explain for the poor efficiency of the male effect outside the limited period preceding the spontaneous onset of the breeding season. First, the inability of the female to respond to males due to a photoperiod-dependent refractoriness of the female to the male stimulus [9, 33, 34]. Second, it may be due to a low quality stimulus provided by the males which are,

as the females, in seasonal rest. Indeed, during the non-breeding season, all sexual characteristics of rams and bucks decrease dramatically [35–37].

The limitation on the quality of the stimulus may be particularly important under latitudes where the photoperiodic inhibition of female activity is not too strong. Thus, studying the male effect in subtropical conditions offers a good opportunity to understand how the various sensory cues from the male interact to stimulate reproduction in anestrus females. This happens in local bucks from subtropical Mexico, which derive from the Spanish Granadina, Murciana and Malagueña breeds and crossed with Alpine, Saanen and Anglo-Nubian breeds. These bucks have a well defined non-breeding season, which lasts from January to May–June. During this period, the plasma concentration of testosterone, the sexual behavior assessed by ano-genital sniffing, nudging and mounts and the sexual odor of bucks are at a low level [8, 38, 39]. We hypothesized that if the sexual characteristics of the bucks are improved by stimulating their sexual activity during the non-breeding season, males may be able to induce the sexual activity of females at any time during the seasonal anestrus period. Therefore, we developed photoperiodic treatments to stimulate the sexual activity of local bucks from subtropical Mexico, and tested the response of females exposed to treated males.

3.1. Stimulation of the sexual activity of male goats during the period of seasonal sexual rest

In Mexican bucks, photoperiod is the main factor determining the annual changes of sexual activity. While artificial treatments with short days stimulate reproductive activity, it is inhibited with long day-treatments [30]. In summary, in this breed, alternation of long and short

days allows the controlling of the bucks' sexual activity. While long days may be provided by extra periods of illumination indoors or outdoors, short days can be mimicked by natural or artificial daylight, or by melatonin administration. In males kept indoors, 2.5 months of long days (16 h of light/day: lights-on 0600 h, lights-off 2200 h) starting on November 1 (mid-breeding season), followed by an application of two subcutaneous (s.c.) ear melatonin implants (18 mg each), induce an intense sexual activity during the non-breeding season [40]. In treated males, testosterone secretion is higher than in controls from February to April (non-breeding season). Sexual behavior, assessed by anogenital sniffing, nudging and mounts, is also higher in light treated males exposed to anestrus female goats than in controls [8, 41]. Similar results are obtained in males raised in open pens and subjected to 2.5 months of long days using a combination of natural and artificial illumination, followed by melatonin implants. In this case, artificial light is given from 0600 to 0900 and from 1800 to 2200 h to obtain 16 h of light/day [41, 42]. Interestingly, in males raised in open pens and treated with 2.5 months of artificially long days only and no melatonin implants, testosterone secretion and sexual behavior are stimulated during the non-breeding season and do not differ from those of males receiving melatonin implants [42]. Finally, sexual activity of male goats maintained in constant long days (16 h of light/day) from November 1 to June 15, is stimulated from March to June [43]. In males submitted to constant long days, plasma testosterone concentrations increase in March, as in bucks treated with 2.5 months of long days followed or not by the insertion of 2 ear s.c. melatonin implants. However, testosterone plasma levels do not decrease in April as in bucks treated with 2.5 months of long days, but remain high until June. These treated males, display a more intensive sex-

ual behavior than controls when exposed to estrous females [43].

These data show that in local male goats from subtropical Mexico, the alternation between long days and short days or melatonin implants, stimulates their sexual activity during the non-breeding season. These treatments can be applied in light-proof buildings or in open sheds using natural or artificial light and melatonin implants, improving all sexual characteristics of males during the non-breeding season. Those stimulated bucks may be effectively used as teasers.

3.2. Response of female goats exposed to active males in different months of the non-breeding season

Through several studies performed in our laboratory, we have demonstrated that bucks treated with long days and melatonin implants are able to stimulate the sexual activity of anestrus goats during the seasonal anestrus period [8, 41]. In March, bucks maintained in a light-proof building or in open sheds, treated with long days and melatonin, stimulated estrus in more than 80% of females, compared with 10% obtained when females were exposed to sexually inactive males [8, 41]. Similar results have been obtained using bucks treated only with artificially long days. Indeed, all females (19/19) exposed to photoperiodic treated males were detected in estrus, while only 10% of these in contact with non-treated males displayed estrus [42]. Interestingly, those males treated with long days only were able to stimulate estrus in a higher percentage of females grazed in our extensive conditions (85%) than sexually inactive males (30%) [30, 44]. Finally, bucks submitted to constant long days from November to June are also able to stimulate the sexual activity of does from April to June, during mid-seasonal anestrus [45–47]. In April, light-treated,

sexually active males stimulated estrous behavior in a higher percentage of females (90%) than non-treated, sexually inactive males (0%). In contrast, in May or June the percentage of females displaying estrous behavior was similar with treated or untreated bucks. The lack of difference is likely to be due to the onset of the natural sexual activity in control bucks, which starts in May [39].

These results show that sexually active males are able to stimulate the sexual activity of does during the non-breeding season and suggest that, at least in our conditions, the sexual behavior of bucks is the main limitation for the efficacy of the male effect during the seasonal anestrus period.

4. RECENT OUTCOMES FROM THE MALE EFFECT STUDIES OBTAINED IN GOATS

The use of sexually active and inactive males as teasers gives the opportunity to determine the role of the different cues involved in the stimulating mechanisms. Thus, by comparing the response to teasing by sexually active or inactive males, we have determined the importance of buck odor, male sexual behavior, buck vocalizations, continuous presence of males and previous separation between sexes in the success of the male effect.

4.1. Importance of buck sexual behavior and olfactory cues

In sheep and goats it is well established that both sexual behavior and olfactory cues are involved in the response of the females exposed to the males [9, 21, 25, 48]. Using sexually active and inactive males, we tested in vivo the role of these cues in the response of females to the male effect [49]. Two control groups of females ($n = 10$ each; 1 buck/group) were exposed

to a sexually inactive buck, that was either awake or sedated in order to prevent the display of any male sexual behavior. Two other groups ($n = 10$ each, 1 buck/group) were exposed to a buck rendered sexually active by 2.5 months of long days (treated), also either awake or sedated, as in the control groups. Plasma LH concentrations were determined every 15 min for 4 h before and 4 h after male introduction, and again for 4 h on the next day. Regardless of whether they were awake or sedated, sexually active males stimulated LH pulsatility (2.7 ± 0.2 pulses/4 h vs. 2.5 ± 0.3 pulses/4 h, respectively) in does. In contrast, in females exposed to sexually inactive males LH pulsatility was not increased (1.2 ± 0.1 pulses/4 h vs. 1.4 ± 0.2 pulses/4 h), regardless of whether bucks were awake or sedated. However, the following day, 20–24 h after male introduction, LH pulsatility remained high in does exposed to the awake sexually active male (2.1 ± 0.3), whereas in does exposed to the sedated sexually active male LH pulsatility had returned to levels that did not differ from those found before the introduction of the buck (1.6 ± 0.2 vs. 1.1 ± 0.1). These results suggest that in the first 4 h of contact between the male and females, olfactory cues alone are sufficient to trigger LH secretion. However, sexual behaviour of males seems important to maintain a high level of LH secretion for longer periods of time.

4.2. Importance of buck vocalizations

Some preliminary results from our laboratory suggest that buck vocalizations may stimulate estrus in local anovulatory female goats during the anestrus period [50]. One group of goats was joined with two sexually active bucks (SA group, $n = 5$). The second group was exposed to buck vocalizations coming from the previous group (VOC group, $n = 6$), reproduced through a microphone-amplifier-

loudspeaker system. The third group was isolated from any male stimulus (C group, $n = 6$). The five females stimulated by bucks ovulated, whereas only 2/6 did so in the VOC group and none in the control group (Fisher exact $P_b = 0.06$ and $= 0.002$). However, the proportion of females displaying estrus did not differ between the does in contact with males (5/5), and those submitted to male vocalizations (5/6), and was higher in these two groups than in the isolated group (0/6, Fisher exact $P_b < 0.02$). These data suggest that male goat vocalizations may induce estrous activity in anestrus female goats, even though they do not seem to influence ovulation itself.

4.3. Importance of the duration of contact between sexes

Using sexually active males, we have demonstrated that the continuous presence of males until ovulation is not necessary to maximize the response to the male effect. Indeed, in local goats from subtropical Mexico exposed to bucks for 16 h per day, the percentage of females that showed estrous behavior (96%) was similar to that of control females which were in contact with a male for 24 h (92%) [51].

4.4. Importance of previous separation between sexes

Early studies assumed that females must be preconditioned by a period of isolation from males in order to obtain a good ovulatory response [5, 15]. However, recently we found in subtropical Mexican goats that maintaining contact with bucks does not induce refractoriness of females to the re-introduction of other males [52, 53]. Indeed, when seasonally anovulatory goats were maintained in contact with a buck in sexual rest under natural photoperiod variations during three months before the male

effect, the introduction of a sexually active male induced sexual behavior in 82% of females. This percentage did not differ from that registered in goats which had been totally separated from males before teasing during the same period of time (91%). In contrast, when teasing was performed with bucks maintained under natural variations of the photoperiod – and thus inactive at the time of teasing – no females showed estrous behavior, regardless of whether they had been isolated or not from the buck before teasing. It remains to be tested if the previous presence of sexually active males affects the response to the introduction of other sexually active males. These results indicate that the previous isolation of seasonally anovulatory female goats from bucks is not critical to stimulate their reproductive activity by the male effect, if sexually active males are used, at least under our subtropical conditions.

5. CONCLUSION

The results obtained in our laboratory in goats underline the major importance of the quality of the males used for the outcome of the male effect. Although the type of goats used in these studies clearly show seasonal reproductive activity, the bucks' stimulation with photoperiodic treatments and melatonin administration ensures a proper activation of sexual behavior and production of sexual odors. As a result, very high rates of success in inducing estrus and ovulation can be obtained in goats in sexual rest. Indeed the use of active bucks allows disregarding many of the conditions that normally have to be taken into account for the success of teasing (e.g. time of the year, previous separation, continuous contact). It remains to be investigated to which extent this would also be true under more temperate latitudes and with more seasonal breeds.

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