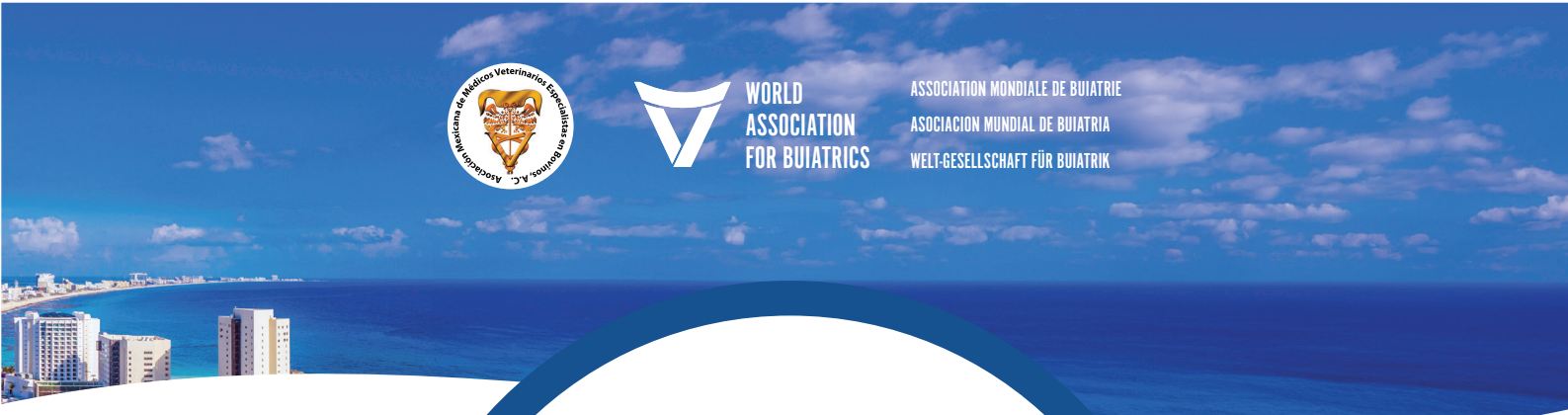

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Sheep and goats

Sustainable control of caprine reproduction through sociosexual interactions

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Background

Reproductive seasonality is a characteristic of male and female goat breeds from temperate and subtropical latitudes. The sexual season, charactrerized by maximal spermatogenetic and sexual behavior activities in males and in estrus behavior and ovulatory cyclicity in females, generally occurs in autumn and winter. However, males are generally starting and ending earlier their sexual season than females, this advance being more marked in subtropical latitudes (i.e. 3 *vs* 1 month). This reproductive seasonality causes a seasonal production of milk and meat. Regardless of the latitude of origin of the goats, this seasonality is, in both sexes, mainly synchronized by the annual variations in photoperiod, which induce changes in estradiol and testosterone negative feedbacks on LH secretion, constituting the main neuroendocrine mechanism responsible for reproductive seasonality. Nonethless, the sociosexual interactions between bucks and goats and between bucks themselves can break the natural inhibition of sexual activity during the seasonal sexual rest. Indeed, the introduction of a male into a group of seasonal anestrous goats immediately leads to a resumption of the activity of the hypothalamic-pituitary-gonadal axis, allowing females to display estrus and ovulations within few days after joining (Walkden-Brown et al., 1999). This is the "short-term male effect". Recently, we described that the permanent presence of bucks made sexually active by photoperiodic treatments stimulate sexual activity during seasonal anestrus and allows females to ovulate throughout the year (Delgadillo et al., 2015). This is what we called the "long-term male effect". Finally, we recently described that, as in females, the introduction of a sexually active buck into a group of seasonally inactive bucks in sexual rest immediately leads to a resumption of the activity of the hypothalamic-pituitary-gonadal axis, improving spermatogenetic and sexual behavior activities of recipient bucks. This is what we called the “buck-to-buck-effect”, or more generally, the “male-to-male effect” (Delgadillo et al., 2022). These three sexual biostimulation techniques to control caprine reproduction in a sustainable way, without the use of exogenous hormones, will be described in the present article.

The short-term male effect

The introduction of a male into a group of seasonal anestrous goats stimulates immediately the secretion of LH, then followed by ovulation generally associated with estrous behavior, within the first five days after joining. The first ovulation occurs 2-5 days after joining, but some ovulations are not associated with estrous behavior. Regardless of the presence or absence of estrus, most females have a short ovulatory cycle and ovulate again 6-9 days later; this second ovulation is generally associated with estrous behavior and followed by a normal luteal phase duration. Most females,

therefore, can become pregnant at this second male-induced ovulation following the short cycle. This is the "short-term male effect", which has been widely studied by the scientific community and used to induce and synchronise estrus and ovulations in anestrous goats since the 60's. A limit of this "short-term male effect" is that when used in strongly seasonal breeds, the sexual response of females is dramatically reduced, or even null, when teasing is performed during the mid-anestrus (Restall, 1992). This response is improved when using bucks made sexually active during the sexual rest by previous exposure to two months of artificial long days in autumn and winter followed by natural photoperiod. This photoperiodic treatment stimulates their LH and testosterone secretion, improves their spermatogenetic activity, sexual behavior and sexual odor about 6 weeks after the end of the long day period, rendered them much more efficient to trigger the endocrine and sexual activites in seasonally anestrous goats than untreated, sexually inactive bucks. Indeed, in March, April and May, the proportions of goats that displayed estrous behavior or ovulations (>80 %) and kidded (> 70%) were much higher in females joined with sexually active bucks than in those joined with sexually inactive bucks (<20%; Delgadillo, 2011). In June, most goats respond to the introduction of untreated bucks who display intense sexual activity because the sexual season of these males has already begun (Figure 1). In addition, the sexually active bucks advance billy goats puberty and reduce the duration of postpartum anestrus (Delgadillo et al., 2020). Interestingly, the sexually active bucks have allowed to reject some "dogmas" about the "short-term male effect". One of these dogmas indicated a prior separation of the two sexes before achieving the male effect to successfully induce estrus and ovulations. However, the proportions of females that ovulated when joined with the sexually active males did not differ between females separated (40 days) or not from the bucks (>85 %; Zarazaga et al., 2017). Therefore, when sexually active bucks are used, a prior separation between sexes is not necessary. These results are important from a practical application of the "short-term male effect" because it facilitates its use by not having to separate the sexes. Altogether, these findings indicate that sexually active bucks are especially efficient to stimulate the endocrine and reproductive activities of goats during the seasonal anestrus and indicate that the intensity of males' sexual behavior is a crucial factor that should be taken into consideration to successfully achieve the "short-term male effect".

Considering that the estradiol negative feedback on LH secretion is the main neuroendocrine mechanism responsible for seasonality, it is likely that the sexually active bucks are able to reduce or overcome this negative feedback. Indeed, in ovariectomized goats bearing subcutaneous implants releasing estradiol (OVX+E), exposure to sexually active bucks increased LH secretion within 15 min of exposure, but exposure to the sexually inactive males did not stimulate this secretion. Therefore, the sexually active bucks probably modify the estradiol negative beedback on LH secretion and activated the kisspeptin neurons located in the arcuate nucleus, which control GnRH secretion (Delgadillo et al., 2020).

The long-term male effect

Recently described, although it undoubtedly sometimes occurs in natural conditions, the "long-term male effect" probably represents one of the regulators of the reproductive seasonality in goats.

Permanent presence of males among females

The permanent presence of bucks among a group of females reduce the duration of anestrus because the sexual season begins earlier and end later than in goats isolated from males throughout the year. However, it does not prevent the appearance of the seasonal anovulation (Restall, 1992). These findings were obtained when bucks were subjected to the natural variations of photoperiod, exhibiting periods of sexual rest, which roughly coincide with those of females. This latters indicates a possible influence of males on the triggering of the seasonal ovulatory activity of females when the two sexes are in permanent contact.

Onset of ovulatory activity during season anestrus

Considering that about 6 weeks are necessary after the end of long days for the sexual activity of males to begin, and that sexual behavior is a crucial factor to successfully achieve the "short-term male effect", we wonder what would happen if goats were in contact with photoperiodic-treated bucks when their sexual activity starts after the long days? Would these females ovulate? During these 6 weeks after the end of the long days, the bucks are still in seasonal sexual rest with very low sexual activity and if they are introduced into a group of females at the beginning of anestrus, for example in February, they do not cause a "short-term male effect" (and also because goats are still cycling). But their gradual resumption of sexual activity in March, induced by the previous photoperiodic treatment, gradually leads to the ovulatory activity of the females and all of them ovulated in April, in the middle of the anestrus period (Delgadillo et al., 2015). This is what we called the "long-term male effect".

Suppression of seasonal anovulation

Considering the previous results, we wonder what would happen if goats remained in permanent contact, during seasonal anestrus, with sexually active males? Would these females maintain ovulatory activity throughout the year? From January and for a period of 18 months, a group of goats remained isolated from bucks, while another one remained in permanent contact with vasectomized control bucks submitted to the natural photoperiod, and displayed periods of sexual activity and sexual rest. Another group of goats remained in permanent contact with vasectomized bucks made sexually active during the period of sexual rest (January-June) by previous photoperiodic treatments applied during autumn and winter (three groups of bucks were used successively). As expected, a longer duration of anestrus (March-September) was observed in goats isolated from bucks, than in those in permanent contact with the control bucks (April-June). By contrast, almost all (12/14) of the goats that remained in permanent contact with sexually active bucks were in cyclical ovulatory activity for the entire duration of the experiment, including the two seasons of anestrus observed in isolated females. To demonstrate that it was indeed the presence of the bucks which induced permanent sexual activity, they were removed from half of the cyclic females in May of the second year; the activity then stopped immediately (Figure 2; Delgadillo et al., 2015).

This "long-term male effect" using sexually active bucks, as in the case of the "short-term male effect", passes through the stimulation of the central nervous system.

Indeed, in OVX+E goats kept in permanent contact with the sexually active bucks, the plasma concentrations of LH remained elevated during the seasonal anestrus, while it decreased in those kept with control bucks (Delgadillo et al., 2020). These findings indicate that, as in the "short-term male effect, in the "long-term male effect", the sexually active bucks also neutralize the negative feedback of estradiol on LH during the seasonal anestrous goats once they start their sexual activity after the end of the long days.

The buck-to-buck effect

As in female goats, in bucks, the sociosexual interactions can also break the natural inhibition of sexual activity during the seasonal sexual rest.

The "buck-to-buck effect" stimulates bucks in sexual rest

The introduction of a buck into a group of other bucks in sexual rest can stimulate the secretion of LH and testosterone, as well as their spermatogenetic activity and sexual behavior. This is what we called the "buck-to-buck effect". The response of bucks to the "buck-to-buck effect" depends of the intensity of sexual behavior displayed by the stimulatory males. Indeed, exposure of bucks in sexual rest to bucks made sexually active by a photoperiodic treatment induced an immediate increase in plasma LH and testosterone concentrations. By contrast, exposure to sexuallty inactive bucks did not induce any significant increase in these two hormones (Figure 3; Delgadillo et al., 2022). Thus, the "buck-to-buck effect" strongly resembles the classic "short-term male effect" that is observed in female goats. As in females, the "buck-to-buck effect" immediately and effectively "bypasses" the seasonal inhibition of the photoperiod on the central nervous system. This stimulation leads to a resumption of sexual activity of bucks during the seasonal sexual rest, which can be interesting on a practical level.

"The buck-to-buck effect" is maintained as long as the sexually active inducers males are active

In bucks joined with sexually active males, plasma testosterone remained significantly higher for at least 30 consecutive days more than in those joined with control bucks (Figure 4). In the same way, sexual behavior of bucks joined with sexually active bucks is higher than that of males joined with control bucks and remains of the same order as that of males that received previously the photoperiod treatment (Delgadillo et al., 2022). It is likely that the sexual activity of stimulated bucks gradually stops because that of inducing bucks does as well. However, it is interesting to note that the sexual behavior of stimulated bucks begins to be stimulated from the first day after contact with sexually active males, undoubtedly under the influence of testosterone, which also increases from 6 hours later and, perhaps also under the influence of other hypothalamic hormones.

Males induced by the sexually active males are also effective for a classic "short-term male effect"

Considering the previous results, we wonder if bucks stimulated by the "buck-to-buck effect" could be able to induce sexual activity in seasonal anestrus goats through the "short-term male effect"? In April, one group of anestrous goats was joined with the bucks stimulated by the "bucks-to-buck effect", while another group was joined with

bucks made sexually active by a photoperiodic treatment. Interestingly, the bucks stimulated by the "buck-to-buck effect" were as effective as bucks made sexually active by the photoperiodic treatment in inducing high ovulatory and estrous activities, leading to fertility which were not significantly different from one group to another (Fertility: 80 % vs. 85 %, respectively; Delgadillo et al., 2022).

Conclusions

The "short-term male effect" allows to induce and synchronize the sexual activity in anestrous goats. The "long-term male effect" also allows to induce and synchronize the sexual activity of goats during the seasonal anestrous, and allows goats to ovulate throughout the year. Finally, the "buck-to-buck effect" stimulate the endocrine and sexual activities of bucks during the seasonal sexual rest. Among the key factors in the success of these three biosexual stimulations, it is undoubtedly the use of the sexual active bucks which has attracted the attention and this is certainly what must be the subject of precise recommendations to breeders. The sexually active bucks reduce or overcome the negative feedback of estradiol and testosterone on LH secetion, by “bypassing” the very strong seasonal inhibition of the photoperiod on the hypothalamic-pituitary-gonadal axis. Altogether, these findings show the power of sociosexual relationships in controlling the seasonal reproduction of caprine species and it rebalances the relative weights of these relationships, in relation to the photoperiod, in the final control of seasonal reproduction during the year.

Keywords: Caprine, Reproductive seasonality, Photoperiod, Male effect, Buck-to-buck-effect.

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Figure legends

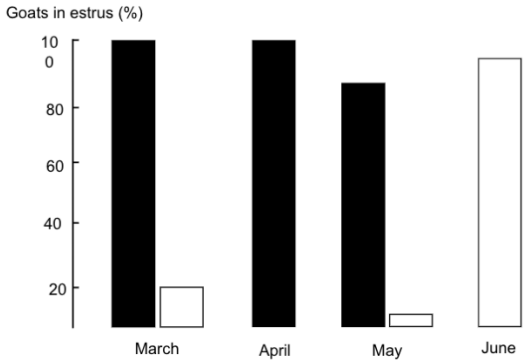

Figure 1. Goats displaying estrus when joined with bucks made sexually active (■) by photoperiodic treatments or untreated, sexually inactive bucks (□). In June, at the beginning of the natural sexual season, the untreated bucks displayed intense sexualy behavior allowing them to induce most goats in estrus (Delgadillo et al., 2011).

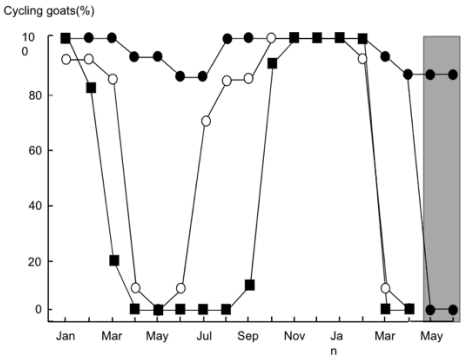

Figure 2. Ovulatory activity of goats isolated from bucks (■) or in permanent contact with vasectomized control bucks kept under natural variations of photoperiod ( ) or with those made sexually active by photoperiodic tretaments (●) during the seasonal sexual rest. Most goats joined with the sexually active bucks ovulated throughout the year. The grey area indicates when bucks were removed from half of the cycling goats; the ovulatory activity stopped in isolated goats (Delgadillo et al., 2015).

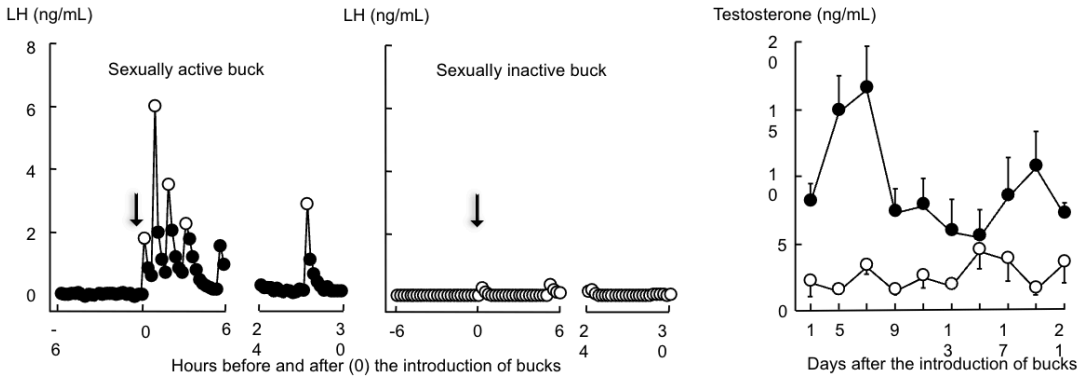

Figure 3. Individual example of LH pulsatility and testosterone concentrations (mean ± SEM) in bucks joined during the seasonal sexual rest with bucks made sexually active (●) by photoperiodic treatments or untreated, sexually active bucks (○). The arrows indicate the introduction of bucks; both hormones increased after the introduction of the sexually active bucks (Delgadillo et al., 2022).

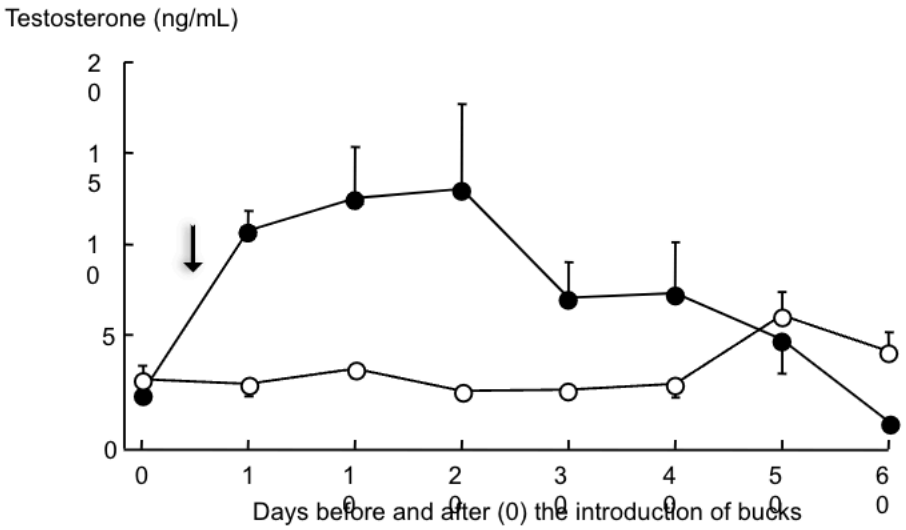

Figure 4. Long-term plasma testosterone concentrations (mean ± SEM) in bucks joined during the seasonal sexual rest with bucks made sexually active (●) by photoperiodic treatments or untreated, sexually active bucks (○). The arrow indicates the introduction of the bucks (Delgadillo et al., 2022).